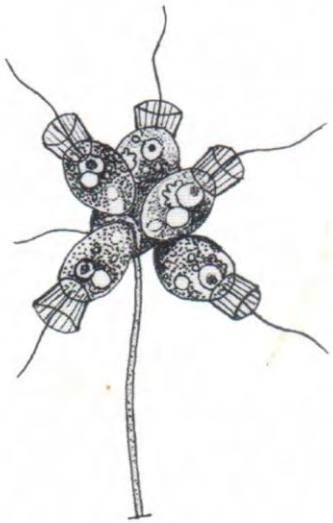
A Century of Protozoology in Britain



Keith Vickerman
Michael Sleigh

Barry Leadbeater and Sharon McCready

The British Section of the Society of Protozoologists

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of Protozoologists (BSSP)

Cover Design: Background pattern – Shell membrane of *Gromia oviformis*; centre illustra
Codosiga gracilis drawn by Mrs Liz Roberts.

About the Authors

Professor Keith Vickerman FRS was Regius Professor of Zoology in the University of Glasgow, Scotland, from 1984 to 1998. He graduated from University College, London in 1955. After postgraduate work in Exeter and Edinburgh Universities, he returned to UCL as lecturer in Zoology in 1958. From 1963 to 1968 he was Tropical Research Fellow of the Royal Society. He then moved to Glasgow University as Reader in Zoology and Director of a Protozoology Unit funded by the Nuffield Foundation. He became Professor in 1974 and was Head of the Zoology Department from 1979-1985. He was a member of the World Health Organisation Panel of Consultant Experts on Parasitic Diseases 1973-1998. His research interests have centred on understanding the complex life-cycles of disease-causing protozoan parasites in relation to parasite survival strategies and the generation of chronic infections. He has a long-standing interest in sorting out the free-living heterotrophic flagellate protozoa. In 1998 he retired from the Regius Chair and now conducts research on soil protozoa. He is an Honorary member of the American and French protozoological societies and an Honorary member of the British Society for Parasitology. He was elected F.R.S.E. in 1971 and F.R.S. in 1984. In 1994 he gave the Leeuwenhoek Lecture of the Royal Society and in 1996 the Linnean Society awarded him its Gold Medal for services to the science of Zoology. He was a founder member of the BSSP in 1962, Treasurer from 1962-66 and President from 1978-81.

Professor Michael Sleigh took his BSc and PhD in the Zoology Department at Bristol University, where Jack Kitching introduced him to Protozoa and John Harris supervised his research on the coordination of cilia. After completing National Service in the RAF, his first teaching post was at Exeter University where his colleagues included Julian Hawes and John Corliss (on a one-year exchange). When Kitching moved to the University of East Anglia in 1963, Michael was appointed lecturer at Bristol, where he taught protozoology and cell biology, among other things, for 12 years, and continued research on cilia. After appointment to a Chair of Biology at Southampton, his interests in protozoa widened to include research on ecology, first of freshwater protists and later of those in marine habitats. The writing of his text *The Biology of Protozoa* stimulated an interest in protistan phylogeny. Although he was a member of the BSSP from its first meeting, he was more heavily involved with the Society for Experimental Biology, as Secretary and Symposium Convenor, during the 1960's, and only in the 1970's did he become active in administration of the BSSP, first as a Committee Member from 1972, then as Vice-President and President from 1978 to 1984. He has also served the Society of Protozoologists as its Vice-President and as Chairman of the International Affairs Committee.

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FOREWORD

It is a well worn cliché that the start of a new millennium is not only a time for looking foward but also a time for taking stock. But it was with this sentiment in mind that I first broached the idea of the BSSP producing a book which combined the history of protozoology with the history of the BSSP and yet still provided a good read.

A further spur was the fact that I had just been involved in a book entitled *The Flagellates* and had been fascinated to read for the first time something about the personages whom I knew merely as authorities to type descriptions. It transpired that many of the men and women who had devoted their careers to protozoological studies were quite remarkable people and it seemed desirable that their stories should be told and brought together for the first time.

The BSSP, which was founded in 1962, is now celebrating its 38th year of existence. Many of the founder members have either passed away or retired and there is a risk that if we do not commit to paper an account of our history now, this information will be lost for ever. It was with these thoughts in mind that, at the 1999 Easter meeting of the BSSP in Reading, I consulted with colleagues as to whether the production of a book would be a good idea. The responses were universally encouraging and so I gave more serious thought as to how this enterprise might be achieved. I approached Professors Keith Vickerman and Michael Sleigh, both of whom have broad protozoological interests, are past presidents of the BSSP and are still participating members. To my pleasure they accepted the challenge. The results of their labours are presented here and have far exceeded my original expectations.

In deciding on the content of this book it seemed sensible to relate the story of the founding and history of the BSSP to the wider context of twentieth century protozoology in Britain - hence the title. But the twentieth century history was also dependent on what had gone before and this had a more international flavour. Hence the book, although a continuous story, is in three parts, the first of which, written by Barry Leadbeater and Sharon McCready, deals with the founding of protozoology from van Leeuwenhoek until the end of the nineteenth century; the second part, written by Keith Vickerman, presents the story of protozoology in Britain related under themes and the third part, written by Michael Sleigh, deals specifically with the BSSP and protozoology in post-1945 Britain. There has been no attempt to impose a uniform editorial style and so there are inconsistencies in format such as citing of the references. However, I hope that any inconsistencies are more than made up for by the freshness and immediacy of the content.

In a venture of this kind, there are many people whom I wish to thank. Above all, of course, are Keith and Michael for their splendid texts. Time constraints were severe and yet both managed to achieve their goals without demur. I am indebted to Hobbs the Printers of Totton, Hampshire, who have given us much valuable advice on the preparation of the text and have, on at least two occasions, extended the deadline for receipt of the edited document. David Ruffles of the Birmingham Biosciences Photographic Unit has kindly assisted with preparation of some of the illustrations. I also wish to thank the following colleagues for supplying or locating photographs or other illustrations (sometimes at short notice): John Baker, Geoffrey Beale, Elizabeth Canning, Tom Cavalier-Smith. John Corliss, Frank Cox, Colin Curds, John Darbyshire, John Dodge, Stephen Droop, Nicholas Leadbeater, Stephen Phillips, Richard Scott and Alan Warren. Many thanks also to Lawrie Bannister for providing the sketches located in the text and to Mrs Liz Roberts for her drawing of *Codosiga gracilis*. I am grateful to The Royal Society, The Wellcome Trust, The Corporation of London and other authorities and colleagues mentioned in the list of illustrations for giving permission to reproduce their materials.

Finally, at the outset it seemed like a good idea for us to produce this book using desktop publishing techniques. Ms Sharon McCready kindly agreed to undertake the task. However, like all good ideas this one mushroomed until it became an enormous task coping with over 200 pages of text and 100 illustrations. Sharon has coped magnificently with many trials and tribulations and I am deeply grateful to her for her unstinting assistance.

Barry Leadbeater
Birmingham
March 2000

Use of Names in the Text

Whilst it was an objective of this book to be inclusive and to cover the subject matter in its broadest sense, it is inevitable that not all protozoologists in Britain are mentioned in the text. This should not be taken in any way as a reflection of the authors's opinions but rather the inevitable limits of time and space.

Familiar names, both for persons and organisms, have been used throughout and again there will be some inconsistencies. In general, forenames and surnames have been used without titles but with a few exceptions. If colleagues were known specifically by their initials rather than their forenames, these have been used in the text. The index, to some extent, relates initials to forenames where appropriate.

PREFACE

The idea to produce this book was mooted too close to the deadline for its publication to allow a scholarly history of British protozoology to be written. The intention has rather been to produce a series of essays each dealing with a particular aspect of the growth of the subject or the seminal contributions of particular individuals.

The burgeoning of science has been one of the most obvious features of the last century. In Britain, as elsewhere in the developed world, professional scientists have become much more numerous with the expansion of the university system and the multiplication of research institutes funded by the Research Councils, by industry or by private trusts. Within the practise of science another feature has been the transition from the individual scientist working alone in his laboratory, or as 'a man, a boy and a dog' set-up, to the team of workers often extending over several laboratories in the same institution or in several separate institutions, even in different countries. For the first half of the century, even into the sixties, advances in science could be almost unequivocally attributed to particular individuals, or to collaborating pairs. This situation changed with the availability of sizeable research council grants and the growth of multidisciplinary approaches over the last thirty years; research units and teams became the norm, and the scope for individual research diminished. Publications have correspondingly progressed from one or two authors to several: the individual scientist is less and less the innovator.

Increasing reliance on international funding agencies such as the European Union, moreover, has made joint work between different nationalities increasingly common and the singling out of British contributions difficult. Indeed, the very idea of "Britishness" seems to be something strongly discouraged by our current political masters in the United Kingdom. These are all reasons why in the early days - before the founding of the BSSP - the individual is more to the fore in discussions of the advance of science, and why those particular characters we used to like to believe were peculiarly British - dogged determination combined with a laidback amateurism - seem more highly developed in the pioneers of the subject.

Finally, it is, of course, impossible to consider British protozoology apart from the subject as it developed in the rest of the world. The influence of Germany at the start of the century and the USA over much of its latter part is all too obvious. Yet, although throughout the last century protozoology was never a major feature of biological science in Britain, at the end of it it somehow seems in better heart than in some of the subject's former strongholds and let us hope that it continues to thrive in the century now starting.

Keith Vickerman, Glasgow

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"And Pauls is burned, and all Cheapside. .... I up to the top of Barkeing steeple, and there saw the saddest sight of desolation that I ever saw. Everywhere great fires"

Samuel Pepys. Diary 4th/5th September, 1666

PART 1

CHAPTER I

HOW IT ALL BEGAN

"And the motion of most of these animalcules in the water was so swift, and so various, upwards, downwards, and round about, that t'was wonderful to see."

Antony van Leeuwenhoek. Letter 6 to Mr Henry Oldenburg (Secretary of the Royal Society of London) September 7th 1674. Translation C.C. Dobell (1932)

'Wee Animalcules'

One of the great landmarks in English history of which every school child in Britain must be aware is the Great Fire of London in 1666. This disaster, which followed so close on an outbreak of plague during the previous year, started in Pudding Lane on Sunday September 2nd 1666 and lasted for four days. At the end of the conflagration much of the City of London, including old St Paul's cathedral [Fig. 1], had been destroyed and an estimated 60,000 citizens made homeless.

Set against this and other disasters, the mid-seventeenth century was a period of great intellectual, scientific, cultural and economic activity. London, with a population of about half a million was the home of such luminaries as John Milton (1608-1674), Isaac Newton (1642-1727), Robert Boyle (1621-1691), Christopher Wren (1632-1723) and Samuel Pepys (1633-1703) to name but a few. This period was presided over by King Charles II (1630-1685) and it was during his reign, in 1660, that the Royal Society of London was founded.

Part of the scientific expansion during the mid-seventeenth century involved the development of microscopes and the study of novel microscopical objects. Compound microscopes, with ocular and objective lenses, were devised around the end of the sixteenth century. Robert Hooke (1635-1703) had access to such a microscope and by the age of 30 had published *Micrographia* (Hooke, 1665) in which he illustrated the cellular substructure of plant material. Hooke was not only a painstaking observer of a wide range of microscopical specimens, but he was also an outstanding artist as evidenced by the exceptionally high quality of the illustrations in his first edition of *Micrographia*. Unfortunately for posterity, it seems likely that the originals of his drawings were lost in the Great Fire and the move from St Paul's churchyard when the print shop was destroyed.

There is still debate over who first observed an individual protozoan cell. Robert Hooke has been credited with the observation of a fossil foraminiferan, possibly *Rotalia beccari* (Cole, 1926), although Dobell (1932) disputes this. Hooke (1865), viewing *"a parcel of sand"* describes how he studied a *"small white spot on both sides, and edge-ways, and saw it to resemble the shell of a small water-snail with a flat spiral shell"*.

By general consent Antony van Leeuwenhoek (1632-1723) [Fig. 3] is considered to be the 'Father of Protozoology'. Leeuwenhoek's connection with microscopy is unconventional in almost all respects. He was born in Delft, The Netherlands in 1623 into a family in which the men were traditionally basket makers. He worked as a draper and carried out various civic duties in Delft. He visited England in or about 1668 but did not meet Robert Hooke. He was clearly inspired by *Micrographia* and it is possible that it was Hooke's observations on the substructure of woven textiles that drew Leeuwenhoek's attention. However, it was not until 1673 that Leeuwenhoek emerged as a microscopical investigator. From then on, until his death 50 years later in 1723, Leeuwenhoek devoted his life, first part-time and then full-time, to his microscopical studies. His observations were not published as papers in learned journals but rather as letters many of which were sent to the Secretary of the Royal Society in London. Unlike Hooke, Leeuwenhoek lacked artistic flair and most of his observations take the form of lengthy descriptions.

In spite of the availability of compound microscopes at the time, Leeuwenhoek used a hand-held instrument with a single lens. The magnifications obtained with his microscopes (still extant) vary from 50 – 300 diameters. Nevertheless, it is the descriptions of his observations that put Leeuwenhoek, the draper from Delft, into the first rank. He was elected a Fellow of the Royal Society of London in 1680 probably as a result of Robert Hooke's recommendation although Hooke did not actually nominate him.

Leeuwenhoek's observations on the free-living protozoa date back to 1674 when he reports the discovery certain *"very little animalcules"* in freshwater (Leeuwenhoek, 1674). In a letter to the Secretary of the Royal Society of London he referred to *"These animalcules had divers colours..... others again were green in the middle, and before and behind white.... I judge that some of these little creatures were above a thousand times smaller than the smallest ones I have ever yet seen..."*. Dobell (1932) interprets these green and white animalcules as being *Euglena viridis*. In a letter dated October 9th 1676 and published in 1677, now known as the *Letter on the Protozoa*, Leeuwenhoek (1677) describes for the first time the animalcules that he observed in standing rainwater. Dobell (1932) has attempted identifications from Leeuwenhoek's descriptions and these include *Vorticella*, where Leeuwenhoek clearly



Fig. 2 *Volvox* (Leeuwenhoek, 1700)

observed movements of the stalk *"which was coiled up serpentwise, after the fashion of a copper or iron wire"*. Dobell (1932) also considers that Leeuwenhoek observed *Monas* sp., probably *Monas vulgata* and *Bodo* sp. Later Leeuwenhoek (1700) recorded in detail a description and illustration of *Volvox* colonies [Fig. 2]. He observed these colonies in sealed glass tubes over a period of several weeks and noted their movement, rotation and the release of daughter colonies. The foraminiferan *Poystomella* was described and illustrated by Leeuwenhoek in 1702. In the same letter descriptions of *Chlamydomonas* and *Haematococcus* are given with the first description of flagella: *"...their bodies seemed to be composed of particles that presented an oval figure; therewithal they had short thin instruments which stuck out a little way from the round contour, and wherewith they performed the motions of rolling round and going forward"*. Other protozoan genera Dobell considers Leeuwenhoek to have seen include: *Stylonchia, Carchesium, Coleps, Kerona, Anthophysis, Elphidium, Polytoma* etc.

Leeuwenhoek is credited with the first description of parasitic protozoa. Bearing in mind that he did not attempt to name the organisms he observed, and we only have his descriptions occasionally accompanied by sketches or drawings, it is difficult to be certain what he did, in fact, see. However, he is generally credited with being the first to observe *Opalina* (really an opalinid species of the genus *Cepedea*), *Chilomastix, Giardia* (in his own stools) and *Trichomonas* sensu lato. In 1683 Leeuwenhoek reported *"In the month of June, I met with some frogs whose excrement was full of a innumerable company of living creatures, of different sorts and sizes... The whole excrement was so full of living things that it seemed to move"*.

In the period intervening between the first discovery of the Infusoria by Leeuwenhoek (1674) and his later contribution in 1703, a number of descriptions emanated from British microscopists. These include Sir Edmund King FRS (1629-1709), physician to Charles II whom he attended during his last illness. King viewed droplets of pepper infusion and illustrated ciliates that are now interpreted as *Enchelys* and *Euplotes*. The Revered John Harris FRS (1667-1719), Rector of Winchelsea in Sussex, recorded *"vast numbers of animalcula"* seen in water. He also observed *Euglena viridis "...the most remarkable were those which I found gave the water a green colour, and were oval creatures, whose middle part was grass green but each end was clear and transparent. They would contract and dilate themselves, tumble over and over and then shoot away like fishes....."*.

Stephen Gray FRS 1696, a physicist, devised a 'water microscope' which comprised a sphere of glass in which was placed a sample of water. The filled sphere served as a magnifying lens. Using this instrument he observed transverse fission in *Halteria grandinella* (Kent 1880-82). By the end of the seventeenth century the existence of protozoa and bacteria had been established; Leeuwenhoek was recognised as the 'father of protozoology' whilst Hooke, Buonanni, King, Harris and Gray were amongst the first generation of protozoologists.

What's in a name?

At the beginning of the eighteenth century there was still no standard system of nomenclature – as we have seen Leeuwenhoek's observations were recorded in the form of lengthy textual descriptions. Theories of evolution abounded but it was still 150 years before Charles Darwin (1859) published *The Origin of Species*. The doctrine of *spontaneous generation* was hotly debated and it rumbled on for another 150 years until finally laid to rest by Pasteur (1822-1895) and Koch (1843-1910). What emerged in the eighteenth century were glimpses of the magnitude of diversity of protozoa and early attempts to name and classify them. Pivotal to these developments were the contributions of two Scandinavians, Carl von Linnaeus (1707-1778) and Otto Friderich Müller (1730-1784).

The first Treatise on the Infusoria was that of Louis Joblot (1718), a Frenchman, who first described a contractile vacuole. Unfortunately, his imagination ran away with his pen and he embellished many of his illustrations with fantastic features including the heads of satyrs. Joblot gave vernacular names to the organisms he saw including 'chausson' to *Paramecium* which is still in use today as the *slipper animalcule*.

In Britain Sir John Hill (1716-1775) [Fig. 4], an amateur microscopist, assigned



Fig. 3 Antony van Leeuwenhoek. Fig. 4 Sir John Hill. Fig. 5 Otto Friderich Müller.

names to some protozoa including *Paramecium*. Although this predates the binomial system introduced by Linnaeus (1758) the name, with Hill as the authority, is still in current use.

With respect to nomenclature in general, since minute animalcules were closely associated with infusions of one sort or another, they became known as *'infusion animals'* (Ledermuller, 1763) and this was formalised to Infusoria by Wrisberg (1765).

Abraham Trembley observed *Stentor* and other 'trumpet animalcules' and gave the first description of their mode of division. His primary interest was *Hydra vulgaris* which was then known as a freshwater polyp. The similarity in form between *Stentor* and *Hydra* led Trembley to describe species of *Stentor* as white or blue funnel-shaped polyps. Linnaeus (1758), following Trembley's lead, included the trumpet animalcules under the title *Hydra stentora* (Kent, 1880-82).

Henry Baker (1698-1774), a Londoner who 'dabbled' in science and published books for the popular market including such titles as *'Employment of the microscope'* described the luminescent dinoflagellate *Noctiluca* and the 'swan' ciliate *Lacrylmaria olor* which he called *Proteus*. In his description of the latter he reported: *"I could discern no eyes, nor any opening like a mouth in what appears to be a head; but its actions plainly prove it an animal that can see... for its dexterity of movement would be wholly unaccountable, should we suppose it to be destitute of sight"*.

The Swedish botanist Carl von Linnaeus, is renowned for his work on the systematics of plants and higher animals. However, it was not until the 10th edition of *Systema*

Naturae (Linnaeus, 1758), the starting date for zoological nomenclature, that the flagellate *Volvox* was recorded. Linnaeus grouped all that was known about the protozoa in the Class Vermes and its last order zoophyta. Apart from a few foraminifera and vorticellidae – placed under the molluscs and polyps respectively – all the protozoa that he recognised comprised the single genus *Volvox* containing only two species. In his 12th edition, Linnaeus expanded on this by including three genera; *Volvox, Furia* and *Chaos*. All the infusoria described are lumped together in *Chaos infusonium*. Linnaeus had neither an interest in, nor knowledge of, the Infusoria to improve on this treatment and so it is to his contemporary, Otto Frederich Müller [Fig. 5], a Danish marine invertebrate zoologist, that we must look for a seminal treatment of protozoan taxonomy.

Müller observed and described many Infusoria giving them distinctive generic and specific titles in line with Linnaeus's then newly introduced binomial system of nomenclature. In *Vermium Terrestrium et Fluviatilium* (Müller, 1773), he was the first to recognise dinoflagellates (*Bursaria* (= *Ceratium*) *hirundinella* and *Vorticella* (= *Peridinium*) *cincta*) which he included in the *Animalium Infusonium*. In his later, posthumous work, *Animalcula Infusoria Fluviatilia et Marina* (Müller, 1786), he included within the Order *Infusoria* descriptions of many ciliates, flagellates and heliozoa that are still recognised today. In particular, *Gonium* and *Monas* are flagellate genera originally named by Müller (1786). In addition to Protozoa as now construed, Müller's *Infusoria* also included bacteria, diatoms, vinegar worms, planarian worms, cercaria larvae, rotifers and other members of the subsequently instituted Metazoa.

The nineteenth century

Eighteenth century science was generally the preserve of wealthy, educated individuals who had enough money and time to practise their interest as a hobby. Hence the involvement of members of the aristocracy and amateurs, including clergymen, who presumably could afford to take time off from their ministrations. In summary, life was still fairly leisurely, the effects of the industrial revolution and the philanthropy of industrial entrepreneurs were still some way off. However, the nineteenth century saw a quickening of the pace with changes in all directions – in scientific theories; improved technology including microscopes; exploration abroad and the building of the British Empire (see Chapter 2). Similar changes were taking place across Europe but the influence of being an island, and thus a seafaring nation, was to have a profound effect on the course of British history. For biology, in general, and protozoology, in particular, the changes in store were to change science from being a hobby to be pursued at leisure to an integral part of life.

In biology two important landmarks associated with the nineteenth century are the

cell theory and evolutionary theory based on the publication in 1859 of Darwin's *The Origin of Species*. The contribution of these theories was to bring together disparate observations in a unifying and secure framework. Of course it wasn't as plain sailing as that since new theories challenged long-held beliefs. Nevertheless, by the end of the nineteenth century the foundations of protozoology that were set to dominate the twentieth century were securely laid.

At the beginning of the nineteenth century the Infusoria comprised a vast array of organisms spanning in size and complexity from bacteria to small invertebrates including worms and crustacea. In 1817 Goldfuss (1817) [Fig. 6] introduced the term *Protozoa* to include polyps, medusae, infusoria and phytozoa (plant-animals). By 1839 Schleiden (1838) and Schwann (1839) had developed what became known as the *cell theory* in which it was acknowledged that the cell was basic to all organisms and therefore organisms consisted of one or more cells. Following this discovery, matters moved fast with respect to the infusoria. Meyen and Dujardin (1841) independently recognised that many protozoa were single cells with a high level of internal organisation comparable to plant cells. Barry (1843), in a publication entitled *The Infusoria compared with Cells*, argued that *Monas* and other flagellates comprised single cells that had a nucleus which corresponded to the cell nucleus of higher forms. von Siebold (1845) [Fig. 7] formulated the *doctrine of the unicellular nature of Protozoa.* He divided the Protozoa into two classes, the *Infusoria* and *Rhizopoda* (see Dujardin below), the former being sub-divided into two groups, the ciliates (*Stomatoda*) and the flagellates (*Astomata*). The rotifers he removed to the *Vermes* and the bacteria and *Volvox* were placed in the plant kingdom.

In 1852 Perty (1852) instituted the *Archezoa*, equivalent to von Siebold's (1845) Protozoa, with the Stomatoda re-named the *Ciliata* and the Astomata (flagellates) re-named the *Phytozoida* (plant-animals). Cohn (1853) is recognised as the originator of the term *Flagellata*. He confirmed that the green colouration of some flagellates was due to chlorophyll and that pigmented flagellates were photosynthetic plants. Diesing (1866) [Fig. 8] instituted the name *Mastigophora* (= whip bearer) for flagellates and many subsequent classificatory systems have used this terminology.

The combination of exploration and science became a feature of the nineteenth century. Captain James Cook's celebrated voyages of discovery, initially to observe the transit of Venus, extended from 1768 until his death in 1779 and set the tone for a series of highly productive sea-going cruises, including the Beagle (1832-1836) and HMS Challenger (1872-1876), during the nineteenth century. All were to return with vast collections of new plants and animals and all were to stimulate great scientific interest. At the practical level, cruises returning with so much new material required

shore-based scientists to make the time consuming observations and so it was the material was shared out on return. The nineteenth century is noted for its monographs of new species based on collections of one sort or another.

Christian Gottfried Ehrenberg's (1795-1876) [Fig. 9] monumental monograph, entitled *Die Infusionthierchen als Vollkommene Organismen* (The Infusion Animals as Complete Organisms), published in 1838 established the Infusoria, including protozoa, bacteria, diatoms, desmids and rotifers, as a major separate group of animals (Ehrenberg 1838). Ehrenberg, a native of Leipzig and trained in medicine, had great observational ability which is manifest in the quality of his illustrations in this and other works, furthermore he was also interested in micropalaeontology and described many fossils. However, his classification of the single celled Infusoria, including the flagellates, into the *Polygastrica* on account of *their many stomachs* and his belief that these organisms were organised in the same way as higher animals was to deflect his attention from a more fundamental understanding of cell structure. He added a large number of new genera, including *Euglena, Bodo,* and many diatom species to the literature, most of which are still in valid use today genera (Schlegel and Hausmann, 1996; Williams and Huxley, 1998).

Félix Dujardin (1801-1860) [Fig. 10], a Frenchman and contemporary of Ehrenberg, was a physiologist, morphologist and taxonomist who concentrated his attention on living foraminifera, amoebae and certain ciliates. He introduced the term *sarcode* to describe the streaming cytoplasm of amoeboid cells. His observations on cell structure, including feeding experiments involving pigmented granules, convinced him of the error of Ehrenberg's polygastrica theory and rapidly lead to the theory's demise. Dujardin's (1841) treatise entitled *Histoire Naturelle des Zoophytes*, like Müller's and Ehrenberg's before, is noted for the number of new genera and species described and also for the quality of the illustrations. Dujardin was the first to describe three types of free-living forms, *les flagélles*, *les rhizopods* and *les ciliés*. He discovered the flagellated cells of sponges, although he did not observe their collars, and held that they were nothing more than colonies of Infusoria. Dujardin's (1841) classification of the Infusoria into four orders according to the means of locomotion established the system for classifying protozoans that was ultimately used throughout the nineteenth and twentieth centuries.

Friedrich Ritter von Stein (1818-1885) [Fig. 11], another in the spirit of Müller and Ehrenberg, working at the German-speaking University of Prague, produced four beautifully illustrated volumes on free-living protozoa entitled *Der Organismus der Infusionthiere* (Stein, 1859-1883). Again he was the originator of many names still in use today. The controversial Ernst Haeckel, Professor of Zoology at Jena, also made a major contrtibution to protozoology in the form of exhaustive microscopic

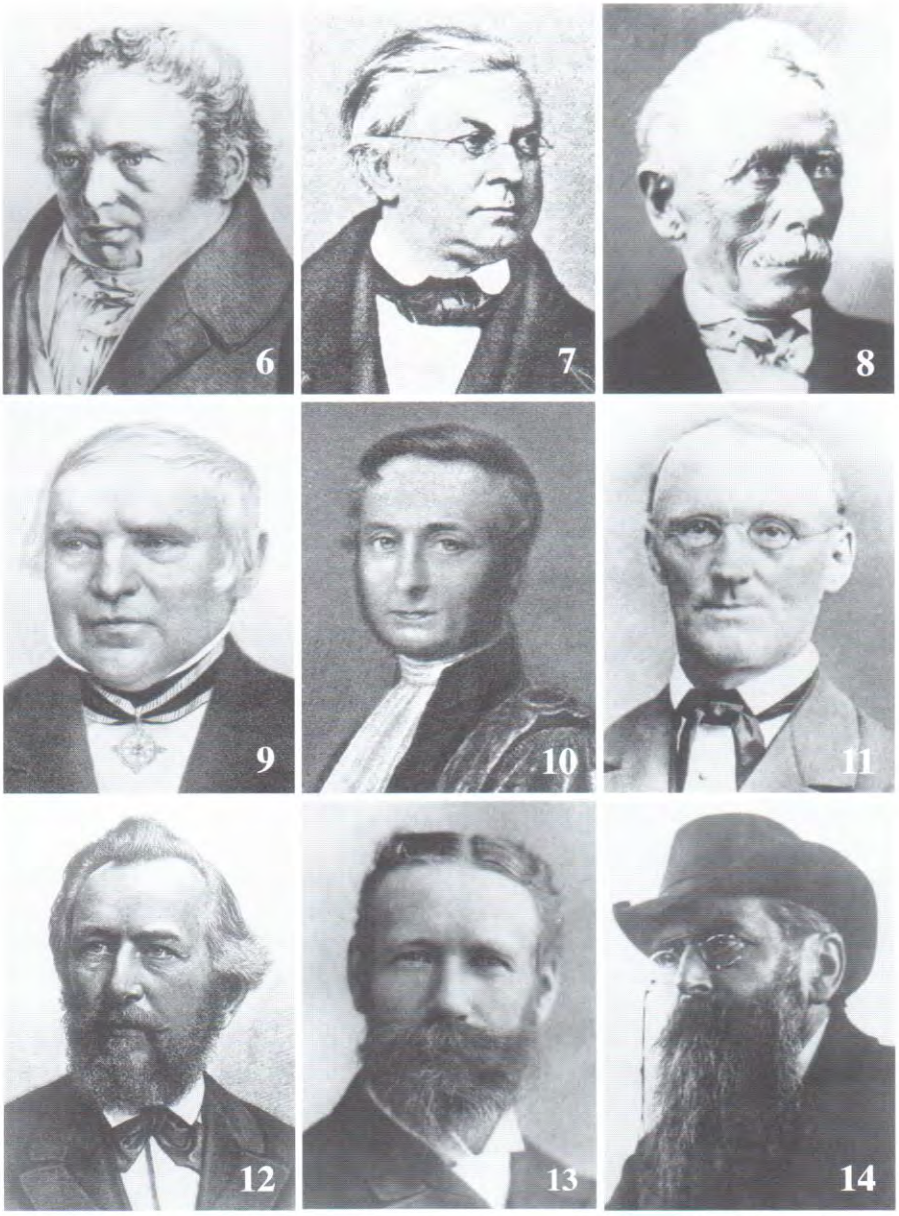


Fig. 6 Georg August Goldfuss. Fig. 7 Karl Theobold von Siebold. Fig. 8 Karl Moritz Diesing. Fig. 9 Christian Gottfried Ehrenberg. Fig. 10 Félix Dujardin. Fig. 11 Friedrich Ritter von Stein. Fig. 12 Ernst Haeckel. Fig. 13 William Saville Kent. Fig. 14 Otto Bütschli.

studies on the radiolaria. He coined the term Protista and named the Heliozoa and Radiolaria.

As we have seen Dujardin (1841) laid the foundations for a classification of the Protozoa. Dujardin considered the sponges to be colonies of Infusoria. However, Haeckel (1869, 1878) [Fig. 12] argued that sponges should be excluded from the Protozoa and in doing so identified himself with von Siebold's (1845) view that the Protozoa were unicellular animals. In 1878 Haeckel (1878) published his most famous systematic generalisation, the division of the animal kingdom into the Protozoa and Metazoa. Haeckel (1878) gave the sponges independent status within the Metazoa since, in his opinion, they more nearly approximated to the Coelenterata. A long, and at times acrimonious, dispute now raged within the literature between those who considered that the Sponges were a separate metazoan group (Haeckel, 1869, 1870, 1873) and those including, Carter, James-Clark (1868) and Kent (1880-1882) [Fig. 13], who considered the sponges were closely related to the Infusoria, and in particular the recently recognised choanoflagellates. Haeckel's defense of the argument involved his *Gastraea theory*, whereby he postulated that all Metazoa have a common ancestor involving a *gastrula* stage. James-Clark (1878) and Kent (1880-1882) argued against the sponges having a gastrula phase in the sense in which Haeckel interpreted it and laid great emphasis on the morphological similarity between the choanoflagellates and the choanocytes of sponges. The latter, by this time, were fully recognised as having conical-shaped *hyaline* collars (James-Clark 1866, 1868, 1878). The finding by Kent (1880-1882) of *Proterospongia*, a colonial choanoflagellate, appeared to settle the proximity of the relationship between choanoflagellates and sponges but in the light of recent information the closeness of this relationship is still in doubt.

Kent (1880-1882) considered that amoeboid forms were the progenitors of all other groups of protozoa. The choanoflagellates were separated from the remainder of the flagellates and were associated with the sponges. The ciliates were separated from the Suctoria (Tentaculifera) and the opalinids. Kent omitted the recently instituted Sporozoa (Leuckart, 1879) although he included some gregarines in his overall scheme. Kent's three-volume publication *Manual of the Infusoria* [Fig. 15] was produced during a very varied and active professional life. He was befriended by both Thomas Henry Huxley (to whom he dedicated his *magnum opus*) and Richard Owen. After a succession of jobs in Britain during the 1870s and 80s, he moved to Tasmania to work on Australian fisheries where he initiated oyster fisheries and arguably started commercial cultivation of pearl oysters. He died in Bournemouth after a short illness in 1908.

Otto Bütschli (1848-1920) [Fig. 14], the *great architect* of systematic protozoology

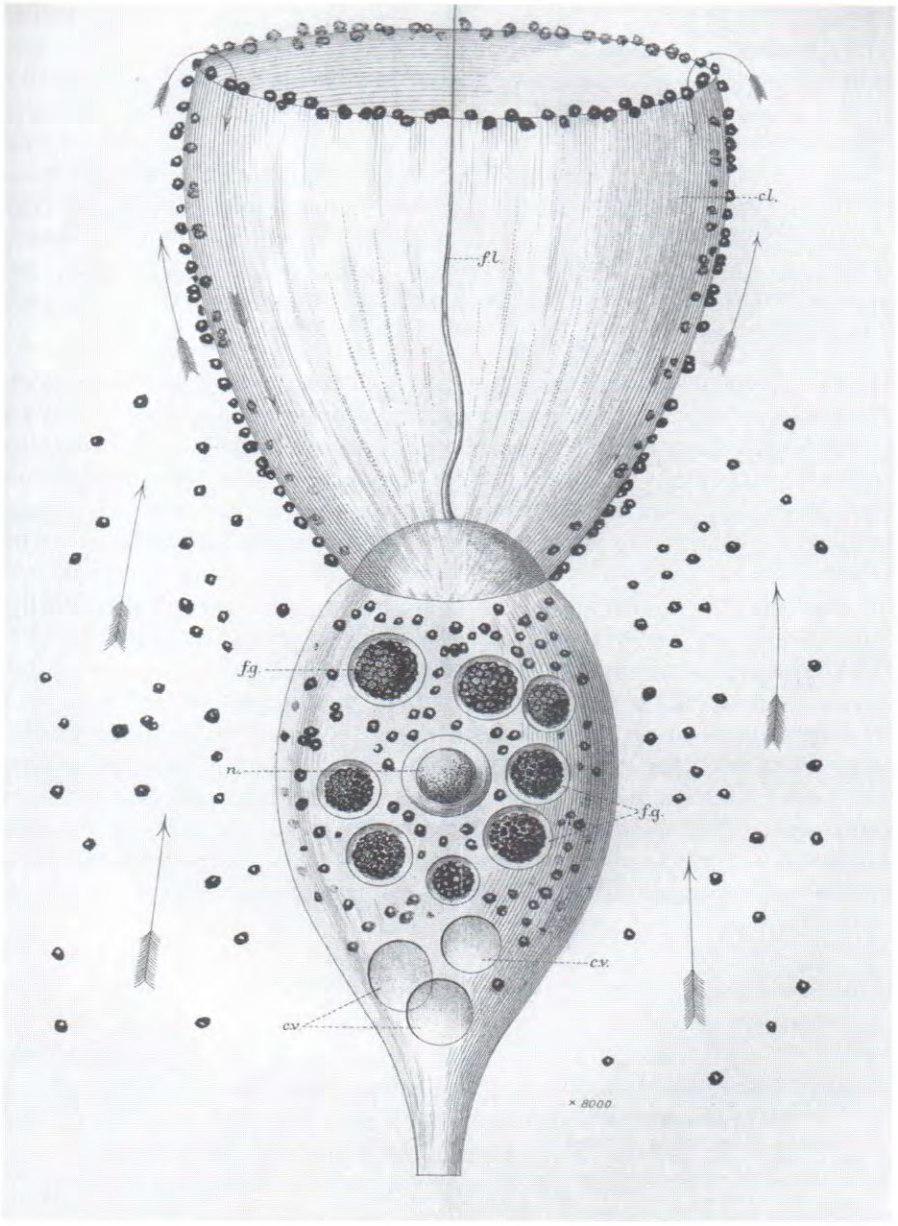


Fig. 15 *Monosiga Gracilis* Kent (Frontispiece, Kent 1880-82)

(Dobell, 1951; Corliss, 1978) published his classification and evolutionary arrangement of the Protozoa. The basis of his system at the class level was still primarily the means of locomotion. Bütschli's (1880-1889) system instituted five classes, namely: the *Sarcodina* (amoebae), *Mastigophora* (flagellates), *Infusoria* (ciliates), *Sporozoa* and *Radiolaria*. The flagellates occupied four orders (*Flagellata, Choanoflagellata, Dinoflagellata* and *Cystoflagellata*) within the class Mastigophora. He grouped the ciliates and Suctoria within the class Infusoria and from this time onwards the term *infusoria* has been restricted to the ciliates. Bütschli's (1880-1889) system had the advantages of order and relative simplicity and probably for this reason has formed the basis of the systematics of Protozoa for the better part of a century.

The end of the nineteenth century marked a high point in protistological studies. The cellular substructure of living matter and evolutionary theory had been established even if these theories were not accepted by all. The extent of biodiversity was becoming apparent, particularly in relation to the oceans. The complex, multi-phasic developmental cycles of parasitic protozoa that caused so much disease, particularly in tropical countries were in the process of being unravelled (see chapter 2). The classification and systematics of the protozoa had at long last been brought into some sort of order. It is striking how these achievements so neatly fitted in with the end of the century Kent (1880-82); Haeckel (1878), Ross (1901), Bütschli (1880-89). These were no mean achievements and were to set high standards for the coming century. Looking back at this period it is striking how long it took protozoology to move on in the twentieth century. Students in the 1960s and 70s (and some now for all we know!) were still being taught the Bütschlian view of Protozoan systematics. It required the advent of electron microscopy in the 1950s onwards to improve on the exquisite cellular detail available in the best of the nineteenth century monographs. And in spite of the achievements of Ross and others in the study of protozoan diseases, parasitic protozoa are still responsible for widespread human misery and mortality.

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PART 2

CHAPTER 2

ARMY AND EMPIRE

"All knowledge must arise within social contexts - even the most obvious factual matter based on direct and simple observation - for one must first ask the right question to secure the proper observation, and all questions arise from contexts."
SJ Gould 1999: Leonardo's mountain of clams and the diet of worms.

" The day of small nations has passed away. The day of Empire has come."
Joseph Chamberlain, Secretary of State for the Colonies 1904.

It may be unfashionable to extol the British Empire but there can be no doubt that the Empire was a major driving force in the development of Protozoology in Britain. In 1900 the United Kingdom stood at the centre of the largest empire the world has ever known: it occupied a quarter of the earth's surface. Much of that empire was in the tropical and subtropical realms where infectious disease plays no mean part in determining the health, wealth and happiness of their peoples. The understanding and conquest of that disease was a major goal of science in the late nineteenth century and remained so in the early twentieth. British scientists played a vital part in demonstrating that the causative agents of many tropical diseases were protozoa and that these agents had complicated life cycles linked to transmission of the disease. But almost of necessity these British scientists did their important work in the Empire rather than in the United Kingdom, and most of them were army men obliged to fit in their research between regimental duties. I shall start with the achievements and genius of two giants of this movement whose major discoveries acted as its opening fanfare - Sir Ronald Ross and Sir David Bruce.

Sir Ronald Ross and the developmental cycle of malaria parasites

The year 1901 saw the award of the first Nobel Prizes to researchers who had made outstanding contributions to science. In 1902, the second crop of these prizes included that for Physiology or Medicine to Sir Ronald Ross (1857-1932) [Fig. 16] for his work on the transmission of malaria. The most important protozoan on earth in terms of human mortality is the parasite of human malignant tertian malaria, *Plasmodium falciparum*. Ross had demonstrated a cycle of development of a parasite in the mosquito vector culminating in the production of long thin sporozoites in the insect's salivary glands [Fig. 20] and their subsequent injection into the parasite's definitive host to initiate infection. He had confirmed the theory of insect transmission

of malaria promoted by his mentor, Sir Patrick Manson (1844-1922) [Fig. 17], by demonstrating the exact route taken by the parasite in the mosquito. His spectacular findings were reported in his absence by Manson to the British Medical Association meeting in Edinburgh in 1898. They brought forth thundering cheers from the audience.[1] A triumph for British Protozoology - or was it?

The prize was certainly a triumph for Ross and for Britain as his was the first British Nobel award in Medicine. But whether Ross ever thought of himself as a protozoologist or a parasitologist is doubtful. His story deserves some elaboration here, however, as it presages much that was to come in the development of protozoology in Britain in the early years of the century: the challenge of vector-borne disease in relation to the British Empire, the transition from humanitarian to curiosity-driven research and from amateur adventurer to professional and perhaps above all the role of contingency in great discoveries.

The parasite of malaria was discovered by a French army surgeon and future brilliant protozoologist, Charles Laveran, in 1880 when he observed the flagellated microgamete moving in recently-drawn blood from a malaria patient. He noted the relation of the motile filaments to pigment-containing bodies (gametocytes) and was convinced he had found the causative agent of the disease, but more influential microbiologists, Edwin Klebs and C. Thomassi-Crudeli thought that a bacillus isolated from swamp water a more likely candidate and Laveran's view when published was not taken seriously. During 1884-85, the Italians E. Marchifava and A. Celli identified the amoeboid trophozoite phase of a parasite inside red blood cells of patients, however and established the erythrocytic cycle of development of *Plasmodium malariae* while Camillo Golgi related the reproductive activities of the parasite to the fever cycle and recognised the three major species of human malaria by their clinical effects. Morphological study of the parasite was greatly facilitated by the discovery of a suitable staining method demonstrating the parasite's nucleus by the Russian D.L. Romanowsky in 1891. The nature of Laveran's flagellating body meanwhile remained unknown.

Mosquitoes had been suspected of transmitting malaria since an Italian called Lancisi had suggested it in 1717, but it took Patrick Manson in 1894 to draw up a satisfactory hypothesis of how this might happen and how his theory might be tested. Manson, had to his credit demonstration of the transmission of human filariasis by culicine mosquitoes and was very much the UK's leading figure in tropical medicine. Manson's hypothesis was: (1) that the parasite had to have forms which permitted

[1] Ross's main regret in life was that he never heard those cheers! After his return to Britain he eagerly sought out those who were there, entreating them to describe the scene.

its development and multiplication inside the human host (as studied by the Italians); (2) that it had to have forms that ensured its development outside the human host when it was in transit from one person to another. He identified the crescentic gametocytes of *Plasmodium falciparum* as seen by Laveran as the second of these forms and the motile filaments seen by him as new forms intended to develop in a different host. He postulated that this different host was a biting insect and most probably a mosquito. Interestingly, he had no views on how the mosquito parasite might be returned to humans at the time, though later he admitted that he believed that it escaped from the dying female mosquito at the time of egg laying and that man became infected by consuming contaminated water!

It was in 1894 that Ross came to see Manson. After being pushed by his father into studying medicine at St Bartholomew's Hospital, Ross had put himself at the disposal of the army and entered the Indian Medical Service. It was some eleven years later, however, that he became interested in malaria (1892-93), and not until he returned to England on leave in 1894 and met Manson was his imagination fired to solve the problem of transmission of the disease. Manson showed him how to stain the parasite in blood smears and impressed him with his theory that malaria was transmitted by mosquitoes. After his return to India in 1895, Ross in Secunderabad set about trying to infect mosquitoes by releasing the insects under a net covering the recumbent malaria patient and capturing them singly after they had fed. He had to discover how to handle and dissect mosquitoes and tell one from another; having dissected them he had to examine their internal organs microscopically to determine how far the parasite had developed in them. He found that crescentic stages of *Plasmodium falciparum* underwent exflagellation in 10-20 mins after the dapple-winged mosquitoes (*Anopheles*) had imbibed infected blood but was not sure of the fate of these flagellated organisms.

After being diverted into sanitary work in Bangalore, Ross returned to Secunderabad in April 1895 and set to work on the malaria problem whenever his regimental duties permitted. He now delayed dissection of the infected mosquitoes for a few days, On August 20, 1897, (commemorated by Ross ever afterwards as "mosquito day") he examined mosquitoes that had fed on crescents four days previously and found 12-16mm pigmented cysts (oocysts of the parasite) in the insect gut wall. The pigment served as a parasite marker because Ross worked only with living and not stained material. Not until Manson interceded with the Secretary of State for India to have Ross freed from regimental duties to concentrate on his research, did Ross make further progress, however. By this time he had heard from Manson of a note published in November 1897 by W.G. MacCallum in Baltimore, proving that the "flagella" of *Haemoproteus* (then *Halteridium* - a *Plasmodium*-like parasite of birds) are male elements (microgametes) that fertilise the pigmented spheres or female

elements (macrogametes): from the zygote, a motile vermicule (ookinete) develops. The news was just what Ross needed. Finding difficulty in obtaining human malaria cases owing to the onset of the healthy dry season, Ross was converted to comparative protozoology and took to studying bird malaria, specifically *Plasmodium relictum* (then called *Proteosoma*) in caged sparrows and larks. *Culex fatigans* was employed as transmitter. Ross saw the vermicules develop into oocysts in the mosquito gut wall and then grow in size over successive days. When the cysts attained a diameter of ~60mm, they burst, liberating "germinal rods" (sporozoites) into the insect's coelomic cavity from which they entered the salivary glands and were injected through the proboscis with the saliva when the insect bit. These results constituted the definitive proof of how malaria is transmitted.

There can be no doubt that Ross's motivation in studying the malaria parasite was entirely humanitarian: it was undertaken with the sole aim of preventing transmission of one of mankind's greatest afflictions. But his success in large measure depended on a piece of curiosity-driven research in comparative protozoology - MacCallum's work on gametogenesis in the life cycle of *Haemoproteus*. Ross had had little training in scientific research. True, he had some background in bacteriology but it had been of virtually no help to him. That great British protozoologist, C.M. Wenyon (see Chapter 6) later remarked: "One is led to wonder whether Ross would have achieved so much had he been better trained in more orthodox methods of research. His want of special knowledge drove him to work out his own salvation and gave scope for that genius which he undoubtedly possessed".

Ross's research career, incredibly, spanned only five years. As a Major in the Indian Medical Service, conducting research in his spare time, he had endured heat "like the blast of an engine furnace", difficult working conditions and the repeated frustration of being moved on by the army just as his research was getting somewhere. After the frustration being diverted by the army into studying kala azar, Ross resigned his commission in the Indian Medical Service in 1899 and left India for England and a new career at the recently founded Liverpool School of Tropical Medicine (Chapter 6). It was left to the Italians under the leadership of Battista Grassi to demonstrate later in 1898 developmental forms of human malaria parasites in *Anopheles maculipennis* (then *A. claviger*) similar to those described by Ross. Unfortunately Grassi claimed priority and a bitter quarrel ensued between the two of them, with wide repercussions, but the Nobel Committee decided for Ross alone. For, as Harrison[2] has so succinctly put it "It makes no sense to couple the names of Ross and Grassi together as co-discoverers - as is often done - without noting the

[2] Harrison, G, (1978) Mosquitoes, malaria and man. John Murray, London. An excellent read on the 'history of hostilities since 1880.'

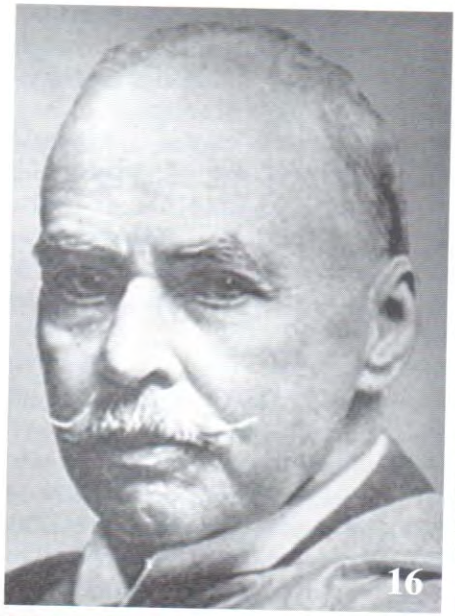








Fig. 16 Sir Ronald Ross FRS. Fig. 17 Sir Patrick Manson FRS. Fig. 18 Sir David Bruce FRS. Fig. 19 Sir William Leishman FRS.

very large difference between the explorer at the helm and those who rode his decks and helped make a landing".

Sir David Bruce and the developmental cycles of African trypanosomes

Unlike Ross, who took it upon himself to study mosquito transmission of the malaria parasite, David Bruce (1855-1931) [Fig. 18] was asked to investigate the cause of Nagana, a severe wasting disease of cattle in Africa. A naturalist by inclination and a medic by training[3], he entered the Army Medical Service in 1883 and made a spectacular start to his career when he was ordered to Malta to investigate Malta fever among the troops there. He quickly identified the carrying agent (goat's milk) and the causal bacterium (later named *Brucella mellitensis* in his honour). The Governor of Malta at the time, Sir Walter Hely-Hutchinson, subsequently became Governor of Zululand and Natal and when Bruce was moved by the Army to South Africa, he invited Bruce to look into the Nagana problem. Within a year (1895) Bruce had submitted a report incriminating trypanosomes as the causative agent and the tsetse fly as their transmitter. He went on to demonstrate that game animals served as a reservoir of the disease. The parasite was named *Trypanosoma brucei* by Plimmer & Bradford (1899), who studied it in an infected dog shipped back to Britain in 1896, and used it as a source of laboratory infections by passage of infected blood through laboratory animals such as rodents and rabbits.

Bruce acknowledged the influence of two great men in his unravelling of the nature and transmission of nagana - the Scottish explorer David Livingstone (1813-73) and that German giant in the history of medical science, Paul Ehrlich (1854-1915). Livingstone had drawn the attention of the scientific world to the ravages of the tsetse fly on cattle and horses - though he believed that the fly injected a lethal venom into its prey. Ehrlich had made the examination of blood in disease fashionable. The fashion relied heavily on the selective staining of blood components (including pathogens) by particular dyes. Ehrlich, who had a passion for use of the new products of the German dye industry, later extended his study of selective staining to explore the use of cell-fixed dyes as selective drugs in infected hosts, and so laid the foundations of rational chemotherapy. It was in a carbol fuchsin-stained blood smear that Bruce first observed "a curiously shaped object lying among the corpuscles". He later found the living trypanosomes in fresh blood.

Bruce was initially more concerned with demonstrating that the trypanosome was the cause of nagana than with its mode of transmission by the tsetse fly. In his report

[3] Bruce entered Edinburgh University to study zoology but was persuaded to change to medicine. Among Edwardian protozoologists the trend was in the other direction (see Chapter 5).

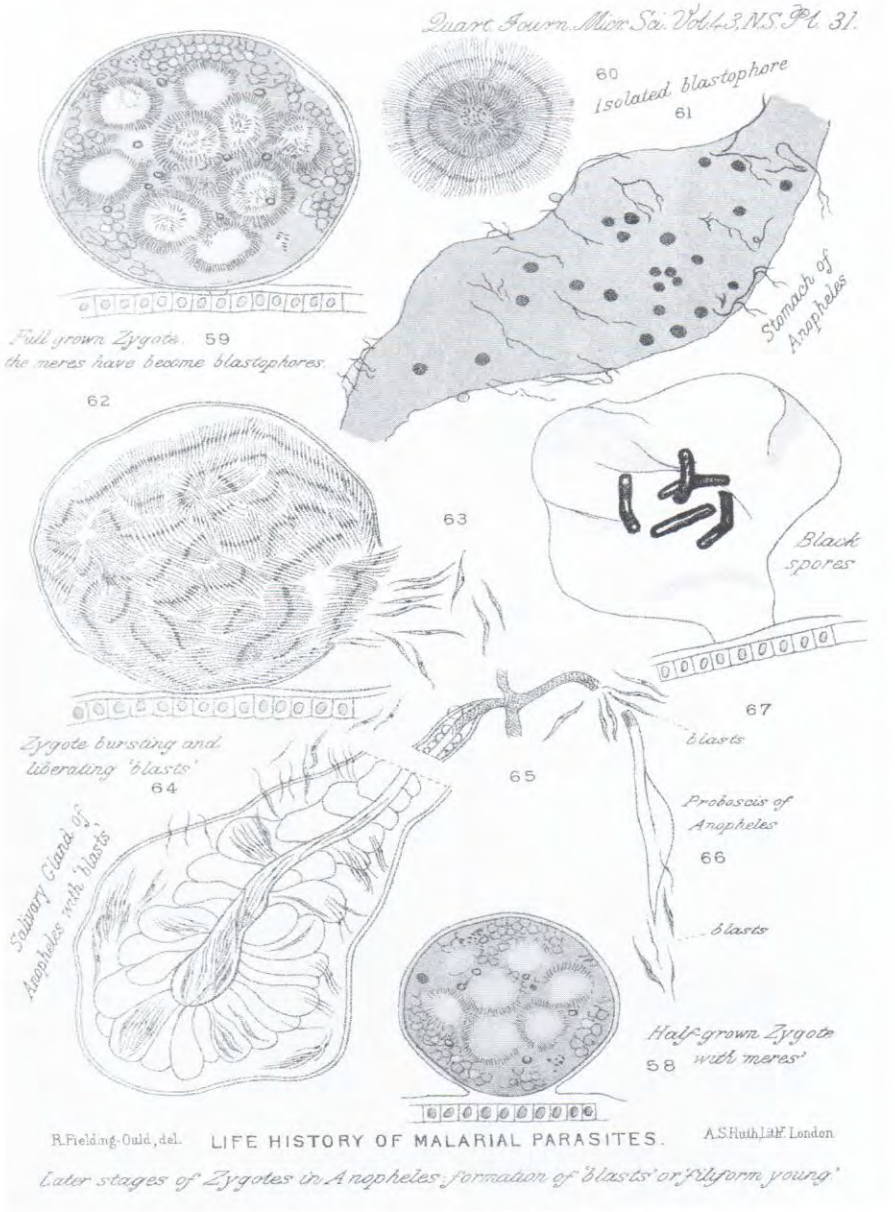


Fig. 20. Development of sporozoites in oocysts of *Plasmodium* in mosquito stomach (Ross, 1900. QJMS, vol 33, Pl. 31.).

to the Governor of Zululand, Bruce concluded that he was "almost certain" that the trypanosome was the true cause of nagana because: (1) it was found in the blood of every animal suffering from the disease and was absent from healthy animals; (2) the onset of fever corresponded with the first appearance of trypanosomes in the blood; (3) as the disease progressed the destruction of red blood cells paralleled the increase in numbers of trypanosomes in the blood; and (4) transfer of the smallest amount of blood from an infected to a healthy animal set up disease in the latter. He did conduct experiments on transmission, however, by exposing healthy animals from outside tsetse-infested areas to fly attack and then following the development of the disease in them.

Louis Pasteur (1822-95) would not have accepted this evidence that the trypanosomes were the disease-causing agent. He would have insisted that serial culture of the suspected pathogen *in vitro* over several generations was necessary before reinfection attempts were made in order to dilute out any contaminant such as a filter-passing virus. In other words Bruce should have tried to fulfil Koch's postulates for demonstrating the relationship between microorganism and disease. This deficiency was not unique to Bruce's discovery: protozoa are bad candidates for fulfilling Koch's postulates. They have complex life-cycles involving differentiation events and more elaborate structure than bacteria. These features do not endear them to microbiologists trained as bacteriologists because they lead indirectly to difficulties in cultivating protozoa *in vitro* and hence in fulfilling Koch's postulates. On the other hand it is precisely these features that do endear them to microscopists and zoologists as I shall discuss later in Chapter 3.

The red herrings provided by concomitant infections with harmless microorganisms, and which Koch's postulates are designed to exclude came to haunt the identification of the causative agent of human sleeping sickness. With the outbreak of the Boer War in 1899, Bruce was compelled to serve as a surgeon to the British troops, but for his outstanding contributions to medical science was elected FRS in the same year. After the war he returned to the UK but was soon seconded by the War Office to take charge of the Royal Society's Second Sleeping Sickness Commission in Uganda (1903-1906). The causative agent of the epidemics of sleeping sickess then sweeping through East Africa was unknown. Aldo Castellani, one of the young investigators dispatched with the first Commission in 1902, had submitted a paper for publication in the Society's *Proceedings* claiming that a streptococcus was responsible. Bruce was not convinced and had blocked publication. Ironically, Castellani had found trypanosomes in the blood of sleeping sickness patients, but having experienced one red herring, the blood nematode *Dirofilaria perstans* initially believed by the team to be the cause, he was reluctant to countenance a possible second. Bruce returned from Uganda with near-conclusive evidence that the streptococcus was a secondary

infection and that sleeping sickness was due to infection with a trypanosome transmitted by the tsetse fly *Glossina palpalis*. He identified the trypanosome as *Trypanosoma gambiense* (now *T. brucei gambiense*) described by Everett Dutton in 1902 as a parasite associated with fever in a West African riverboat captain (see Chapter 6). Whether Bruce or Castellani should get the credit for the identification of the aetiological agent of East African sleeping sickness has been another subject of chronic controversy in the history of tropical medicine.[4]

Bruce's original experiments on the transmission of nagana by the tsetse fly did not reveal what took place in the vector during transmission, as Ross's investigations on malaria transmission had done. Indeed Bruce, being a bacteriologist by training (including a spell in Robert Koch's laboratory in Berlin) was unaware that elaborate protozoan developmental cycles taking place in the vector might be the whole key to parasite transmission. As he reported to the British Association in 1904, he envisaged simple mechanical transmission of the trypanosome on the tsetse proboscis. His view was reinforced in 1901 by Leonard Rogers' demonstration of the mechanical transmission of *Trypanosoma evansi* in India by tabanid flies. In fact *T. evansi* in the blood of horses and camels had been linked with Surra - a nagana like disease - by its discoverer Griffith Evans, a Welsh veterinary officer serving in India, as far back as 1880, but Evans believed the animals acquired the infection from polluted drinking water in which he had found "infusoria", despite the fact that the locals associated transmission of the disease with horse-flies!

It was a German worker, F.K. Kleine, who in 1909 showed that tsetse (*Glossina fuscipes*) fed on mammals infected with *T. brucei*, transmitted the infection to clean animals only after an interval of 18-20 days, thus indicating that the parasites underwent a definite cycle of development in the insect vector before they become infective. Bruce thereafter revised his opinion and with his colleagues Hamerton, Bateman and McKie went on to show (1911) that only the metacyclic stage in the fly's salivary glands are able to infect the mammalian host. This was the beginning of our understanding that each stage in the life cycle of a protozoan parasite has undergone a differentiation process that allows it to proceed to the next stage.

Unlike Ross, Bruce went on to develop his interest in protozoology. He headed further Royal Society Sleeping Sickness Commissions - in 1908 to Uganda, in 1911 to Nyasaland (now Malawi) - which resulted in a long series of papers on different trypanosome species of man, cattle and game animals and their life cycles. Throughout the first World War he was Commandant of the Royal Army Medical College. In

[4] See Boyd, J, (1973) The Castellani-Bruce controversy. *Notes & Records of the Royal Society* 28: 93-1

1915 he summarised his vast experience on trypanosomes in his Croonian lectures to the Royal College of Physicians, dealing with them in a taxonomic framework of the *T. brucei*, *T. congolense* and *T. vivax* groups, later to be elaborated on by C. A. Hoare (see Chapter 6). Bruce's researches gave Britain a lead in African trypanosome research which lasted late into the twentieth century.

Sir William Leishman and leishmaniasis

The third major contribution to parasitic protozoology around the turn of the century was made by another army doctor, William Boog Leishman (1865-1926) [Fig. 19][5]. In 1900, while an assistant professor of pathology at the Army Medical School, Nettley, later to become the Royal Army Medical College, Leishman had developed his own version of Romanowsky's staining procedure for blood films. In 1901 in the course of an autopsy on a soldier who had died of "dum dum fever" - what we now know as kala azar - he examined spleen smears stained by his new technique and found the microscope field strewn with small oval bodies. Each contained two masses of chromatin-staining material, one circular, the other rod-shaped (nucleus and kinetoplast we now know!). The appearance was one he had not previously encountered, and he made careful notes but did not publish his observations. Two years later when examining smears from rats experimentally-infected with *Trypanosoma brucei* and that had died some hours previously, he noted degenerating trypanosomes which forcibly reminded him of his earlier observations; he now saw a reason for publishing them. Human trypanosomiasis had just been described by Dutton and Todd (see Chapter 6), so Leishman hazarded a guess that kala azar was a disease of similar causation and suggested that a search should be made among cases of the disease in India during life.

Later in 1903, Charles Donovan a British professor of physiology at Madras University sent sketches of a parasite he had found in the spleen of a patient with fever and splenic enlargement to Ronald Ross. Ross recognised the parasites seen by Leishman and Donovan as the same organism and created the genus *Leishmania* in honour of their discoverer; the parasite of kala azar became known as *Leishmania donovani*. In 1904, L Rogers cultivated the parasite *in vitro* in citrated blood, under which conditions it transformed into flagellates resembling those of the genus *Leptomonas* described by Bütschli. The significance of the flagellated form was not missed by Leishman who pointed out the probability that this was the stage that would be found in the insect vector. In the case of the *Leishmania* parasites, the search for the vector continued for nigh on 40 years, and not until 1942 did H.E. Shortt and

[5] A Glasgow graduate and friend of Sir John Graham Kerr who encouraged protozoology in Glasgow early in the century (Chapter 4).

colleagues (see Chapter 6) in the Indian Army Medical Service succeed in demonstrating their transmission by sandflies. Like that of Ross, Leishman's excursion into protozoology was brief. He went on to make his name in typhoid vaccination in the First World War.

Importance of work on vector-borne protozoa

British workers were not the first to show that arthropods can act as carriers of protozoan parasites: this honour fell to Theodore Smith and F E Kilborne (1893) in the USA who demonstrated that the recently-discovered piroplasm, *Babesia bigemmina*, causative agent of redwater fever in cattle was transmitted by the tick, *Boophilus annulatus*. The above account is intended to show the unique and original contribution made by British workers to our understanding of protozoa as agents of disease and how they are transmitted.

The consequences of this work for the development of protozoology in the UK were far-reaching. First it opened up a new means of control of disease based on attacking the vectors; Ross devoted the remainder of his career to practical aspects of this control and it dominated tropical medicine for much of this century.[6] Second, it led to the realisation that protozoa with their complex life cycles and recurring differentiation processes are fundamentally different from bacteria, and to their exclusion from a science of microbiology that was based largely on bacteria. Third, it led to the foundation of important research institutes staffed by professional scientists who could devote themselves to the study of protozoa, as outlined in chapters 3 and 5. And lastly, of course, they led eventually to an increased interest in protozoa all round.

[6] This advance was noted by one, Albert William Brown, of Stoke on Trent, the compiler of the Protozoa section for the *Zoological Record* in his report for 1900. "The discoveries of the relation of the Haematozoa to malarial fever afford a strong justification of the utility of Biological Science" he wrote, as though he had just discovered this.

CHAPTER 3

MICROSCOPY AND PHILOSOPHY

"Looking through a microscope... I feel overwhelmed. All the hairs on the back of my neck stand up."

Richard Dawkins Interview in TheSunday Telegraph 1999

"The full and earnest cultivation of Science - the Knowledge of Causes - is that to which we have to look for the protection of our race - even of this English branch of it - from relapse and degeneration."

E. Ray Lankester: Degeneration: a chapter in Darwinism, 1880

As the twentieth century dawned, Germany remained the fountainhead of research on Protozoa, and microscopy the principal occupation of those who worked on them. Otto Bütschli's monumental contributions on Protozoa to Bronn's *Klassen und Ordnungen des Thierreichs* (1880-1889) were the revered benchmark on the systematics of these organisms. In 1846 the optician Karl Zeiss had opened a workshop in the town of Jena and started what was to become Europe's biggest optical instruments industry giving Germany a head start in microscopy. In turn of the century Britain, there was mounting interest in protozoa among academic zoologists but protozoology was not an all-consuming passion of anyone. There was no obvious successor to Saville-Kent as a dedicated explorer of the infinite diversity of these organisms, but a dilettante interest in this diversity.

Zoology in general was in the grip of the dynastic concept of evolution. The course of evolution was being unfolded in the form of pedigrees or family trees, an approach made popular by the writings of the Great Sage of Jena, Ernst Haeckel (1834-1913) [Fig. 11]. While proclaiming himself an apostle of Darwin, Haeckel introduced the notion of progress into his evolutionary trees. He, in fact, carried over into his evolutionary thought the tenets of the *Naturphilosophie* movement - the scientific incarnation of German romanticism. According to the "naturephilosophers," the flux of nature was from lower to higher, from initial chaos up to Man - the highest configuration of matter on earth. On Haeckel's phylogenetic trees, Man was at the very top, at their base the unicellular protozoa [Fig. 21]. His thinking embraced the concept of the "Great Chain of Being" or *Scala Naturae* - the idea, dating back to Plato, that there must be a continuous gradation of rationally-imagined creatures from the simplest and humblest all the way up to the divine. Also crucial to Haeckel's view of evolution was the "Biogenetic Law", that ontogeny recapitulates phylogeny. In his climactic work *The History of Creation* Haeckel argued with characteristic assurance: "An irrefutable proof that such single-celled primaeval animals really

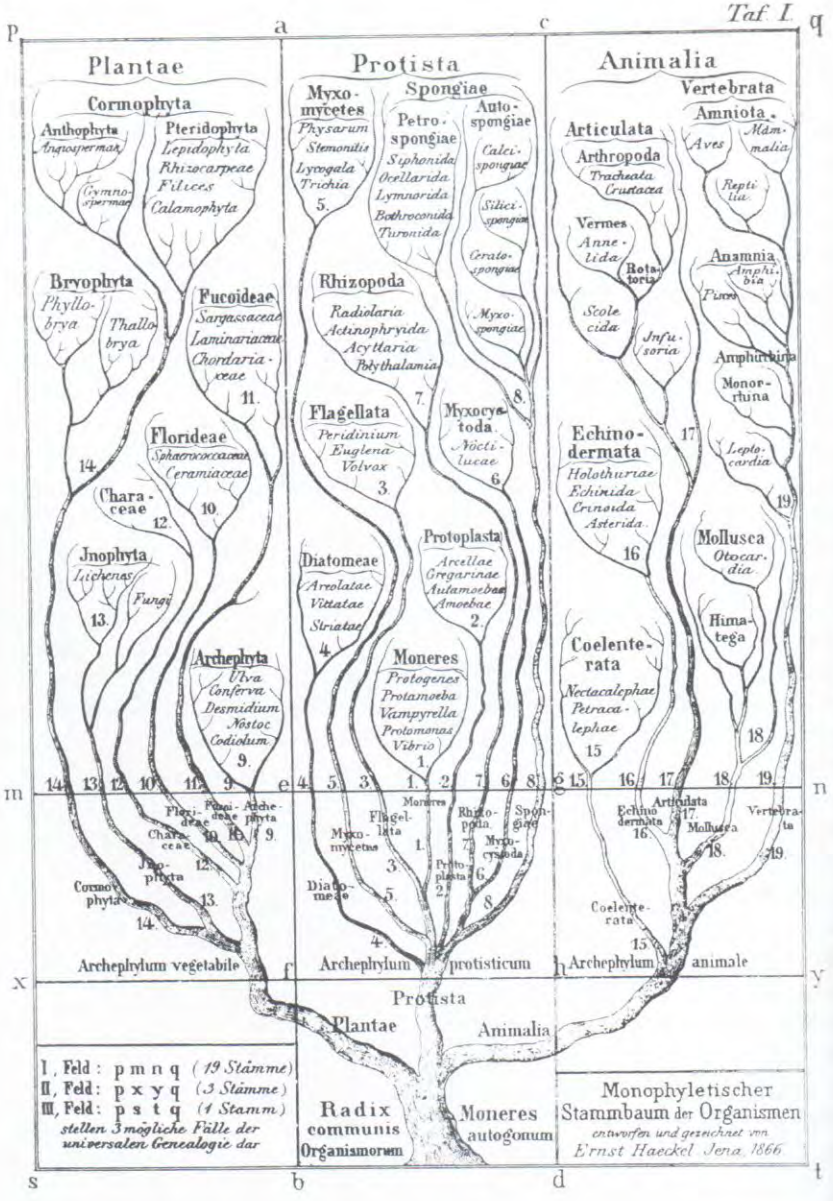


Fig. 21. Haeckel's (1896) phylogenetic tree (John Corliss).

existed as the direct ancestors of Man, is furnished according to the fundamental law of biogeny by the fact that the human egg is nothing more than a simple cell". This two volume work was thought to be of such importance by the British zoologist E.R. Lankester that he translated its eighth edition into English for publication in 1892. Its influence lingered on until well into the twentieth century.

Sir Edwin Lankester and the QJMS

A good example of the dilettante interest in protozoa characteristic of many British zoologists at the turn of the century is to be found in the career of Sir Edwin Ray Lankester (1847-1929) [Fig. 22], Professor of Zoology first at University College London (1874-91), then at Oxford until he became Director of the British Museum (Natural History) from 1898-1901. Lankester was widely regarded as the successor to that giant of Victorian zoology, Thomas Henry Huxley (1825-95) [Fig. 23]. As Ruse[1] has put it - Lankester was born to the purple in British zoology. His father, Edwin Lankester M.D., FRS was a respected microscopist and founder of that important publication, the *Quarterly Journal of Microscopical Science* (QJMS for short). Lankester junior became co-editor in 1869, just after his graduation from Oxford, and, eventually, sole editor from 1878-1920. During the period of his editorship the journal became the principal outlet for British research on Protozoa - indeed for zoology in general. In 1900, Ronald Ross published his "Diagrams illustrating the life history of the parasites of malaria" in it - and Lankester could not resist following Ross's paper with one by himself commenting on its importance. *The Archiv für Protistenkunde* founded by Fritz Schaudinn in 1902 specifically for research on protists, eventually attracted some British authors though their numbers fell sharply with the onset of the 1914-18 war with Germany.

In 1863, E.R. Lankester, aged 16, published his first contribution to QJMS on a gregarine protozoan. This paper was the prelude to a series of researches on free-living and parasitic protozoa.[2] These encompassed Apicomplexa (his name is commemorated in the genus *Lankesterella*), trypanosomes, Proteomyxa (see below) and foraminifera, both extant and fossil. Lankester's principal interest was in comparative anatomy and embryology, however, and his best work was on the development of invertebrates. He was one of the first British scientists to work at the *Stazione Zoologica* marine station in Naples, and his friendship with the Director,

[1] Ruse, M. (1996) *Monad to Man: the concept of progress in evolutionary biology*. Harvard University Press.

[2] To credit Lankester with the discovery of protozoan parasites, as his Oxford successor, E S Goodrich, did in Lankester's Royal Society obituary, is surely going too far! Goodrich's argument was that Lankester recognised parasites that had previously been classified as worms, as protozoa.

Anton Dohrn, profoundly affected his thinking on evolution. Lankester's marine interests came to fruition when he later founded the Marine Biological Association of the United Kingdom and its Plymouth Laboratory.

Lankester's Treatise on Zoology

Lankester is perhaps best known for his popular writings and encyclopaedic works. The first decade of the 20th century saw the publication of two important zoological encyclopaedic works in Britain, each with detailed treatment of Protozoa. In the eminently readable *Cambridge Natural History* (1906), edited by S.F. Harmer and A.E. Shipley, this was undertaken by the relatively unknown ex-Trinity man Marcus Hartog, Professor of Natural History at University College, Cork. The more scholarly *A Treatise on Zoology* was edited by Lankester, and regrettably never finished as has been the fate of all such ambitious comprehensive works. It was a strange publication. The editor boasted that "The two fascicles of the first part of this treatise give a more complete account of the Protozoa than is to be found in any similar work hitherto published." Fascicle 2 (Foraminifera, Sporozoa and Infusoria) appeared (1903) before Fascicle 1 (Proteomyxa, Heliozoa, Mycetozoa, Lobosa, Radiolaria Mastigophora and Haemoflagellates) which did not emerge till 1909. Lankester originally hoped to have *Treatise* contributors who were Oxford to a man (as a counterblast to the *Cambridge Natural History*, presumably!) but as it turned out, apart from E.A. Minchin (see Chapter 4), the contributors on protozoa were all Cambridge or London products. They were a rum lot! S.J. Hickson, who contributed the sections on Proteomyxa, Lobosa, Mastigophora (jointly with A.Willey) and Infusoria was a coelenterate man (as was Willey); W.F.R. Weldon (Lankester's successor at both UCL and Oxford) who was senior author (with Hickson) on the Heliozoa was a distinguished biometrician but had no published papers on this group. The most scholarly contribution was that on Sporozoa by Minchin, but at the time he wrote it the author was a sponge expert and had published next to nothing on protozoa, nor had F.W. Gamble any papers on radiolarians. True, the young H.M. Woodcock who wrote the haemoflagellates section had published one paper on them in QJMS in 1906, but only J.J.Lister could claim to be a recognised authority on his groups, the Foraminifera and Mycetozoa. And he admitted that for his section on the latter he had been heavily dependent upon the work of his father, A. Lister, who had published a massive British Museum monograph on the group in 1894. The overriding impression is that early in the first decade of the 20th century, Britain was not exactly well-off for authorities on Protozoa, but that some workers in other fields of zoology found the protozoa sufficiently interesting to devote a great deal of their time to reading about them. On the other hand, it could have been just as difficult to recruit authoritative contributors to this kind of multi-authored work then as it is today!

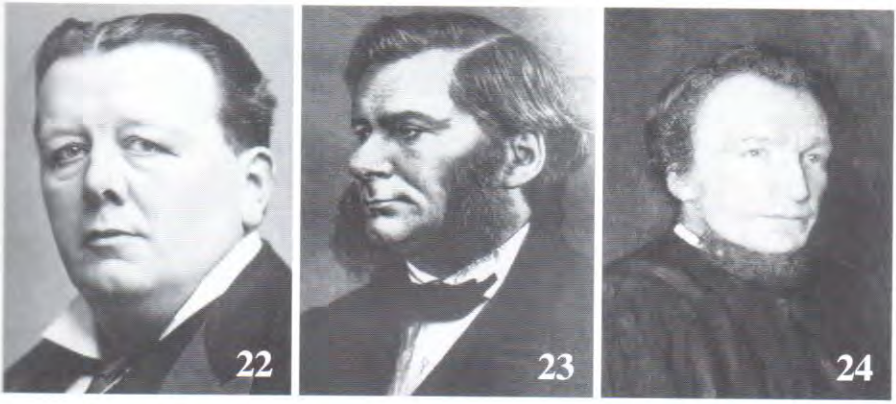


Fig. 22 Sir Edwin Ray Lankester FRS. Fig. 23 Sir Thomas Henry Huxley FRS. Fig. 24 Rev. Dr William Dallinger.

Philosophical questions

Lankester contributed only the Introduction to the Protozoa volumes in the *Treatise*. This was essentially a more hurriedly-written version of the discussion introducing his entries on protozoa in the *Encyclopedia Britannica* that he published separately in bound form as *Zoological Articles* (1891). These discussions are of value as in them he outlined the principal problems seen by him as facing protozoologists at the *fin de siecle* and, as the standing of a subject is often judged by the questions being asked by its practitioners, it seems appropriate to consider them here. These questions were: How should we define Protozoa? What constitutes an individual protozoon? Do all protozoa have nuclei? What were the first protozoa like? These questions might be viewed by some as philosophical, even Naturephilosophical, but they were very much in tune with the biology of the day.[3]

Lankester had no hesitation in defining protozoa as unicellular animals and thus seeing their study as part of zoology. Their animal nature was of paramount importance and they could be studied independently of unicellular plants (which at that time included bacteria). "There is no doubt" he stated with characteristic Victorian authority, "that organisms present themselves to us in two great series, starting in both cases from simple unicellular forms". He rejected motility as a deciding animal

[3] Hartog in his 1906 *Cambridge Natural History* treatment of Protozoa described Lankester's article in the *Encyclopedia Britannica* as being "of epoch-making quality in its philosophical breadth of thought." Unlike Hartog, Lankester did not consider spontaneous generation a topic worthy of philosophical discussion. in relation to protozoa.

characteristic (as many plant spermatozoa possess it) and saw no convincing argument for Haeckel's Protista, nor Hogg's Protoctista. He admitted that "the evil we have to avoid is that some small group of unattractive character should be rejected by both the botanist and the zoologist. He made little of the individuality problem presented by colonial protozoa. "Their coherence" he said, "has no economic significance, unlike the cells composing the bodies of multicellular animals." At the time he was presumably unaware of the debate over whether the individual ciliate or the entire clone that develops from an ex-conjugant corresponds to the individual metazoan - a view held by Bütschli in Germany and Calkins in the USA (see Chapter 5).

Lankester was less certain about the universal presence of a nucleus among protozoa. Although he said that nuclei had now been demonstrated in Foraminifera and Mycetozoa (where at one time they had been believed to be lacking) "we are not yet justified in concluding absolutely that there are not some few protozoa in which this central differentiation of the protoplasm does not exist." He mentioned Flemming's recent discovery of chromatin fibres (later called chromosomes) in dividing cells and that they had not been universally observed in dividing protozoan nuclei. Sutton had not yet drawn a parallel between the behaviour of chromosomes and that of "Mendel's factors" (later called genes) because Mendel's work had not yet been discovered by de Vries. And of course the distinction between prokaryote and eukaryote came decades later.

Protozoa as first life and the concept of protoplasm

The great Bütschli had promoted protozoa as ideal material for the study of the nature of protoplasm - the "physical basis of life" as T.H. Huxley called it. His hefty tome*Investigations on Microscopic Foams and on Protoplasm* had been translated into English by the young Oxford zoologist, E.A. Minchin, in 1894. Bütschli had the good sense, however, to recognise, that despite his exertions, the question of the nature of protoplasm was "as yet so little ripe for final treatment."

Lankester's biggest embarrassment was a sensed duty to pronounce on the "nature of the first protoplasm which had evolved from non-living matter on the earth's surface." He plumped for the Mycetozoa before they developed elaborate fruiting bodies as most closely resembling such organisms. Among his special protozoan interests were the Proteomyxa - a taxon he created himself for amoeboid organisms in which "the cell protoplasm is a naked undifferentiated slime." It is interesting to recall that Haeckel himself (no doubt pondering on the Great Chain of Being), suspected the existence of organisms consisting of naked protoplasm or "*Urschleim*" and lacking nuclei: he called them Monera. The Lankesters (father and son) considered this concept of such importance that they translated Haeckel's papers on

Monera and republished them in the QJMS (1869).[4] It is plain that the appeal of amoeboid protozoa to jack-of-all-trades zoologists at the turn of the century lay in the conviction that in watching them they were viewing the physical basis of life in all its rawness. And they really believed in protoplasm as a sort of pervasive biological ether that endows the otherwise inanimate with life.

Degeneration and the question of simplicity

A notable and distinctive feature of Lankester's thought was his view (acquired from his friend Dohrn, the Haeckel protégé who founded the Naples Marine Station) that, against a background of progress from simple to complex in evolution, we often find organisms exhibiting degeneration from complex to simple. If ontogeny recapitulates phylogeny, then such animals as ascidians (sea squirts) and barnacles that have actively mobile larvae and sedentary adults of simpler structure have clearly followed a similar evolutionary path. Lankester postulated that any environmental change that rendered food and safety more easily obtained could lead to degeneration. He was inclined to regard bacteria as degenerate plants. Parasites, in particular, were degenerate and he would have pounced with joy on recent phylogenetic work that has resulted in the expulsion from the protozoa of the wholly parasitic Microspora - once believed to be early branches on the tree of life but now shown to be derived from Fungi - and the entirely parasitic Myxozoa, now undoubtedly derived from Metazoa! Lankester's view was important in relation to Dobell's criticism (see Chapter 5) of the almost universal assumption that because protozoa are not divided into cells they are obviously primitive. Lankester raised the possibility that they could equally be degenerate.

The enthusiastic amateur

Largely due to the determined efforts of T.H. Huxley, professional biologists began increasing in numbers in UK universities at the tail end of the nineteenth century. While Lankester and the contributors to his Treatise were paid for their labours in the science departments of Universities, however, the Victorian amateur microscopist lived on, publishing in less citation-worthy journals than QJMS, such as the *Monthly Microscopical Journal*. No account of the development of British protozoology should omit the Rev. Dr William Henry Dallinger FRS (1839-1909) [Fig. 24], by profession a minister in the Methodist Church, but a formidable amateur microscopist who took up cudgels in the debate on spontaneous generation and was indefatigible in

[4] T.H. Huxley described in the QJMS (1868) such a creature from the ocean depths, naming it *Bathybius haeckeli* in honour of the Sage of Jena. It was later deemed to represent a colloidal precipitate of calcium chloride thrown down by the action of alcohol on seawater!

his pursuit of protozoan life cycles. In his determination to refute the evidence for *de novo* origin of life in vegetable and animal infusions presented by Henry C. Bastian's his pursuit of protozoan life cycles. In his determination to refute the evidence for *de* massive 1115 page tome *The Beginning of Life* (1872), he and his medical friend John James Drysdale (1817-1892) would spend as long as 72 hours on the trot observing flagellates to ensure that new always arose from old, often with several metamorphoses accompanying the process. With a bed suitably placed nearby they were able to change over and rest at intervals, but Dallinger unaided could peer down the microscope for nine hours, having trained his wife to spoon-feed him when he deemed it necessary.

Dallinger challenged not only H.C. Bastian and his ilk, but even the Great Sage of Jena himself! He did not like Haeckel's third Kingdom of life, the Protista, one bit, and went out of his way in one of his three day stints at the microscope to demonstrate sexual congress in the flagellate *Cercomonas,* as Haeckel viewed the protists as asexual. Dallinger was elected President of the Royal Microscopical Society and eventually Fellow of the Royal Society. He even won approbation from Darwin himself, who wrote to Dallinger: "Allow me to add that I have read all your papers.... and they seem to me to possess higher value than anything that has been published on such subjects, though I am too ignorant to have any right to express such an opinion. But I have a full right to say that they are extremely interesting".[5]

[5] See Haas, J.W. (2000) The Reverend Dr William Dallinger FRS (1839-1909). Notes & Records of the Royal Society, 54: 53-65 for a recent appraisal of Dallinger's work.

CHAPTER 4

FIRST PROFESSOR, FIRST TEXTBOOK, FIRST WOMEN

"There is a mask of theory over the whole face of nature."
William Whewell 1837

"Many men have broken their hearts for a woman, but I shall be known as the man who broke his heart for a flea!"
E.A. Minchin (in letter to E.R. Lankester as editor of QJMS)

If, at the start of the first decade of the twentieth century, protozoology in Britain was a subject moping among dilettante naturephilosophers or practised only in the outposts of empire, by the middle of the second decade it was in full flower. This transformation was in no small measure due to two scientists who raised the standards of scholarship and critical approach in both observation and experiment - E.A. Minchin and C.C. Dobell. In character they were at opposite ends of the charisma spectrum. What Minchin tried to achieve by example, Dobell sought to achieve with a caustic tongue. Minchin was the only incumbent of the only established chair in protozoology that Britain has ever had.

First Chair: Edward Minchin

The creation of the Chair of Protozoology by the University of London at the recently-founded Lister Institute of Preventive Medicine in 1905 could only reflect the perceived importance of the subject. That such perception came in the first place from the Colonial Office is not surprising. The importance of protozoa as agents of disease in the tropical countries of the British Empire was by then well-recognised as a result of the work of Manson, Ross, Bruce, and others. What was surprising was that, unlike most appointees to chairs, the new professor of Protozoology had practical experience of his subject measurable in months rather than years, and this had been acquired in the actual year of his appointment. Yet by 1912 he had written the first British comprehensive textbook on protozoa.

Edward Alfred Minchin (1866-1915) [Fig. 25] acquired his interest in natural history during his boyhood in India. After graduating in Zoology from Oxford in 1890, he spent time at the Naples marine station and learned cytological technique in the laboratories of Butschli in Heidelberg and Richard Hertwig in Munich. In 1894 he published an authorised English translation of Bütschli's *magnum opus* on *Microscopic Foams and Protoplasm*, but his principal interest was in the structure, development and spicule formation of calcareous sponges. This topic he pursued

initially as Lankester's assistant and later while holding various college fellowships at Oxford. His investigations on sponge development finally separated the sponges from coelenterates and the triploblasts. His memoir "Materials for a monograph on the Asconidae" published (naturally!) in QJMS in January 1898, was deemed the model of a carefully-written treatise with clear exposition of facts and philosopical discussion of conflicting views. It earned him the Jodrell Chair of Zoology and Comparative Anatomy at University College London, in 1899 when Lankester's successor there, F.W.R. Weldon, replaced Lankester at Oxford.

On his appointment to the Protozoology Chair, Minchin had not published a single original paper on protozoa. Clearly, his proven capacity for painstaking cytological investigation was seen as being of paramount importance for the future of protozoology. But the dramatic switch in Minchin's career had come earlier in 1905, when he was invited to join the Royal Society's Sleeping Sickness Commission in Uganda, under David Bruce. Within a year he had justified the confidence of his selectors with a paper on trypanosomes in tsetse flies. In assessing his candidacy for the Chair, however, we must not forget his earlier (1903) outstanding and massive review of the Sporozoa in Lankester's *Treatise*, now memorable for its opening confession:" A retrospect of the history of our knowledge of Sporozoa further brings into prominence the fact that, as an obscure group of no obvious practical importance, they did not for a long time appeal to the 'common sense' Englishman."

Life-cycles and their lessons for parasitologists

Minchin was thrown into trypanosome research at the deep end. When he went to Uganda he began to sort out the trypanosomes infecting the tsetse fly *Glossina palpalis* - transmitter of *Trypanosoma gambiense*. Minchin showed that flies were infected with a second trypanosome found by itself in flies from an island uninhabited by humans and lacking *T. gambiense* infection. The notoriously-critical Robert Koch (the great German father of microbiology himself!) in his dabblings with sleeping sickness had confused the two trypanosomes. Minchin's identification of possible natural hosts for the second trypanosome (hippos, crocodiles water birds) showed the keen eye of a congenital naturalist. *T. grayi* was, in fact, later shown by C.A. Hoare (Chapter 6) to be a crocodile parasite with infective metacyclic forms produced in the vector's hindgut (posterior station) unlike *T. gambiense* whose metacyclics are produced in the fly's salivary glands.

His brief spell in Uganda showed Minchin the difficulties of working out the complete life-cycles of protozoan parasites, especially in the vector, and after taking up his appointment at the Lister Institure he instituted a programme of research on a "model" trypanosome - the readily available rat parasite *Trypanosoma lewisi* in its vector, the

rat flea *Ceratophyllus fasciatus*. His choice of this system was influenced by the small size of the vector's gut (millimeters long as compared with the several centimetres of tsetse fly gut) and the fact that the Director of the Lister Institute, C.J. Martin FRS, had a programme on the transmission of plague bacillus (*Yersinia pestis*) by the rat flea. This particular trypanosome life cycle was the subject of much interest at the time. In Germany Noller and in the UK the formidable G.H.F. Nuttall (see Chapter 6) and the bright young C.M. Wenyon (see Chapter 6) were providing competition.

Minchin was a consummate histologist and cytologist. One must remember that he worked in the era of the oil lamp as a source of illumination in microscopy! In 1909 he published in QJMS a lengthy critique of the structure of *T. lewisi* in relation to microscopical technique. The influence of his translation of Bütschli's monograph was evident here. He had faith in use of wet-fixed material only and use of osmium tetroxide fixation for preservation of fine detail. He came out strongly against use of the Romanowsky techniques (Giemsa, Leishman, Wright) on dried smears to demonstrate structural details, and the subsequent near-universal faith of parasitologists in what are essentially crude diagnostic techniques, however convenient, would for him have beggared belief. Yet for much of this century whole careers in parasitology have been based on little else.

Minchin's work had other important lessons for parasitic protozoologists. In addition to the problem of sorting out mixed parasite infections, he deemed it important to be able to recognise degenerating stages of the parasite and not to construct fanciful life histories based on them. Again this lesson has not been heeded for much of this century so that even today life cycles with branches leading nowhere are described without the investigator questioning whether Natural Selection would tolerate such wanton wastage.

The final outcome of Minchin's work on *T. lewisi* was an enormous memoir (229 text pages plus 18 plates) in the QJMS with his assistant J.D. Thompson as junior author. It won universal admiration. One controversial finding was the occurrence and multiplication of intracellular trypanosomes in cells of the flea's stomach. Subsequent work has suggested that such forms were not imaginary, they do occur, but not in all infections and like the similar wandering forms of *T. brucei* in tsetse gut cells may simply have lost their way. Thanks to Minchin's exemplary cytological technique we can be assured that they were certainly not degenerating forms.

Minchin's evolutionary views

In keeping with the phylodendrographic obsession of his age, Minchin speculated

on certain aspects of protozoan evolution. His views on trypanosome phylogeny were startling at the time he proposed them, and have been viewed askance until quite recently. Unlike Leger, who in 1904 considered the ancestors of the vector-borne (digenetic) trypanosomes to be monogenetic parasites of bloodsucking insects, Minchin (1908) believed that the ancestors of trypanosomes were originally intestinal parasites of vertebrates. Initially transmitted by cysts from the gut, they later passed into the blood of vertebrates from which they were taken up by bloodsucking invertebrates and adapted themselves to life in their alimentary tracts, continuing to produce cysts which were transmitted to new vertebrate hosts by contamination. He drew on his studies on *T. grayi* of the crocodile which he believed to produce cysts in the hindgut of its tsetse fly vector. Minchin's view was by and large rejected by subsequent trypanosome evolutionists including C.A. Hoare (see Chapter 6), the doyen of 20th century trypanosome systematics, but not by F.G. Wallace the foremost 20th century student of insect trypanosomatids. In the 1990s, however, phylogenetic trees based on SSU rDNA gene sequencing indicated clearly that the genus *Trypanosoma* branched off from the trypanosomatid evolutionary tree before monogenetic genera (*Leptomonas, Crithidia, Blastocrithidia*), thus supporting Minchin's original hypothesis. By 1914, unfortunately, Minchin had been converted to the Leger camp and regrettably espoused a Haeckelian Naturephilosophy view of trypanosome evolution believing that the epimastigote phase of the trypanosome life-cycle recapitulated the development that occurred in the ancestor which was originally a parasite of the invertebrate alone.

Textbook and memorial

Minchin's scholarship, his experience in two different worlds - marine biology and parasitology, his training in cytology in Germany, and the vast number of correspondents that he had built up, made him the ideal author for the first British textbook of protozoology - *An Introduction to the Study of the Protozoa* (1912). He was an active member of several expanding learned societies, Zoological Secretary of the Linnean, and President of the Queckett Microscopical Club; he clearly liked to keep his finger on the pulse of biological research. Add to all this that his style of writing and ability to criticise with courtesy and diplomacy were much-admired, and one can see why his book was well-received. It outshone the other two protozoology textbooks of the new century - Calkins' *The Protozoa* and Doflein's *Lehrbuch der Protozoenkunde* in bringing together an enormous amount of information in a relatively concise manner and it stands as a worthy memorial to his name.

From childhood, Minchin's health was far from robust. His premonition that his heart would let him down was recorded in his letter to Lankester accompanying

submission of his *magnum opus* on the *T. lewisi* life cycle (see head of chapter) for publication. His swansong was an attempt to reconstruct the early evolution of nucleated cells and written as his presidential address to Section D (Zoology) of the British Association meeting in Manchester in 1915. Sadly, he was much too ill to deliver it, and it was presented on his behalf by his friend E. Heron-Allen (see Chapter 7). When Minchin died shortly afterwards at the early age of 49, the obituary writers could not contain their grief and I defy anyone to read Heron-Allen's account of his last days without experiencing a lump in the throat.

Muriel Robertson and the first British women protozoologists

When Minchin died in the middle of the First World War, the chair of Protozoology expired with him. No successor was ever appointed, but protozoology continued at the Lister Institute. Minchin had male assistants who made valuable contributions to the subject, notably H.M. Woodcock on sporozoans, bird trypanosomes and coprozoic flagellates. But in 1909 Minchin acquired as assistant a young woman who was to carry the torch for protozoa at the Lister Institute into the late 1950s. Her name was Muriel Robertson (1880-1970) [Fig. 26]. In time, she became a very distinguished protozoologist, one of the first women to be elected to the Royal Society (in 1947) and the first woman zoologist to be so honoured.

She was one of the first students taught by John Graham Kerr, Regius Professor of Zoology at Glasgow University from 1902 to 1936. Although very much a vertebrate man, Graham Kerr's obsession with microscopy and his love of protozoa for introducing the animal world to students, led him to encourage protozoology in his department - and to launch the careers of three remarkable women. He was a vigorous promoter of women students in a university world still not at ease with them. Before moving to Glasgow in 1902, he had taught zoology to students of Girton and Newnham colleges when his superior at Cambridge, Adam Sedgwick, refused to do so. In Glasgow he insisted on teaching women alongside men in the University instead of separately in Queen Margaret College as was the custom. While still an undergraduate, Robertson had rediscovered Cienkowski's *Pseudospora volvocis* (an enigmatic helioflagellate that Lankester put in his Class Proteomyxa) in class material of *Volvox*, and published a paper on it in QJMS. After graduating MA in 1908 she pursued research on parasites of fish in the Clyde Estuary, especially the skate trypanosome and its development in its vector, the giant leech *Pontobdella*, and later on turtle blood parasites on a visit to Ceylon. She then joined the Royal Society's Sleeping Sickness Commission in Uganda (post-Minchin) and worked out the developmental cycle of *Trypanosoma gambiense* in *Glossina palpalis,* thus making a lasting contribution to tropical medicine. Her most important observation was on the significance of pleomorphism (then called dimorphism or polymorphism) in the









Fig. 25 E.A. Minchin FRS. Fig. 26 Muriel Robertson FRS. Fig. 27 Margaret Jepps FRS. Fig. 28 Doris Mackinnon.

bloodstream stages of the sleeping sickness trypanosomes. She pointed out that the long slender dividing forms were responsible for continuing the infection in the mammalian host while the non-dividing short stumpy forms are the ones that infect the vector. Minchin, in his first paper on the trypanosome had fallen for current fallacy that the slender forms were males and the stumpy forms females and that syngamy must occur at some stage but no one knew when. The "mask of theory" - as that great philosopher of science, William Whewell (see chapter heading) would have called it - in this case was derived form the life cycle of the malaria parasites with their male and female gametocytes. Controversy dogged Robertson's interpretation for decades, until the writer (1965) demonstrated the metabolic significance of Robertson's observation. This is that the stumpy forms have embarked upon the activation of mitochondrial respiratory pathways - which are greatly augmented in the fly, whereas in the slender forms the mitochondrion is still repressed so the stumpy forms are pre-adapted to life in the vector's gut. Some workers still continued to insist that the stumpy forms are simply degenerating parasites and constitute a dead end in the cycle, however, until Michael Bosschart's careful *in vitro* culture work put an end to this heresy in 1998.

Diminutive in stature but ferocious in argument, Muriel Robertson remained a formidable figure in protozoology into her ninth decade. After being diverted into the study of anaerobic bacteria in World War I, she later worked on the effects of radiation on protozoa and on host immune responses to them. After 'late' retiral from the Lister Institute she continued research on *Trichomonas foetus* with her former student A.S. Pearse at Babraham, Cambridge, for a while. On her 80th birthday she delivered the Marjorie Stephenson Lecture to the Society for General Microbiology before finally returning to her family home in Northern Ireland where she died in 1970, aged 90. The last words I heard from her were at the Cambridge meeting of the British Society for Parasitology in 1961, where the resolution was taken to found the BSSP. Amid the din of the reception given by the University she remarked that "Hell cannot possibly have any torment to compare with the modern cocktail party."

Being a woman student in the early years of the century cannot have been easy but few women can have endured the difficulties encountered by Sister Monica Taylor, for many years head of Biology at Notre Dame College, Dowanhill, Glasgow. After a long battle with the Roman Catholic hierarchy she was allowed to attend Graham Kerr's classes as a private student but was obliged to remain separated by a curtain from other students and to register for a London University External rather than a Glasgow degree.[1] She developed large scale farming of *Amoeba proteus*, the mainstay

[1] Sister Monica's trials were not all academic. In the second world war she was arrested on suspicion of being a German parachutist disguised as a nun. When asked to prove she was a woman, she simply pointed to her feet!

of Graham Kerr's introductory practicals and isolated in culture from Loch Katrine and elsewhere this and other large chaosid amoebae for use in experimental research throughout the world, for example in the nuclear transplantation researches of J.F. Danielli (see Chapter 9). She refuted Calkins' claim for a sexual cycle in *Amoeba proteus* but her extraordinary story of spore production in this amoeba from chromatin blocks extruded by the nucleus[2] has never received a satisfactory explanation - or confirmation! Yet it found its way from QJMS into the *School Science Review* and was long regarded as Holy Writ by schoolteachers, indeed in revision courses for schoolteachers I have often been castigated for daring to cast doubt on it.

Sister Monica's interest in amoebae was shared with Dr Margaret Jepps [Fig. 27], an expert on parasitic amoebae and foraminifera and early collaborator with Clifford Dobell (Chapters 5 & 6) with whom she described a new parasite of the human colon, *Dientamoeba fragilis*. Her researches on foraminifera are discussed in Chapter 7. Invited by Graham Kerr to be lecturer on Protozoology in Glasgow, she taught there from 1923-1952. Two recipients of her lectures, future professors A.J. Haddow and W.H.R. Lumsden recorded their admiration for her teaching in a famous valentine card, [Fig. 29] decorously adorned with protozoa, and recently exhibited by the Natural History Museum. In retirement, she produced a book *The Protozoa Sarcodina*.[3]

On the other side of Scotland, a little later than Muriel Robertson, a young Aberdeen graduate, Doris Mackinnon (1883-1956) [Fig.28], started her career in protozoology. After training in R. Hertwig's laboratory in Munich and G.H.F. Nuttall's Molteno Institute in Cambridge (see Chapter 6) she became assistant to that giant among Scottish Professors of Natural History, Sir D'Arcy Wentworth Thompson. Her job was to stand at the door of his lectures and collect fees from students as they entered.[4] From research on encystation in *Actinospherium* she progressed to sorting out the innumerable flagellate parasites of insects. In 1934 she succeeded Julian Huxley (see Chapter 6) in the Chair of Zoology at King's College London, thus becoming the UK's first woman professor of Zoology. But this subject was still considered a somewhat indecent interest for a woman in some quarters and her appointment was

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[2] Shades of Richard Hertwig's dotty "chromidia" hypothesis here. See Chapter 5.

[3] Both Dr Jepps and Sister Monica (then in her nineties) plus her assistant Sister Carmela Hayes, attended the inaugural meeting of the BSSP organised by the writer at UCL in the Autumn of 1963.
Unable to climb the stairs to the tea room, Sr Monica asked my technician if there was somewhere they could rest on the ground floor until the start of the meeting. I was horrified to find that he had parked them in room full of 'free-range' chickens infected with coccidiosis! There they sat in stately dignity claiming that they were not in the least incommoded.

[4] One of her successors in this role was Katherine M.G. Adam, first secretary of the BSSP.



Fig. 29. Valentine from A.J. Haddow FRS and W.H.R. Lumsden to Margaret Jepps.

greeted by howls of protest from the Divinity Faculty who were outraged at the thought of her dissecting a male mammal in front of students. When she died in 1956, she left an unfinished textbook, *An Introduction to the Study of Protozoa*, with detailed treatment of the more important species on a 'type' basis. This was completed for publication in 1963 by her former student Julian Hawes of the University of Exeter. A gracious and charming lady, she was the embodiment of those civilised values so noticeably absent from universities today.

CHAPTER 5

A MATTER OF PRINCIPLES

"Here in these mere specks of animated jelly, which rarely measure more than one hundredth part of an inch, we find, in their simplest form, the manifold processes of the living organism."

G.N. Calkins 1902

"Protozoa are whole organisms whose structure corresponds to that of a single cell of metazoan tissue. Whether they are described as single-celled or 'non-cellular' is a matter of indifference to all except Naturephilosophers who have ensured their livelihood by inventing pseudoproblems and discussing them earnestly and at length...!"

P.B. Medawar 1984

Why study protozoa? The pragmatic answer to this question - that understanding their life-cycles is essential for control of the diseases that they cause - is fine for parasitic forms, for even the relatives of those species that are of obvious medical or veterinary importance may have much to tell us in this respect as illustrated by Ross's work on the malaria parasites of birds, but what about free-living forms? An alternative answer that embraces both free-living and parasitic forms is that because of their enormous diversity of form and function they present ideal material for the investigation of innumerable fundamental biological problems. It was this view that attracted the young Clifford Dobell (1886-1949) [Fig. 30], one of the most illustrious protozoologists that Britain has ever produced and undoubtedly among the most arrogant, critical and caustic of scientists of all time in his dealings with others. He objected in particular to the view - prevalent, indeed virtually universal, at the time that protista (protozoa and protophyta) were "elementary, unicellular, primitive lower organisms displaying life at its simplest." His contempt for this view came to a head in his 1911 paper in the *Archiv für Protistenkunde* entitled 'The Principles of Protistology.' His blunt Introduction declared "The present paper is largely analytic and destructive, but it is so of necessity, for it is useless to build on a rotten foundation." He was all of 24 years old when he penned these words.

Education of a protozoologist

Dobell decided on graduation in the Natural Sciences Tripos from Cambridge University in 1906 to abandon his plans for a career in medicine and devote himself to protozoology instead. He had been heavily influenced in this decision by his tutor, Adam Sedgwick, Reader in Morphology. Sedgwick had undergone a similar

conversion from medicine to comparative embryology and was in the process of building up one of the finest schools of Zoology in the world, with emphasis on his own speciality, though protozoology was also a subject that he wished to encourage. When in 1907 Sedgwick at long last inherited the Chair of Zoology in Cambridge he was prevailed upon to abandon it and in 1909 take up T.H. Huxley's Chair of Zoology at Imperial College, London. He, in turn, persuaded Dobell to join his department as lecturer in Protistology and Cytology in 1910.

Dobell's education in protozoology had been catholic to say the least. As an undergraduate he had been taught by J.J. Lister (of Foraminifera fame, see chapter 7) and G.H.F. Nuttall (immunologist, bacteriologist and parasitologist, see Chapter 6). As a novice graduate he was put to work with W.S. Perrin - a Von Prowazek-trained protozoologist, then a demonstrator in Zoology (but later to abscond into medicine and achieve fame as a surgeon). The two of them thought nothing of working 16-17 hours a day and seven days a week, so enthralled were they by their subject. At the end of 1907, Dobell went to the University of Munich to study at the feet of Richard Hertwig. Germany was then the Mecca to which all biologists made pilgrimages. Though his relations with Hertwig and his colleague F. Doflein (author with Reichenow of the biggest ever textbook of protozoology!) were good, he was "utterly repelled by the speculative views and slapdash methods" of the majority of protozoologists he met. These were the pupils of Fritz Schaudinn, who though recently dead seemed even more of an icon than when living. Dobell was so unsympathetic to their prevalent uncritical attitude that he was very unhappy during his six-months stay, and his experiences there at an impressionable age (22!) influenced his feelings to the entire country for the rest of his life. German culture remained totally antipathetic to him.

Later travels took him to the Stazione Zoologica at Naples where he collected most of the material for his famous and gigantic paper on the life cycle and cytology of the coccidian *Aggregata eberthi* (Dobell, 1925) and to Ceylon where he spent several months as guest of A. Willey FRS, Director of the Colombo Museum, working on various parasitic protozoa. Before moving to Imperial College and delivering his lambast ("The Principles") to protistologists everywhere, he had published on flagellates, amoebae, coccidians and ciliates, as well as bacteria which he seems to have counted as protists. His productivity was prodigious.

"The cell theory must be abolished"

The cardinal points that Dobell made in his "Principles" paper were these. First, the Cell Theory and the Theory of Evolution have led biologists to the view that protists are unicellular organisms, i.e. homologous with a single cell of a metazoan o

a metaphyte, and this view is erroneous. If we define Metazoa and Metaphyta as organisms possessing a cellular structure, we should define the Protista as organisms possessing a non-cellular structure. Second, protists are complete organisms and the view that tends to homologise a clone of protists formed by division between one sexual event and the next with a multicellular organism derived from a fertilised egg is "absolutely erroneous." Third, the protists are not properly called "simple, lower or primitive." These terms have arisen through misconceptions generated by the Cell Theory and the Theory of Organic Evolution. Finally, since protists constitute a group of living beings organised quite differently from all others, an analysis of their vital phenomena will afford us a large mass of knowledge for comparison with that derived from multicellular animals and plants upon the vital phenomena of which almost all biological generalisations are based.

It is in many ways amusing to read Dobell's intemperate language today, even to laugh out loud at some of his statements (e.g. "the Cell Theory is a myth;" "the cell theory must be abolished"), but, as Corliss (1999)[1] has pointed out recently in annotating excerpts from Dobell's "insightful classic paper," some of Dobell's thought-provoking statements and admonitions are worthy of sober reconsideration, even today.

"Some people prefer the hypothesis - others, among them myself, the facts" said Dobell in perhaps the most telling statement in the entire essay. Dobell was very much a facts man! Look at the quotation from Dobell, chosen by his former collaborator, Margaret Jepps, to introduce her book *The Protozoa Sarcodina*: "What our science really needs most at present is more Protozoa study... we want more facts". The idea that Science advances through the testing of imaginative hypotheses was not for him.[2] In support of his proposal that Protista should be defined as non-cellular organisms, Dobell barks "This is no cell theory: it is a statement of fact, and therefore greatly to be preferred to any theory."

The decision as to whether protists/protozoa are non-cellular or single cells depends upon how the decider views the cell. If it is as an administrative subdivision of an organism then they are non-cellular; if it is as a tectonic unit then they are unicellular. Dobell was well aware of these distinctions but used the difference of opinion to damn the Cell Theory. In doing so he was, in fact, only parrotting his mentor, Adam Sedgwick, who ranted volubly against it, his distrust of it being based upon his finding that the embryo of *Peripatus* is one big syncytium.

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[1] See *Protist* 150 : 85-98, 1999)

[2] Poor man! Did he never experience the excitement of having an irresistible hypothesis thrust into his head and then the rapture of finding that it stood up to attempts to disprove it?

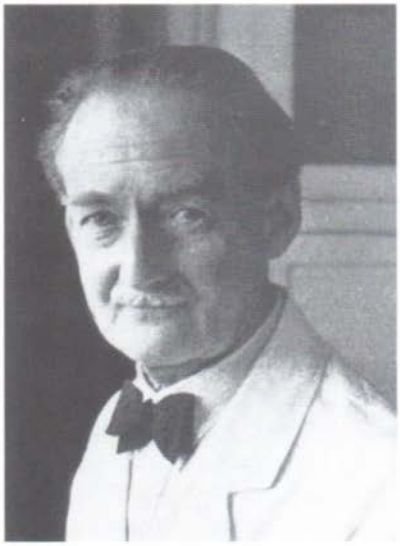


Fig. 30 Clifford Dobell.

Dobell had some good points, but his barbed arrows were misdirected. Far from being a myth, the cell theory is arguably the most important tectonic generalisation in the whole of biology: recall the vitriolic arguments between Golgi and Ramon-Y-Cahal on the structure of the nervous system at the end of the nineteenth century. That this generalisation does not apply to protists is true. But apart from the question of how we define the Protista little turns on the decision as to whether protists are unicellular or acellular. Note the view of Sir Peter Medawar at the head of this chapter.

"As far as the concept 'individual' can be analysed - and I believe that it is at present unanalysable - it is clear that a protist is no more homologous with one cell of a metazoan than it is homologous with one organ (e.g. the brain or liver) of the latter". In this statement, and unfortunately elsewhere in his essay, Dobell confuses homology with analogy. In terms of structure, the protist and the metazoan cell *are* homologous: both are eukaryotic cells, i.e. they have nuclei and organelles. The important distinction between eukaryote and prokaryote cell did not emerge, however, until much later when the American microbiologist Roger Stanier refined and popularised the proposals of the great French protozoologist Edouard Chatton. And, let's face it, the individuality problem is all about analogy and not homology!

The Individuality Problem

It is easy to dismiss the challenge of defining the individual as yet another pseudoproblem invented by Naturephilosophers to give biology an air of profundity, but unlike the protist cellularity problem, important questions do turn on it, particularly in relation to the operation of Natural Selection and to incompatibility in cooperation between cells and organisms. Dobell's discussion of the individuality problem, however, is more focussed than his discussion of protist cellularity.

What inspired his wrath here was Calkins' statement that not the single cell of a protozoon but the entire succession of cells that may be formed from the period of one conjugation to that of the next should be compared with the individual metazoan organism. In support of his view Calkins mentioned Maupas' finding that the clone, like the individual metazoan, goes through periods of immaturity, maturity and senility. Calkins's view was not original, for such eminent authorities as Bütschli and Weismann had previously come to the same conclusion. Dobell commented: "It is to me almost incredible that such a view as this should have found wide acceptance." He pointed out that Calkins' hypothetical aggregate of protist cells would eventually enter conjugation and whoever heard of a metazoan which was composed of nothing but gametes?

Dobell does not mention it and his quote from Calkins does not mention it, but we are clearly talking about ciliates here, and ciliates, like animals, segregate their germ plasm. In ciliates the germ plasm resides in a special diploid nucleus, the micronucleus, whereas in animals (Metazoa) the germ plasm is set aside in special germ cells. The vegetative (transcriptive) functions of the ciliate are undertaken by the polygenomic macronucleus which is derived along with a new micronucleus *de novo* during sexual processes (conjugation, autogamy) from the zygote nucleus. Haploid gamete nuclei, derived from meiosis of the micronucleus, fuse in syngamy to give rise to the zygote nucleus.

If our definition of individuality is possession of a distinctive genome then Calkins has made a plausible analogy and Dobell is wrong. The genetic constitution (micronuclear genome) of members of a ciliate clone derived from an ex-conjugant should be the same, just as the genetic constitution of the cells that constitute the body of a metazoan should be the same as they are formed by binary fission involving mitosis. If on the other hand we define individuality on the basis of separateness and functional integration (i.e. bodies) then clearly each member of the clone is an individual and Dobell's criticism is valid.

We now know that there are flaws in both these arguments. Calkins' analogy assumes

that all members of a clone are genetically identical, but whereas the micronucleus divides mitotically, the macronucleus divides "amitotically" with uneven distribution of chromosomes or of "free-floating genes" derived from them in differentiation of the macronucleus. Ageing of the ciliate clone cited by Calkins to boost his analogy with development of the individual metazoan, is now believed to be a consequence of and therefore not comparable to ageing in metazoans. And the flaw in Dobell's argument macronuclear aneuploidy resulting from such uneven partitioning of macronuclear geneslies in the recent realisation that the members of a clone are not so independent of one another as he imagined. There is accumulating evidence that members of a ciliate clone - indeed possibly all members of a unicellular (or acellular) species - are in constant communication with one another, that their growth is boosted as a result, and that deprived of such communication they may die. They thus resemble multicellular organisms which in the absence of similar stimulation undergo programmed cell death.[3]

In recent years the problem of individuality has perhaps been most discussed in relation to the unit on which Natural Selection acts in evolution.[4] Darwin believed that Natural Selection acted on bodies, that it was individual organisms that struggled for reproductive success. He was particularly vexed by the social insects where the entire colony appeared to serve as the unit of selection. In recent years the theory of inclusive fitness and kin selection has explained away Darwin's difficulties in this respect [5] and it has become obvious that selection may operate at several levels from gene to population. Strangely enough, although Dobell specifically cited heredity, variation and sex as fundamental biological phenomena, our understanding of which would be considerably improved by an input from work on protists, he remained strangely silent on the subject of Natural Selection, in his "Principles" essay, and elsewhere. Perhaps, along with several outstanding geneticists (William Bateson in the UK, in particular) of his time, he would have none of it!

Not simple, lower *or* primitive!

The most valuable part of Dobell's essay was his appraisal of the widely held view that organic evolution goes from simple to complex and that the distribution of forms in time should be applied to the forms distributed at the present moment in space. "Why should it always be taken for granted" he said, "that by evolution is

[3] See Christensen, ST et al. Signalling in unicellular eukaryotes. *International Review o Cytology* 177: 181-253.

[4] See Gould, S J. (1990) *The Individual in Darwin's World*, Edinburgh University Press.

[5] For a discussion of similar problems relating to protozoa see chapter 9.

meant an upward progress from protozoa to man? This is only one hypothesis of organic evolution. That evolution of some sort has taken place in living beings I regard as certain. But that evolution of the Haeckelian amoeba-to-man type has not occurred I regard as equally certain. We can certainly believe in evolution without believing in this dogma."

When, in this essay, Dobell refers scathingly to the "theory of organic evolution", he is in fact deriding the romantic recapitulation theory, or Biogenetic Law, of Haeckel. In particular he disapproves of Haeckel's speculative phylogenetic trees (e.g. that in Haeckel, 1874) in which the primaeval organisms are a mixture of extant protozoa (amoebae, infusoria) and hypothetical organisms reconstructed from the developmental stages of extant multicellular animals.[6] Dobell's view that extant protozoa are themselves the result of a long period of evolution and must not be regarded as ancestors frozen in time is echoed resoundingly by present-day phylogeneticists and by cladists in particular. The widely-held belief that evolution equates with upward progress has been repeatedly criticised by Gould in his essays and at length by the biological philosopher Michael Ruse (1996) in his book *Monad to Man: the Concept of Progress in Evolutionary Biology*.[7] As mentioned previously, molecular phylogenetic studies suggest that two large groups of erstwhile "simple" organisms - the Microspora and the Myxospora - appear to have their next of kin among morphologically more complex forms (fungi and metazoa respectively) and should be excluded from the Protozoa.

Haeckel's biogenetic law took a long time to die. It infected comparative anatomy and hence zoology for several decades into the twentieth century and use of the terms simple, lower and primitive survives to this day in defining the protozoa as can be seen by glancing at any student textbook that deigns to mention them.

So, Dobell's sonorous trumpet blast against German Naturephilosophy did not have the impact that he clearly hoped it would have. Without doubt one reason for this was Dobell's failure to come up with suggested alternative adjectives for defining the Protista. He was right - his *Principles* essay was destructive and it would have had greater impact if he had found something constructive to say as well. But we

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[6] Haeckel's infuriating self-assurance can be gauged from his assertion that "An irrefutable proof that such single celled primaeval animals really existed as the direct ancestors of man is furnished according to the fundamental law of biogeny by the fact that the human egg is nothing more than a simple cell."

[7] Protozoologists will be disappointed to find that monads are not really mentioned and do not appear in the index!

have to admire his courage.[8]

Dobell's critical approach to what the study of protozoa is all about had its most lasting effect in his major contribution to protozoology - the sorting out of the numerous amoebae that inhabit the human alimentary tract. His sterling performance in this area will be discussed later. His talent for weighing evidence was indisputable. I would love to hear a debate between Dobell and the exponents of the "higher dismissiveness"[9] now infecting the philosophy of science. They deny that truth exists and maintain that there are no such things as facts. I can imagine his wrath.

[8] Dobell's other critical reviews were just as trenchant. His critique *Chromidia and the binuclearity hypothesis* (*Arch. Protistenk.*, 1909, 53:279-326) was a bold demolition of his former mentor R. Hertwig's view that protozoa could expel nuclear DNA into the cytoplasm as "chromidia"; his "*A commentary on the genetics of the ciliated protozoa*" (J Genetics 1914, 6: 131-190) makes equally interesting reading.

[9] See Haack, S (1998) Manifesto of a passionate moderate. Chicago University Press.

CHAPTER 6

SOME LEADING RESEARCH INSTITUTIONS AND THEIR LEADING LIGHTS

"It seems too improbable, and so contrary to all past experience that flagellated organisms should occur in the blood."

Sir William Osler British Medical Journal 1887

"Never refuse to see what you do not want to see, or what might go against your own cherished hypothesis, or against the views of authorities. These are just the clues to follow up, as is also, and emphatically so, the thing you have never seen or heard before."

Sir Patrick Manson

The First World War of 1914-1918 cut short the careers of many young men - some of them protozoologists. One such was Geoffrey Smith, Fellow of New College Oxford and tutor of the young Julian Huxley, grandson of T.H. Huxley and one of the best-known biologists of the 20th century. Encouraged by F.W.R. Weldon to take up biometrical studies on heliozoans, Smith inspired an interest in protozoa in his protégé whose first published paper was on an unusual gregarine of crustaceans.[1] Later Huxley dabbled in foraminiferan life-cycles at the Naples station before turning to broader issues - ecology, the Evolutionary Synthesis, The New Systematics (see Chapter 12) and eventually the Directorship of UNESCO. Smith fell in the Battle of the Somme (1916); Huxley succeeded him in his college fellowship in 1919.[2] But for some protozoologists the Great War provided a unique opportunity to advance their subject - and promote their careers, especially those in the newly emerging research institutes catering for the subject.

The National Institute for Medical Research

In 1919 Clifford Dobell resigned his lectureship at Imperial College to accept the

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[1] *Ganymedes anaspidis* - named after the beautiful youth in Greek mythology carried off by Zeus to become cup-bearer of the gods. In syzygy one gamont has a posterior cup into which the head of the other fits!

[2] One of Huxley's tutees was A.C. Hardy, the eminent marine biologist and future Linacre Professor of Zoology at Oxford - another protozoologist manque! Huxley suggested to Hardy that he should follow up his highly successful New Naturalist volumes on *The Open Sea* with one entitled *Ponds, Puddles and Protozoa*. Hardy got no further than the first chapter and a series of rather indifferent water colours of protozoans, however, as the book was displaced by his increasing preoccupation with spiritual matters.

newly-created post of protistologist to the Medical Research Committee (later the Medical Research Council or MRC) at the new National Institute for Medical Research (NIMR). By 1913 he had realised that he did not fit into academic life. "I was not cut out for a professor," he said, " I am not serious enough on some subjects and far too serious about others." During the First World War he had been released from the College and seconded to the Wellcome Bureau of Scientific Reseach (see below) by the War Office to investigate amoebic dysentery and intestinal protozoa among troops. Although by 1914 the causative agent of amoebic dysentery was known, largely as a result of the human infection experiments of the American investigator E.L. Walker in the Phillipines, this knowledge was not general and few of those called upon to investigate the disease during early hostilities were able to recognise or differentiate protozoan parasites in the human host. By the end of the War, Dobell had become one of the world's foremost authorities on these organisms and had been elected FRS (1918) at the age of 32.

Dobell spent 30 years at the NIMR in Hampstead. Initially, he was allowed a great deal of freedom in his research. He praised the MRC's enlightened policy in allowing him to complete 16 years cytological research on the esoteric coccidian *Aggregata eberthi* which has a two-host life-cycle in crabs and cuttlefish: it enabled him to demonstrate that in the Sporozoa proper (Apicomplexa nowadays) meiosis is zygotic and apart from the zygote all other stages in the life cycle are haploid. He was also able to make a number of contributions to the history of protozoology including his masterpiece *Antony van Leeuwenhoek and his little Animals* (1932). His main work, however, was the elucidation of the life cycles of the intestinal amoebae of humans and macaque monkeys - the pathogenic *Entamoeba histolytica* and the non-pathogenic *Entamoba coli, Endolimax nana, Dientamoeba fragilis* (discovered by him and Margaret Jepps and now recognised as an aberrant trichomonad) and *Iodamoeba butschlii* (though this last he never published). The vast knowledge and experience he gained during the war was encapsulate in his monograph *The Amoebae living in Man* (1919) [Fig. 31]and later the *Intestinal Protozoa living in Man* (1921 with F.W. O'Connor). The discovery by Boeck and Drbohlav in 1925 of the first reliable method for cultivation of the intestinal protozoa gave great impetus to his life-cycle work and with Patrick Laidlaw and Ann Bishop (see below) he set out to improve on them. Over 15 years he published his meticulous series of papers entitled *The Intestinal Protozoa of Monkeys and Man* in the journal *Parasitology* founded by G.F.H. Nuttall of the Molteno Institute (see below). These papers represented an extraordinary body of knowledge ("facts" as Dobell undoubtedly thought of them) of permanent value to biology and medicine in the precise detail of observation and experiment. Only the relationship between pathogenic and non-pathogenic *Entamoeba histolytica* eluded him and that particular problem had to await the precise tools of molecular phylogeny at the end of the century to be resolved.

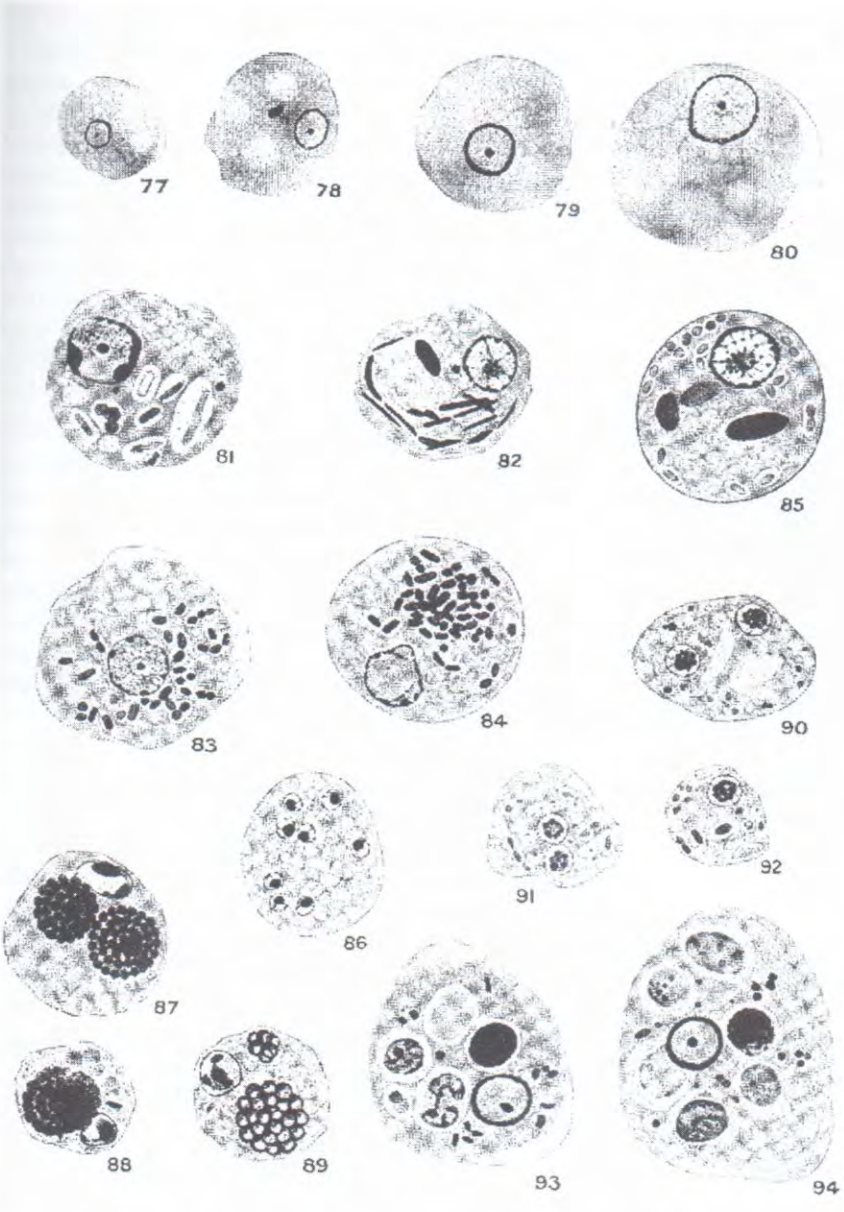


Fig. 31 One of Dobell's paintings of *Entamoeba* from "The Amoeba Living in Man."

Dobell died suddenly, before his much-dreaded retirement age, and on the eve of the equally dreaded move of the NIMR from Hampstead to Mill Hill. After the move protozoological work was contained in the Division of Chemotherapy which eventually changed its name to Parasitology in 1965. Much of the emphasis was on drug action and treatment of parasitic infections under Frank Hawking who moved there from the Liverpool School (see below) though basic biological work has become increasingly to the fore on biochemistry of trypanosomes by J.D. Fulton and James Williamson, antigenic variation in malaria parasites by Neil Brown (see Chapter 10), and, more recently, molecular biology of malaria parasites by Tony Holder and Iain Wilson.

The Wellcome Bureau of Scientific Research

Sir Henry Wellcome was one of those inspired millionaires who, in his own words, "chose to spend his wealth in supporting research as another man might choose to spend his on a racing stable." In 1913 he founded the Wellcome Bureau of Scientific Research, London, which was to be devoted to research on problems related to tropical medicine - including all branches of parasitology. Although its funds were derived from the commercial activities of Burroughs Wellcome and Co., the Bureau was otherwise independent and had a separate administration. Research work was not subordinated to trading interests: scientific staff were free to follow their own lines of investigation. This extraordinary liberty gave British Protozoology two of its most outstanding stars – C.M. Wenyon FRS and C.A. Hoare FRS.

Charles Morley Wenyon (1878-1948) [Fig. 32], a one-time zoology student of Minchin (in his pre-protozoa days) at UCL had gone on to qualify in medicine in 1904. After a few months as a general practitioner he decided on a career in protozoology and successsfully applied for the headship of the newly-created protozoology department at the London School of Tropical Medicine, then situated at the Royal Albert Dock. Its founder, Sir Patrick Manson, had singled out Wenyon as one of his lieutenants and ensured that he gained experience both in continental laboratories (Felix Mesnil at the Pasteur Institute, Richard Hertwig in Munich) and in field work in tropical countries. The latter he acquired during a year spent travelling in a floating laboratory on the Upper Nile in Sudan, where he made observations on blood parasites and trypanosomatids in biting flies. After a spell back in London working on intestinal flagellates (he described *Chilomastix mesnili* as a human parasite), he undertook a detailed study of the leishmaniases: he demonstated that there was no difference between the Indian and Mediterranean types of kala azar (*Leishmania donovani*) and whereas he did not succeed in confirming the suspected transmission of oriental sore (*L. tropica*) by sandflies (he used himself as test animal!) he accumulated a

scholarly body of knowledge on the leishmanias, much of it published in his Kala Azar Bulletin (1911-1912).

In 1914 he resigned from the London School to take up the position of Director of Research in the Tropics at the newly-created Wellcome Bureau of Scientific Research. Shortly after his appontment, however, the First World War broke out and the Wellcome Bureau was placed at the disposal of the War Office. Wenyon joined "Balfour's Travelling Circus" (the Director of the Wellcome Bureau, Andrew Balfour, acted as leader) visiting Egypt, India and Mesopotamia advising on tropical diseases. During this period, Wenyon made some of his most important contributions to our knowledge of human intestinal protozoa, especially amoebae in relation to the amoebic dysentery problem in troops. With F.W. O'Connor, he showed that cysts of *Entamoeba histolytica* in stools do not justify a diagnosis of amoebic dysentery and postulated the existence of pathogenic and non-pathogenic races of the parasite - what Peter Sargeaunt and Graham Clarke at the LSHTM were later to recognise as different species, *E. dispar* (non-pathogenic) and *E. histolytica* (pathogenic). Wenyon also described other non-pathogenic species that might confuse diagnosis - *E. hartmanni* (differing in the size of its cysts form *E. histolytica*) and *Endolimax nana* with a completely different nucleus. He also demonstrated that cysts of *E. histolytica* can pass through the housefly gut with impunity, supporting his view that fly dissemination of amoebic dysentery is plausible. Together with his studies on coccidians (*Isospora belli*) and flagellates (especially *Retortamonas intestinalis*, *Enteromonas hominis*, in addition to *Chilomastix mesnili*), Wenyon made a lasting contribution to the differential diagnosis of human intestinal infections.

The rest of Wenyon's war service was devoted to advising on malaria control centred on Macedonia. He carried out important investigations on epidemiology, transmission, prophylaxis and treatment of the disease including experimental studies on the effect of low temperature on development of *Plasmodium vivax* in its vector. Development of oocysts in the hibernating mosquitoes was arrested during the cold season and was resumed when the temperature rose again giving rise to spring outbreaks of benign tertian malaria.

His uniquely-varied experience with so many different parasitic protozoa and his numerous excursions into the biology of coprozoic free-living forms, made Wenyon the ideal author for a comprehensive textbook on protozoology and, on his return to the Wellcome Bureau after the war, he set about writing one. In 1924 he succeeded Balfour as Director in Chief of the Bureau, but managed to finish his monumental two volume treatise *Protozoology: a manual for medical men, veterinarians and zoologists*. Profusely illustrated with many coloured plates, Dobell dubbed it the book that "no working protozoologist can afford to do without." He was right. It is







Fig. 32 C.M. Wenyon FRS. Fig. 33 C.A. Hoare FRS. Fig. 34 L.G. Goodwin FRS.

formidable and irreplaceable! There is nothing like it in English or in any othe language. For any parasitic protozoologist working in the tropics it is still a goldmine Wenyon's original scientific research may be regarded as useful rather than spectacularly revolutionary but for anyone who works with parasitic protozoa from the wild (as opposed to handed-on lab cultures and cryostabilates) Dobell's prophecy that "no future worker will be able to conduct his researches without frequent reference to these two volumes" still rings true.

As he made clear in his preface, Wenyon was a sincere advocate of protozoology as a discipline in itself: he did not approve of students of parasitic protozoa ignoring free-living forms and vice-versa. He was regarded as the supreme authority on the subject in Britain during his lifetime. When H.E. Shortt and P.C.C. Garnham discovered the exoerythrocytic stage of primate malaria (see below) they sought Wenyon's blessing before announcing it to the world.

Cecil Arthur Hoare (1892-1984) [Fig. 33] was Wenyon's only real pupil. On Clifford Dobell's recommendation, he was appointed protozoologist to the Wellcome Bureau in 1923 when Wenyon moved on to be Director in Chief. Hoare had arrived in England from revolution-torn Russia in 1920. Though his father was British, his mother was Russian and he was brought up by her in her native land. He had left his post as an assistant lecturer in the Military Medical Academy of Petrograd (St Petersburg), with good references (though officially classified as a deserter from the Soviet Army!) and on the strength of these Dobell gave him temporary accommodation at the National Institute for Medical Research in Hampstead. On his retirement from the Bureau in 1957 Hoare had served as Head of the Protozoology

Department for 34 years.

Although Hoare's London DSc was awarded for work on free-living ciliates and he wrote many papers on amoebae and coccidia, as well as publishing his *Handbook of Medical Protozoology* for students, he is universally associated with trypanosomes, their life cycles, nomenclature and evolution especially. He preferred problems relating to the complete natural history of a species. He first investigated the life cycle of *Trypanosoma melophagium* of British sheep (of which 80% were then naturally infected and demonstrated transmission by the sheep ked. In 1927 he was seconded to Uganda where he worked out the complete life cycle of *Trypanosoma grayi* in crocodile and tsetse and demonstrated contaminative transmission of the reptile by hindgut metacyclics, not by cysts as Minchin had supposed. He was the first to elucidate the important role of the peritrophic membrane barrier in development of sleeping sickness trypanosomes in the tsetse fly.

Much of Hoare's research, however, was London-based and a great deal of it devoted to biometrical work validating or refuting the different species named earlier by Bruce and his collaborators, e.g. the independent status of *T. uniforme* from *T. vivax*, the widespread disribution of *T. simiae*, causative agent of porcine trypanosomiasis. He devoted many years, on and off, to *T. evansi*, the causative agent of 'surra' in horses and camels, building up a case that it had arisen by transport of tsetse-transmitted *T. brucei* across the Sahara in camel trains, transmission being maintained outside the tsetse belt in Southern Asia and South America by horse flies (tabanids) transferring the parasite mechanically on their proboscises rather than allowing it to undergo cyclical development in fly gut and salivary glands as did its *T. brucei* ancestor. Recent molecular work by Wendy Gibson in Bristol and others has born out this story.

That research on trypanosomes was able to flourish so successfully in the UK from the 1960s onwards is in very large measure due to Hoare's authoritative systematic approach to these protozoa. He introduced several major innovations. With F.G. Wallace (of Minneapolis, the foremost authority on insect trypanosomatids this century), Hoare made radical changes in terminology of trypanosomatid life-cycle stages, replacing the old genus-based names e.g. leptomonad, leishmanial herpetomonad, crithidial, trypanosomal.... with names reflecting the position of the flagellar origin - promastigote, amastigote, opisthomastigote, epimastigote and trypomastigote respectively. This terminology has been crucial to all subsequent discussion of life-cycles and phylogeny. Within the mammalian trypanosomes, Hoare recognised subgenera based on life-cycle differences e.g. s.g. *Trypanozoon* for the former '*Trypanosoma brucei* group'. Below the species level he introduced the

deme concept of flowering plant taxonomists to distinguish populations which differ from others of the same species or subspecies in a specified property, e.g. serodeme for a population characterised by a particular antigen repertoire, nosodeme for a population defined by the type of disease (e.g. acute/chronic) that it caused and so on.

In 1972, when he had passed his 80th birthday, he published a comprehensive monograph, *The Trypanosomes of Mammals: a Zoological Monograph*, putting his life's work into context. A strong believer in what he called "the didactic approach" he spoke with such authority that one's natural reaction was to believe every word he said.

The Wellcome Bureau later became the Wellcome Laboratories of Tropical Medicine and in 1966 moved from its Euston Road site to Beckenham in Kent. Among those of its members who contributed to it excellence in protozoological studies may be mentioned Ralph Neal whose studies on *Entamoeba muris* of laboratory rodents and that "parasite of the municipal digestive tract" - *Entamoeba moshkovskii* (it is free living in sewage!) greatly added to our knowledge of the genus, and Len Goodwin FRS [Fig. 34] distinguished for his work on pathological mechanisms in trypanosomiasis and chemotherapy of trypanosomiasis and malaria.

The Molteno Institute, Cambridge

When Frederick Quick, a prosperous coffee merchant, died in 1902, he left the bulk of his estate to Cambridge University for the promotion of " study and research in the sciences of vegetable and animal biology." He designated three non-scientific friends as Trustees to negotiate with the University over the best way of utilising the money, and three major fields in the biological sciences were identified: biochemistry, genetics and parasitology - especially protozoology. The Trustees favoured establishing a single prestigious chair and despite the University's preference for the first two subjects (Gowland Hopkins and William Bateson would have been strong contenders for the chair) they favoured the third! After extensive negotiations the University in 1906 made an appointment: the most significant stipulation was that the new professor "should devote himself to the study of protozoa - especially such as cause disease."

George F.H. Nuttall (1862-1937) [Fig. 35] who was appointed first Quick Professor of Biology in the University was more than just a protozoologist. American born, of a British father, he had a University of California M.D. (1984) and an enviable education in science in biological and medical research laboratories in Europe and the USA over the next 15 years. He developed a broad interest in parasitology and

the role of arthropods as vectors in the spread of infectious disease; his research extended into serology and animal relationships as assessed by precipitin reactions. Like Minchin, however, he had a dearth of publications in what one might call protozoology at the time of his appointment (the distribution of anopheline mosquitos in relation to the prevalence of malaria in earlier times hardly qualifies, does it?). After attaining the Quick Chair, however, he settled on piroplasmosis of cattle, sheep, horses and, especially, dogs, and its transmission by ticks, as his major area of research. His discovery that Trypan blue (shades of Paul Ehrlich!) provided a valuable treatment for *Babesia* infections was of great practical significance to farmers throughout the world. It was this development that persuaded Mr & Mrs Percy Molteno, whose family had extensive farming interests in South Africa to take an interest in Nuttall's research and eventually to respond generously to his appeal for a new institute. Opening of the new building on the Downing Street site by a former Governor General of South Africa took place with great ceremony on 29 November, 1921. It was unfortunate that Nuttall himself could not attend on account of a haemorrhage from a duodenal ulcer.

In 1920, at Nuttall's suggestion, the remit of his chair was changed to "the study of Parasitology" and the new building was named The Molteno Institute for Parasitological Research. Even this title does not encompass the interdisciplinary research that went on in it until its incorporation into the Department of Pathology in 1987 as the Molteno Laboratory. [3] David Keilin, who succeeded Nuttall as Director and in the Quick Chair, 1931-1952, continued the founder's interest in arthropods, especially parasitic Diptera, but is best known for his discovery of cytochromes and the respiratory chain. In the latter vein, he sparked off research by protozoologists - notably John F Ryley, whose early work on respiration of *Tetrahymena* led him on to make distinguished contributions to our understanding of the metabolism of trypanosomes (including cytochrome synthesis in *T. brucei*), malaria parasites and coccidians at ICI Ltd.

When Parr Tate took over as Director of the Molteno (1952-66), the Quick Chair became dissociated from the Institute and, sadly, from protozoology. Tate had come initially as Nuttall's Ph.D. student, and spent the rest of his working life there. He continued the dipteran interest but a childhood interest in canary breeding led him to use *Plasmodium relictum* (the malaria parasite employed by Ross in his transmission studies) of canaries in testing antimalarial drugs developed in the 1920s

[3] For a more detailed account of the history of this remarkable Institute which played host to the virologists Kenneth Smith and Roy Markham and the biochemists/molecular biologists Max Perutz, John Kendrew, Thaddeus Mann and E C Slater, among others see R.A. Klein (ed) *The Biochemist* for Feb/March and April/May, 1992.

by the Medical Research Council. His most significant protozoological discovery, with Colonel S.P. James, was the exoerythrocytic cycle of development of avian malaria parasites in endothelial cells of brain capillaries.[4]

Ann Bishop (1899-1990) [Fig. 36] who took over the malaria chemotherapy work from Tate when he transferred to a University lectureship, became one of the UK's most distinguished protozoologists (FRS 1959). Her interest in protozoa started with an undergraduate project on the ciliate *Spirostomum* supervised by Prof S.J. Hickson at Manchester University and continued in Cambridge Zoology Department (where women were relegated to sitting on the first aid box during tea time gatherings). Later she moved to the National Institute for Medical Research as assistant to Clifford Dobell (Chapters 5 & 6) for three years. Here she learned the rudiments of chemotherapy by testing the amoebicidal effects of emetine. She returned to Cambridge and came to the Molteno Institute on a Beit Memorial Fellowship in 1929. Here she pioneered work on the cultivation of a wide range of intestinal protozoa (entamoebae, trichomonads, diplomonads, retortamonads) of various animals. She discovered and cultivated a free-living trichomonad (*Pseudotrichomonas keilini*) and with HP Baynon cultivated a related flagellate, *Histomonas meleagridis*, cause of the disease blackhead in turkeys and a notorious threat to American Thanksgiving Day dinners. But her most extensive work was conducted on acquired drug resistance in malaria, especially to the widely used prophylactic drug paludrine, using *Plasmodium gallinaceum* (the malaria parasite of the jungle fowl) transmitted by *Aedes aegypti* as her experimental system. She demonstrated that resistance could develop quite quickly and survived mosquito transmission. Much of this work was carried out with Elspeth McConnachie and it paved the way for later genetic studies on resistance (see Chapter 10).

On the retiral of Parr Tate in 1966, the Molteno became home to the MRC's Biochemical Parasitology Unit directed by Bruce Newton and in it some extremely distinguished work on trypanosome biochemistry was conducted, especially on the molecular basis of antigenic variation (see Chapter 10).

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[4] My colleague D.W.T. Crompton tells the amazing story of Tate cycling in from Grantchester to the Molteno in the middle of the night to retrieve an infected chicken carcass from the dustbin after realising suddenly that the elusive e-e stages must be in the brain. These were in fact secondary exoerythrocytic forms, the preerythrocytic generation that precedes them was discovered later by H.E. Shortt in India. The presence of this second generation in avian *Plasmodium* spp. provided false clues to the pattern of exoerythrocytic development in mammalian malaria parasites.

The Liverpool School of Tropical Medicine

Ronald Ross, when he left the Indian Medical Service in February 1899, became thefirst member of staff at the recently-opened Liverpool School of Tropical Medicine. Founded by Sir Alfred Lewis Jones,[5] the School organised several important expeditions between 1899 and 1914 that greatly advanced the epidemiology, aetiology and transmission of key tropical diseases. The first of these was led by Ross to Sierra Leone in the summer of 1899 and its main interest was malaria control.

Several fundamental discoveries about parasitic protozoa emerged from these expeditions. First of these was the discovery of *Trypanosoma brucei gambiense* as the cause of sleeping sickness in West Africa by Dutton and Todd (1902). Later came the differentiation of West and East African sleeping sickness trypanosomes by J.W.W. Stephens FRS [Fig.37] and H.B. Fantham (1910) and their naming of the latter *Trypanosoma rhodesiense* (now *T. brucei rhodesiense*). The zoonotic nature of the East African disease was recognised by Stephens, Kinghorn and Warrington Yorke (1912). Stephens also described the fourth human malaria parasite, *Plasmodium ovale* (1922).

After World War 1, Warrington Yorke (1883-1943) [Fig. 38] developed a team to work on chemotherapy of malaria, trypanosomiasis and leishmania: this included J.D. Fulton, E.M. Lourie, A.R.D. Adams and F. Hawking and they developed suramin (1921), pentamidine (1939), antimonials (1939) and antimalarials. With ICI, the School was the first to publish research on the activity of the popular antimalarial prophylactic drug proguanil (paludrine) (1945) and to demonstrate the development of drug resistance to it in the field. Wallace Peters, who occupied the Chair of Parasitology at the School before moving to the Chair of Medical Protozoology at the LSHTM in 1979, wrote a massive monograph *Chemotherapy and Drug Resistance in Malaria* (Academic Press, London, 1970) and pioneered the study of chloroquine resistance using rodent malaria test systems in the 1960s.

The London School of Hygiene and Tropical Medicine

It greatly disturbed Sir Patrick Manson that although 20% of the graduates from British medical schools went on to practise in the tropics, their was no specialist course in tropical medicine to prepare them for their new career. In 1897 he starteddiscussions with the Secretary of the Seaman's Hospital at the Royal Albert

[5] For a detailed account of the history of the School and its work see: Power, H.J. (1999) *Tropical Medicine in the Twentieth Century: a history of the Liverpool School of Tropical Medicine* 1898-1990. Kegan Paul International, London.

Dock about the possibility of instituting a School of Tropical Medicine there, and through to Endsleigh Gardens in Bloomsbury and after Manson's death in 1922 was amalgamated with the School of Hygiene to become the London School of Hygiene and Tropical Medicine (LSHTM) at its present site in Keppel Street [Fig 44]. C.M. Wenyon was one of those who replied to the original advertisement in *The Times* inviting applications for posts in the new School as recounted above. The School quickly became a premier research institution in parasitology, including protozoology.

Wenyon's successor as Director of the Department of Protozoology and later as Professor of Medical Protozoology was John Gordon Thompson, perhaps best known for his textbook *Protozoology: a Manual for Medical Men* (1929) co-authored with his assistant Andrew Robertson. Published only three years after Wenyon's *magnum opus* (and by the same publishers - Balliere, Tindall & Cox), it is only a pale shadow of the latter work (perhaps because unlike Wenyon it did not also cater for veterinarians and zoologists!), but it contains more details on pathology and on culturing parasitic protozoa (Thompson's main interest). Thomson and Robertson are most remembered for their puncturing of the ego of Clifford Dobell by their demonstration that two species of coccidian, *Eimeria oxyspora* and *E. wenyoni* described by him as human parasites are nothing of the kind. Parasitologists have a habit of naming coccidia on characters of the oocyst and Dobell named these two from oocysts he found in large numbers in human faeces. Thomson and Robertson showed that they are identical with *E. sardinae* and *E. clupearum* of Thelohan. Both are found in abundance in the soft roes of sardines and herrings respectively and are found only in the stools of people who have feasted on these fishes.

In protozoology, the LSHTM will always be associated with the names of H.E. Shortt (1887-1987) [Fig. 39] and P.C.C. Garnham (1901-1994) [Figs. 40, 44, 45] and their work on the exoerythrocytic (E-E) cycle of the malaria parasites. As a Colonel in the Indian Medical Service, Hugh Shortt had made a lasting contribution to tropical medicine by conclusively demonstrating using human volunteers, that *Leishmania donovani* was transmitted by sandflies (*Phlebotomus argentipes*). Although sandfly transmission of leishmanias had been long suspected (see Wenyon above), experimental transmission had proved impossible until the discovery by Shortt and colleagues (1942) that the female sandfly had to be maintained on fruit juices between blood meals. While in India, however, Shortt had developed an interest in malaria parasites of lizards and birds, and ensconced in the Chair of Medical Protozoology at the LSHTM in 1945, his interest turned to the missing stage in the development of the malaria parasite in the human host.

Basttista Grassi, Ronald Ross's great adversary, in claiming the honour for demonstrating the development of human malaria parasites in the vector, had



Fig. 35 G.H.F. Nuttall FRS. Fig. 36 Ann Bishop FRS. Fig. 37 J.W.W. Stephens FRS. Fig. 38 Warrington Yorke FRS. Fig. 39 Col. H.E. Shortt FRS. Fig. 40 P.C.C. Garnham FRS. Fig. 41 R.S. Bray. Fig. 42 J.R. Baker. Fig. 43 R. Killick Kendrick.



Fig. 44 The London School of Hygiene and Tropical Medicine

suspected at the turn of the century that *Plasmodium* spp underwent a period of development before they invaded the red cell and began their cycle of development there. However, the description in 1903 by the all-influential Fritz Schaudinn of the direct entry of sporozoites into erythrocytes convinced protozoologists that parasite growth and reproduction was confined to the red cell. Not until differences were noted in the effectiveness of quinine in preventing blood-induced as opposed to sporozoite-induced infections was Schaudinn's observation questioned by Colonel S.P. James in 1931. He proposed that an intermediate phase occurred between sporozoite and erythrocytic stage and went on with Parr Tate (see Molteno Institute, above) to demonstrate the existence of an exoerythrocytic stage in bird malaria.

In 1947, Cyril Garnham, working as a medical officer in Kenya found the exoerythrocytic stage of *Hepatocystis kochi*, then believed to be a *Plasmodium* species, in the liver of infected monkeys. He maintained that *H. kochi* was probably the first parasitic protozoan to be seen by man, though it would not have been recognised as such, the observation having been made in prehistoric times in Africa. The developmental (E-E) stages of the parasite are glistening macroscopic cysts, easily visible on the surface of the liver, and these could scarcely fail to have been detected by African hunters who killed monkeys for food! Shortly after this discovery, Garnham moved to the LSHTM and joined Shortt in a search for the E-E stage of *Plasmodium cynomolgi* (often used as an experimental model for *P. vivax* of humans) in Rhesus monkeys. After feeding 500 infected mosquitos on a single monkey, they eventually were able to demonstrate the E-E forms in liver parenchymal cells. In a later experiment involving infection of a human volunteer with *Plasmodium vivax* via 2000 *Anopheles*, Shortt and Garnham demonstrated the E-E stages in sections of a

liver biopsy. They also managed to find a volunteer to endure a similar experiment with the much more dangerous *P. falciparum* and win the struggle with beaurocracy to actually perform it. When Garnham succeeded Shortt as Head of the Departmentof Parasitology at the LSHTM in 1952, the exoerythrocytic stages of the other two human malarias (*P. ovale, P. malariae*) were still unknown. Garnham tracked down a priest who had returned from Liberia with a *P. ovale* infection and the infection – R.S. Bray, F.I. Awad , R Lainson and J Williamson - were infected for the same purpose and fortunately Williamson developed a gametocytaemia sufficient to infect 77% of 900 mosquitoes. Garnham's chief technician, Willliam Cooper was then infected from almost 1000 bites and 9d after the first 10g of his liver was removed by laparotomy. On his recovery from the operation, Cooper prepared sections of his own liver in which were found two E-E schizonts per gram of tissue. Cooper also illustrated the resulting paper with beautiful water colour illustrations. The E-E stages of *P. malariae* (which will infect apes as well as man) were obtained later by infecting a splenectomised chimpanzee with mosquitoes flown from Romania after feeding on a patient there.

The significance of the relapse infections in malaria was thought to be made plain by the discovery of the E-E stage. If the parasite goes on multiplying in liver cells, re-infecting them and ticking over at a low rate, it could emerge into the bloodstream months or years later. *Plasmodium falciparum*, which does not exhibit late relapses, does not have a persistent E-E stage, dying out in the liver once the red cells have become infected. The question of whether it is possible for re-infection of liver cells to occur was later examined in an exhaustive co-operative study, initiated by Garnham between British and American scientists with a surprising conclusion. Relapses of tertian parasites *P. vivax* and *P. ovale* are due to a dormant hypnozoite stage embarked upon when some sporozoites enter the liver. The hypnozoites become active and start a new bloodstream infection months or years later. Sadly, though he lived to complete his century, Shortt never accepted the hypnozoite story and insisted that the original interpretation was correct.

We shall return to Garnham's pioneering work on electron microscopy of malaria parasites later (Chapter 11). Following his retiral from the Chair of Medical Protozoology at the LSHTM in 1968, he moved to Imperial College Field Station at Silwood Park and continued to work on malaria parasites there.

Garnham had several disciples at the LSHTM who became eminent protozoan parasitologists: R.S. (Bill) Bray [Figs. 41, 44] (malaria, especially E-E stages, *P. malariae* in particular). Ralph Lainson FRS [Fig. 44] and Jeffrey Shaw (ecology of New World leishmanias), John Baker [Figs. 42, 44] (trypanosomes, especially of birds and bats) and Robert Killick-Kendrick [Figs. 43, 44] (*Leishmania* in sandflies),



Fig.45 Left to right; Bill Bray, Cyril Garnham, John Baker, Ralph Lainson and Bob Killi
Kendrick.

to mention but a few. It is easy to see why Garnham inspired so much devotion and admiration in all that he met. His combination of profound scholarship, cultivated tastes (especially in music), gentility and dry humour - mixed with ruthless determination[6] - made him an absolutely delightful companion for the evening or long plane journey to distant places. He was the obvious choice for first President of the BSSP and Presidency of the International Congress on Protozoology in London in 1965, Garnham's magnificent monograph, *Malaria Parasites and other Haemosporidia*, published in 1966, was, with C.A. Hoare's *The Trypanosomes of Mammals* published in 1972, the climax of an extended period of parasitology based on the Romanowsky smear or its modification for tissue parasites, the Giemsa-collophonium technique. Their colour illustrations showing protozoa stained in the colours of the Union Jack are in the Wenyon tradition and somehow peculiarly British!

[6] I witnessed this particular aspect of Garnham's character when he, I and a WHO representative arrived late for the flight from Rio de Janiero to London at the close of the Carlos Chagas Centenary celebrations in 1979. There was only one check-in desk and the queue for it snaked right around the airport. Garnham put on his panama hat and said "Follow me." We did, as he confidenly strode to the head of the queue and dropped his ticket in front of the surprised check-in girl. The WHO man said to her "He is a very important man you know - and we are with him." She checked us in without a murmur from either her or the queue.

CHAPTER 7

CHALK AND THE INTELLIGENT FORAMINIFERAN

"And of all the unicellular organisms, the Foraminifera appear to me to lend themselves most readily to biological investigation. The relatively gigantic proportions of their protoplasmic bodies, the readiness with which they may be collected, and the ease with which they can be kept alive, watched and bred in captivity, all combine to single out the group for the earnest attention of the biologist."

E. Heron-Allen 1915

"We have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast."

D'Arcy Wentworth: Thompson Growth and Form 1942 Edn

It is rumoured that only one Fellow of the Royal Society has ever ridden a horse in the Grand National steeplechase. Certainly, only one FRS has ever been a circus rider, author of books on violins, asparagus breeding, palmistry, Buddhism, barnacles and archaeology - and gained distinction for his research on foraminifera ("forams" for short). This was Edward Heron-Allen (1861-1943) [Fig. 46] - undoubtedly one of the most colourful characters in protozoology, British or otherwise, over the last century or any other for that matter. What is perhaps most amazing is that, in what had by then become an age of professional scientists, Heron-Allen was an amateur.

The attraction of Foraminifera for Heron-Allen is obvious from the quotation above. They are mainly marine protozoa, most being bottom-living deep-water forms, but some are planktonic, for example the common ooze-forming species of the genus *Globigerina*. They are amoeboid with reticular pseudopodia and live in shells that vary greatly in shape; the shells are usually composed of calcium carbonate, more rarely constructed by cementing together sand grains or other particles. As the foram grows it enlarges its shell by adding new chambers, one by one, each larger than its predecessor. Heron-Allen went to great pains to show that, though saddled with the unicellular condition, their behaviour was inexplicably sophisticated.

Foram shells have been preserved in sedimentary rocks from the Cambrian onwards and indeed are a major constituent of chalk and limestone rocks. These protozoa are of great importance as stratigraphic markers of past climates and environments, as well as being indicators for certain important deposits, such as natural gas and petroleum. The 40,000 or so fossil species outnumber living ones ten to one. Because of their importance geologically, living foraminifera have been studied largely by

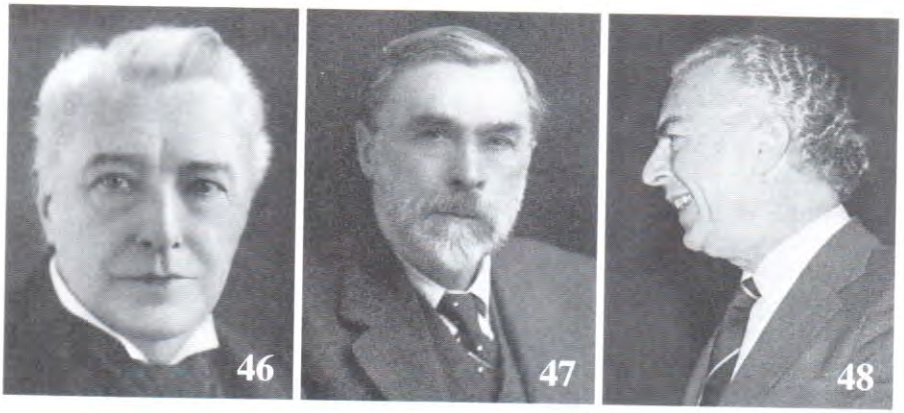


Fig. 46 E. Heron-Allen FRS. Fig. 47 J.J. Lister FRS. Fig. 48 R.H. Hedley.

geologists. One of the criticisms levelled against Darwin's theory of evolution was that many simple organisms had remained unchanged over long periods of geological time. The foraminifera were often cited as organisms that had not evolved!

The above-mentioned criticism of Darwinian theory was the result of a fundamental misunderstanding of the nature of natural selection, which, *pace* Haeckel and his followers, does not have to work in some direction or other. Forams have remained unicellular since their first appearance, but they have evolved. Thus early foram shells were of organic material or cemented sand grains: in the Silurian biomineralised microgranular ($CaCO_3$) shells appeared, and chambered shells in the Devonian. Porcelain-like (magnesium calcite) shells appeared in the Carboniferous and a massive extinction of forams occurred at the end of the Permian. Some survived into the Mesozoic era, however, with planktonic forms appearing in the Jurassic and flowering in the Cretaceous before the catastrophe that wiped out the dinosaurs also eliminated planktonic and shallow water forms. Again survivors continued into the Tertiary, when *Globigerina* appeared and the spectacularly large *Nummulites* evolved in shallow, well-illuminated waters. Shells of the latter form the pyramids and sphinx of Egypt. In the nineteenth century, British students of foraminifera contributed much to this story, especially W.B. Carpenter (author of a Ray Society Monograph [1862] on Foraminifera) and H.B. Brady (the cataloguer of the immense collection of forams retrieved by the Challenger Expedition). In more recent times, the substantial publications of John W. Murray of Southampton University on the ecology and distribution of benthic and pelagic foraminifera (e.g. in Lee & Anderson 1991) have added greatly to British contributions on this group. This chapter emphasises the work of two outstanding British students of the foraminifera, E. Heron-Allen and J.J. Lister whose researches are of more general protozoological interest.



Fig. 49 *Technitella thomsoni* (Heron-Allen).

The effect of a piece of chalk

After leaving Harrow School in 1879 Heron-Allen became articled to Allen & Son, Solicitors, Soho and was admitted Solicitor of the Supreme Court in 1884. But from then until 1889 he led a bohemian life first as Special Commissioner for Music section of the Colonial Exhibition in Italy, then in the USA lecturing on spiritualism, writing novels and short stories and earning his daily bread in various employments - including circus riding. After returning to the family firm of solicitors, he became interested in palaeontology and archaeology - and foraminifera. The gift of a piece of chalk rock containing their shells by his schoolmaster is said to have been the original stimulus for this last consuming interest.

By 1891 forams had become his principal relaxation from the law along with music and literature.[1] Heron-Allen was one of those people who have to share their every interest with the public through publication. His first paper on forams was published in 1894. In 1911 at the age of 50 he retired from the law in order to devote more time to them. He became President of the Royal Microscopical Society - whose council benefited greatly from his legal expertise, business ability and relentless energy during the First World War - and President of the Zoology Section of the British Association. In 1919 he was elected to the Royal Society.

In 1925 he handed over his collection of 90,000 slides of forams and his library of 720 volumes relating to these protozoa to the Natural History Museum, London and served as Honorary curator of Foraminifera there until his death in 1943. His collection added to the 612 slides from the Challenger expedition identified by Henry Bowman Brady and deposited in 1884, and the 2,265 slides of the William Kitchen Parker Collection purchased in 1894.

Intelligence, purpose and the dawn of art

Highly significant in Heron-Allen's career as a student of the foraminifera was the moving of his home in 1907 to Selsey Bill, on the south coast of England where he could study both extant forams from the sea and fossils in the local limestone. He had been attracted to living forams for the reasons cited in the quotation at the head of this chapter and because "nothing is easier than to maintain in healthy and

[1] In 1882 he became part time apprentice to a violin maker and made two violins played upon to great acclaim by Joachim, Sarasate and other leading violinists. He compiled and published an enormous bibliography of the violin (1890-94), was joint editor of the Violin Times, and continued publishing *opuscula* on the instrument up to 1941. He translated literary works from the Persian (including the Ruba'iat of Omar Khayyam). He certainly took his hobbies seriously!

prosperous condition, a series of small observation tanks in the heart of great inland cities." He went on to say that, "the living foraminifera have one supremely valuable quality - that they do not suffer from occasional, unavoidable neglect." A home in Selsey placed him nearer to his collection sites.

In making gatherings of the littoral and shallow water forams of Selsey Bill, Heron-Allen and his collaborator, Arthur Earland, found arenaceous forms that assemble a shell from grains of sand instead of secreting a calcareous covering. Among these they noticed individuals that appear to select and incorporate relatively large fragments of coloured gems and other minerals such as garnet, topaz and magnetite. The specific gravity of these fragments was much higher than that of normal quartz grains, basically used in construction, so the gem fragments were not found in the same layers of sediment as the quartz; they sink below it. The pair found it difficult to know what biological significance to ascribe to this "apparently ornamental use of grains of building material". "I have been constrained to disclaim the attribution of any aesthetic sense to these organisms" wrote Heron-Allen in his 1915 address to the Royal Microscopical Society, but J Arthur Thompson, Regius Professor of Natural History at Aberdeen University, had no such qualms. Writing in *The New Statesman* (Oct 23, 1915) about Heron-Allen's findings he enthused: "When we remember that this is no matter of organic crystallisation (*sic*) but the result of placing extraneous materials in a definite and singularly effective arrangement, we feel that we are approaching the Dawn of Art".[2]

Although he gave public lectures with such titles as "On beauty, design and purpose in the Foraminifera," and despite his lack of formal background in science, Heron-Allen was careful to point out that he disliked anthropomorphic interpretations of the behaviour of unicellular organisms and regretted the inability of objective scientific language to describe what he was witnessing. His reticence contrasts strongly with the current profligate usage of metaphors from the battlefield and the stock exchange in ethology and ecology and rightly dubbed by J S Kennedy (1992) "*The New Anthropomorphism*".

Selecting grains and sticking them together

Two aspects of arenaceous foram architecture fascinated Heron-Allen. First, the exclusive selection of certain materials and second, the manner in which they are used. His favourite example of selection was the exclusive collection of perforated echinoderm plates by *Technitella thompsoni* from sediments in which these plates

[2] My wife, impressed by the incorporation of magnetite in particular by these unicellular architects, has suggested that the Dawn of Feng-Shui is a more appropriate interpretation!

formed an infinitesimal fraction of the total bulk [Fig. 49]. Agglutinating forams commonly select on the basis of particle size alone regardless of composition, others practise mineralogical selectivity as noted. Selection on the basis of size is characteristic of thecamoebae, testate amoebae and tintinnid ciliates in constructing their shells, but the mechanism that permits selectivity is still unknown. In caddis fly larvae, polychaetes and other tube-constructing invertebrates modified appendages and various mechanosensory organs effect selection but of course forams lack such fancy structures.

After the death of Heron-Allen, the protozoan collections at the Natural History Museum fell into neglect until Ronald Hedley [Fig. 48] was appointed as head of the protozoa section (1955-1971) to study the biology and shell structure of recent forams (see Chapter 11). He proposed that the enormous variation in agglutinated tests - which range from pliable fragile structures to rigid, sturdy forms - was related to the extent of biomineralisation in the form of bound iron or calcium salts in the acid mucopolysaccharide cement, though some tests contain collagen-like material. Bowser and his colleagues in the USA have demonstrated the presence of ligament-like cables of bioadhesive connecting sand grains but we are no nearer understanding how the foram transports particles to their final position in the test, nor how it manages to enlarge its shell to accommodate its growth. For over a century micopalaeontologists have examined the test structure of agglutinating forams with respect to texture, composition and cementing material or bioadhesives but the manner of their construction remains a mystery.

J.J. Lister and foram life-cycles

The section on Foraminifera in Lankester's *Treatise on Zoology* (1903) was one of the few written by an acknowledged expert in the field, Joseph Jackson Lister (1857-1927) [Fig. 47], who incorporated many of his own original findings into the work. The Lister family had many claims to scientific distinction. J.J.'s grandfather, also Joseph Jackson (1786-1869), was a Quaker wine merchant and a founder of the Royal Microscopical Society: his contribution to protozoology was indirect - he solved the problem posed by spherical aberration by designing an optical system using achromatic pairs of lenses. One of his (J.J Lister Sr's) sons was Lord Joseph Lister FRS (1827-1912), the eminent surgeon and pioneer of antisepsis and asepsis; as President of the Royal Society at the turn of the century he took a great interest in Ross's work on malaria and devoted his 1900 Presidential address to the subject.[3]

[3] Lord Lister happened to be present at the meeting of Section D (Zoology) of the British Association Meeting in Toronto at which the young W.G. MacCallum read his paper on sexual fusion in *Haemoproteus* - and accorded the speaker a vote of thanks!

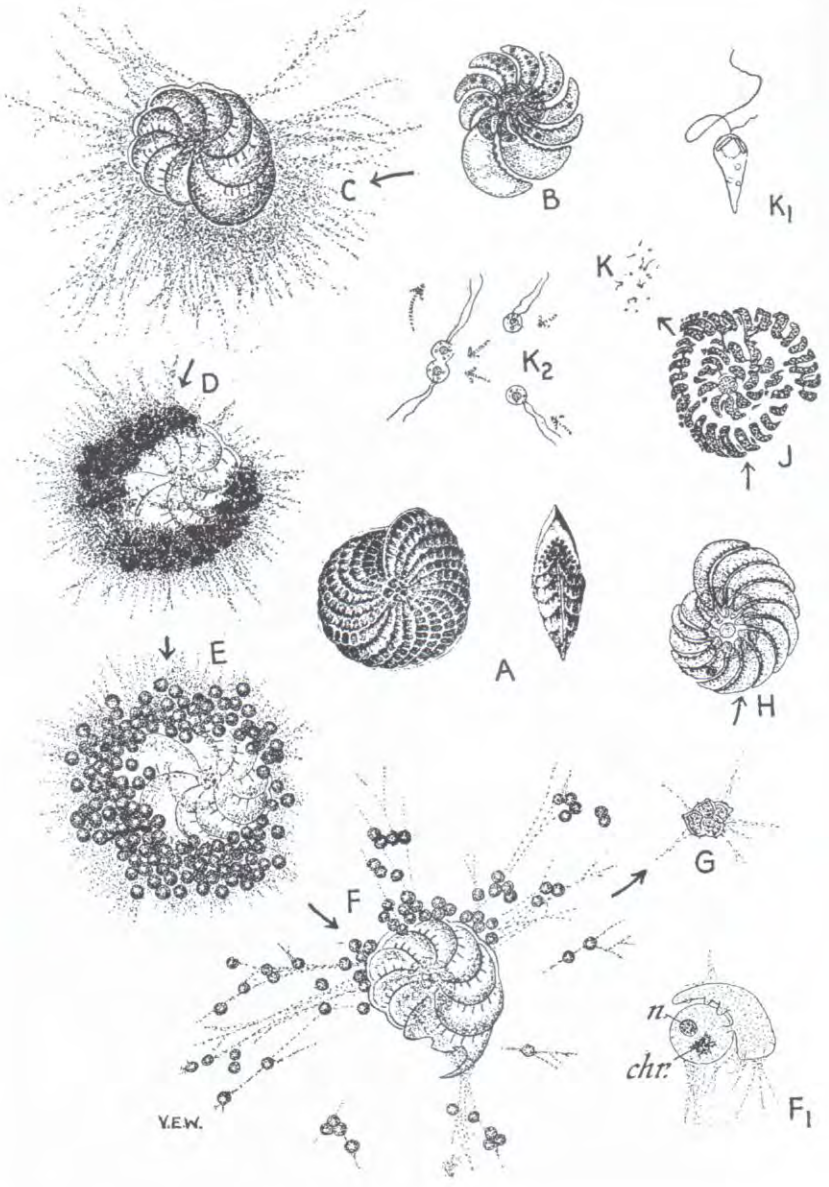


Fig. 50 *Elphidium crispum* (Jepps, 1956).

Lord Lister's brother and father of J.J. Lister Jr was Arthur Lister, another amateur microscopist but also FRS and an acknowledged authority on Mycetozoa. JJ Lister Jr graduated in Natural Sciences at Cambridge and then in Medicine at UCL, but his health being poor his distinguished medical uncle advised him to take long cruises to restore it and not to practise medicine.[4] He acquired an interest in forams on these cruises and returned to Cambridge as a lecturer in Zoology.

J.J. Lister's major contribution to protozoology concerned the life-cycle of foraminiferans, especially the large (1-2mm!) nummulitid *Elphidium crispum* (or *Polystomella crispa* as Lister, Jepps and most Brits preferred to call it rather than employ Cushman's name!) which up to 1950 abounded in one or two collecting grounds near Plymouth. The classic foram life cycle of zoology textbooks, in which there is alternation between a haploid uninucleate gamont generation and a diploid multinucleate agamont generation and in which free swimming (flagellated) gametes are produced by the gamont and undergo syngamy in the open sea to give zygotes that develop into agamonts - is based largely on Lister's careful observations on *E. crispum* (summarised by him in his 1903 *Treatise* contribution) augmented by those of Margaret Jepps (1942) [Fig. 50]. In *E. crispum*, the uninucleate gamont is termed megalospheric because the first chamber of its spiral multichambered shell is large compared with that of the agamont shell, which is described microspheric. The multinucleate microspheric agamont reproduces by "schizogony" in early spring a few weeks after the spring burst in productivity of its diatom food. The elucidation of the life cycle involved setting up laboratory cultures of limited lifespan, and providing diatoms as food. Healthy individuals add a new chamber to their shell every second day. Both Lister and Jepps found that they had to guard continuously against the production of abnormal individuals in such cultures, and criticised Schaudinn, who in 1903 had published his own highly inaccurate version of the *Elphidium* life cycle, for failing to do this. In cold British waters, Jepps estimated that the complete life cycle consisting of one microspheric and one megalospheric phase lasts about two years. On learning this, one can see why - despite Heron-Allen's praise for their capacity to withstand neglect - the living foraminifera have attracted relatively few protozoologists, at the same time being inordinately impressed by the patience and perseverance of the few who have been drawn to them.

[4] The only use he seems to have made of his medical qualification was in the manufacture of artificial limbs for servicemen amputees in World War 1.

CHAPTER 8

ECOLOGY: BACTERIA GOOD, PROTOZOA BAD - OR VICE-VERSA

The earliest studies on protozoan ecology were stimulated by agricultural considerations. Although at the beginning of the 20th century the occurrence of protozoa in soils had been known since the work of Ehrenberg early in the previous century, serious interest in them only really began with the publication in 1909 of work on the effects of partial sterilisation on soil by Sir John Russell FRS (1862-1965) and H.B. Hutchinson of the Rothamsted Experimental Station, Harpenden. They discovered that plant productivity increased after "sterilising" soil samples at 95°C instead of 120°C - the temperature conventionally used for sterilisation. They interpreted this improvement in plant yields as the consequence of removal of some unfavourable biological factor, in short - Protozoa. They suggested that protozoa play a negative part in soil fertility by devouring the bacteria that promote it, in Orwellian language - bacteria good, protozoa bad! Until then protozoa had been regarded as inactive components of the soil microfauna, permanently dozing in their cysts.

Tom Goodey and the dozing protozoa

Russell's first move in following up his ideas was to recruit a young graduate from Birmingham University, Tom Goodey (1885-19530 [Fig. 52]. Highly recommended by F.W. Gamble, the Professor of Zoology there, Goodey moved to Rothamsted in 1910 on a Royal Society Studentship (£150 a year!). Russell's culture technique had mainly isolated the ciliate *Colpoda cucullulus* from soil, and on the assumption that this was the chief protozoan there, Goodey was set the problem of seeing whether it was active or only encysted. By looking at ciliates that emerged from soil immediately after wetting it, he found that in contrast to those taken from the soil surface, which contained abundant ingested bacteria, those taken from below the surface contained none. He concluded (1911) from this observation that cysts were washed down from above by rainfall and that in the soil itself *C. cucullulus* was normally inactive and encysted. His results led him to doubt whether any soil protozoa functioned as grazers of bacterial populations. When his work was published it was so convincing that most biologists were satisfied that the predator theory was finished, but Gamble realising that Goodey had been able to study only the soil ciliates suggested that there was still the possibility that amoebae may be active in the soil. Unfortunately Goodey did not have the opportunity to pursue this idea as his studentship had run out. He returned to Birmingham in 1913 to a post in Gamble's lab where he worked on the characterisation of amoeboid organisms in the soil, and showed that cysts of amoebae and flagellates could retain their viability in stored soil over long periods



Fig. 51 Sir John Russell FRS. Fig. 52 Tom Goodey FRS. Fig. 53 Harold Sandon.

of time. He was sidetracked, however, into looking at an amoeba in the human mouth, *Entamoeba gingivalis*. The recent work on the pathogenicity of *E. histolytica* (see Chapter 6) had raised the possibility that *E. gingivalis* was a cause of gum disease. Goodey and A.W. Wellings concluded that it did more good than harm as a scavenger of bacteria in the mouth. This entry into parasitic protozoology enabled Goodey to spend the First World War as protozoologist to the Southern General Hospital in Birmingham making routine examinations for *Entamoeba* and other intestinal protozoa. After the war in 1920, the staff of the Rothamsted Experimental Station expanded and Goodey returned to Harpenden where he spent the rest of his life. He eventually deserted soil protozoa for soil and plant nematodes on which he wrote an authoritative monograph.

During the first spell in Harpenden, Goodey had studied voice production in London and continued his training back in Birmingham. He became a highly acclaimed tenor soloist during the war and remained in demand as such through much of his life. In the Heron-Allen tradition of versatile protozoologists, he is the only person in this book who had an operatic role written for him (the part of Angus in *Forever Young* - the successor to Rutland Boughton's popular opera, *The Immortal Hour*). Supposedly, it was the embarrassment to his colleagues of his musical broadcasting career alongside his laboratory one that caused him to adopt the stage name "Roger Clayson."

Soil Microbiology at Rothamsted

Despite the cold water poured on Russell's hypothesis by Goodey's work, attempts

to test it continued at Rothamsted. In 1914 C.H. Martin and K.R. Lewin[1] extracted active feeding forms from the soil and study of their relations with bacteria began in earnest. Ward Cutler, Harold Sandon and Lettuce Crump,[2] attempted to demonstrate the relationship between protozoa and bacteria in soil, and between protozoan activity and soil temperature or moisture. Although they found an inverse relationship between numbers of soil bacteria cultured on a nutrient agar and numbers of active amoebae in 86% of their daily observations, they did not find significant correlation between these fluctuations and environmental conditions in the soil.[3] The situation was clearly more complex than envisaged by Russell and Hutchinson.

Cutler and colleagues were handicapped by the computational facilities available to them at the time, and realising that further statistical analysis might prove rewarding, they included all their daily counts for one year in an appendix to their paper. A recent re-analysis of their data relating to common soil flagellates of the genus *Cercomonas* and soil bacteria using more appropriate modern statistical methods, by John Darbyshire and colleagues[4] at the Macaulay Institute of Soil Research in Aberdeen has revealed population oscillations similar to those detected by Gause in his, later (1934), classic experiments on predator-prey relations between *Paramecium aurelia* and *Schizosaccharomyces pombe*.

The substantial work of the Rothamsted Station on soil protozoa up to the mid 1920s was summarised by Harold Sandon [Fig. 53] in his monograph *The Composition and Distribution of the Protozoan Fauna of the Soil* (Oliver & Boyd, Edinburgh 1927). Based on an examination of soils from all over the world, Sandon was able to survey the influences affecting the numbers and distribution of species of protozoa in the soil and the composition of the soil protozoan community insofar as the limited systematics of the Protozoa allowed at the time. Although in his Introduction Sandon expressed disappointment that 17 years of study post-Russell had yielded little really-convincing information, he surmised that the failure had been due in part to an oversimplification of the problem by the assumption that they can all be considered together as leading very similar lives, or that at the most they need only be divided into ciliates, amoebae and flagellates. We now know that some protozoa - including *Colpoda* - can actually stimulate the growth of protozoa in soil

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[1] Martin C.H. & Lewin K.R. (1914) Some notes on soil protozoa. *Phil. Trans. Roy. Soc. London* Series B 205, 77-94.

[2] One wonders whether she ever thought of adopting a stage name.....!

[3] Cutler D.W., Crump L. & Sandon H. (1922) A quantitative examination of the bacterial and protozoan population of the soil, with an account of the protozoan fauna. *Phil. Trans. Roy. Soc. London* Series B 211, 317-350.

[4] Darbyshire J.F., Zwart K.B. & Elston D.A. (1993) Growth and nitrogenous excretion of common soil flagellate, *Cercomonas* sp. *Soil Biology & Biochemistry* 25, 1583-1589.

Sandon's more detailed conclusions, were, however, very helpful. These were: that not even barren soils lack protozoa; that although some 250 species of protozoa have been recorded from soils, many occasional species are not true soil forms, many occur in other habitats, but the true soil forms constitute a fairly well-defined community; that the soil protozoa are world-wide in their distribution, the same species occurring in arctic, temperate and tropical soils; that some species are capable of living under anaerobic or semi-anaerobic conditions; that maximum numbers are generally detected at a depth of 10-12 cms and very few species are found in the sub-soil; that the testate amoebae are generally more numerous on acid peaty soils where bacterial development is poor and scarce or absent in neutral or alkaline soils; that for flagellates, ciliates and naked amoebae the food supply in the form of bacteria appears to be the most important factor affecting the number of species and the highest numbers are found in arable and garden soils. Apart from the species numbers quoted, few would quarrel with these conclusions today. There are considerable practical difficulties in studying protozoan distribution in soil and in assessing their significance there, but they now have a recognised role as secondary decomposers in nutrient recycling in soil. In 1994 John Darbyshire [Fig. 54] edited a useful monograph on *Soil Protozoa* (CAB International) which contains chapters by himself, B.S. Griffiths (Scottish Crop Research Institute, Invergowrie), and A.J. Cowling (IFE) and an international group of experts on these problems.

Sandon followed up his unique monograph with a less well-known one on *The Food of Protozoa*[5]- a valuable catalogue of feeding habits, which was an important contribution to protozoan ecology very much in its embryonic stage. By this time (1932) Sandon had left the UK for a career in the African universities.

Protozoan communities

British ecological studies on protozoa were few and far between until after the Second World War (1939-45). One of the most notable, that of Laurence Picken of Cambridge in 1937, was the first holistic study of protozoan communities in freshwater, and looked at the effect of sewage pollution on changes in substratum provision for the protozoan community.[6] Picken, another in the Heron-Allen mould, did systematic work on the bicoecid flagellates and wrote a thoughtful book on cell organisation[7] just before the dawn of the cell biological renaissance after which he transferred from

[5] The Egyptian University, Cairo. Misr-Sokkar Press, 1932.

[6] Picken, L.E.R. (1937) The structure of some protozoan communities. *Journal of Ecology* 25: 368-384.

[7] Picken, L.E.R. (1960) The organisation of cells and other organisms. Cambridge University Press.

zoology to oriental music in Cambridge, in which at the age of 91 he is still going strong.

The need for systematic work

The need for more precise identification of protozoa if studies on ecological relationships were to get anywhere, was evident in Sandon's monograph, in Picken's work and other pre-World War 2 ecological studies such as the first study in Britain of the role of Protozoa in marine benthos food chains by Mare (1942)[8]. One group causing particular difficulty in soil microbial ecology was the limax amoebae - small naked amoebae with a single pseudopod and vesicular nucleus. The testate amoebae, readily differentiated on the form of the shell, had been magnificently monographed by Joshua Leidy in the USA 1879 and extensively dealt with in the monograph by J Cash, G.H. Wailes and J. Hopkinson (1905-1921)[9], but the small naked amoebae appeared to have few characters of use in differentiating genera and species. In post-war Rothamsted, however, B N Singh made an attempt to introduce systematic order into their chaos with detailed cytological studies of their mode of nuclear division in particular. He recognised the distinctness of the Schizopyrenidae from the Hartmannellidae and within them created several new genera and species.[10]

This start was built on substantially by the American protozoologist Fred Page who moved to Britain with the establishment of the Culture Centre of Algae and Protozoa in Cambridge in 1970 (see below). He emphasised patterns of movement and all life-cycle stage characters in a vastly revised classification summarised in his monographs on freshwater and soil amoebae and later on marine naked amoebae.[11] A particularly valuable aspect of Page's work was sorting out the mix-up between the genera *Acanthamoeba, Hartmannella* and *Mayorella,* widely employed by experimentalists who found in the first genus in particular, ideal lab material for studying various aspects of cell biology. In the UK, Michael Swann's group in Edinburgh in the 1950s was outstanding in this respect and Katherine Adam (firstsecretary of the BSSP) [Fig. 88] who had joined this group in 1952 carried out

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[8] Mare, F (1942) A study of a marine benthic community with special reference to the micoorganisms. *Journal of the Marine Biological Association UK* 25: 517-554.

[9] *The British Freshwater Rhizopoda and Heliozoa*. Vols I-V. London: The Ray Society

[10] Singh, B.N. (1952) Nuclear division in nine species of small free-living amoebae and its bearing on the classification of the Order Amoebida. *Phil. Trans. Roy. Soc.* Series B 236: 405-61.

[11] Page, F.C. (1976) An Illustrate Key to Freshwater and Soil Amoebae. Sci.Publ.Freshwater Biol. Assoc.No.34.Ambleside: FBA; Page, F.C. (1988) A New Key to Freshwater and Soil Gymnamoebae. Ambleside: FBA; Page, F.C. (1983) Marine Gymnamoebae. Institute of Terrestrial Ecology, Cambridge.

pioneer work on the cultivation in chemically-defined media and differentiation of species in this genus based on molecular characteristics. Another important aspect of Page's detailed systematic work was realised after the facultatively parasitic nature of species of *Acanthamoeba* and *Naegleria* was realised in the 1950s and 1960s, and their ability to cause fatal meningitis or encephalitis in humans Although much of the work of medical importance was done in the USA, Belgium and Australia, David Warhurst (LSHTM) and Simon Kilvington (Bath Public Health Laboratory) made valuable contributions as protozoologists to the controversies engendered by it. Both involved in the notorious amoebic meningoencephalitis case at Bath that resulted in closure of the Spa in 1978. Today controversy still lingers over the identification of a third human brain pathogen originally identified as *Leptomyxa* (a genus of multinucleate soil amoebae created by Goodey) but now placed in a genus of its own, *Balamuthia*.

Protozoa in relation to used water treatment and pollution

Economic considerations often fuel advances in academic subjects and the stimulus of Russell's agricultural worries on protozoology in Britain is one example illustrated above. Another is the clarification of liquor in sewage treatment processes. In 1960 B.A. Southgate, Director of the Water Pollution Research Laboratory (WPRL), Stevenage (now the Water Research Centre) while serving as a member of the Board of Studies of Chelsea College of Science and Technology (now part of Kings' College, London) entered into discussion with Eleanor Brown,[12] Reader in Zoology, on this very topic. He remarked that while it was well known that aerobic sewage-treatment plants contain very large populations of ciliated protozoa their role in effluent clarification remained a mystery. He suggested that a research student should be put onto this project and Dr Brown persuaded the College to fund a small laboratory with culture room and a technical assistant to run it. Colin Curds [Fig. 55] was the first of a series of Chelsea research students to investigate the role of ciliates in the activated-sludge process. Later, while holding a postdoctoral fellowship at the WPRL, he was able to show that the presence of ciliates in sewage-treatment processes was vital to achieve high quality effluents (protozoa good, bacteria bad!). Their major role was shown to be the removal of bacteria by predation though a subsidiary role was indirect help in flocculating finely particulate detritus; this conclusion was supported by quantitative feeding studies using batch and continuous cultures, and

[12] Trained by eminent French protozoologists, she had done pioneer work on parasitic ciliates of fishes. Known affectionately to all and sundry as 'Nellie', she was a prominent character in the early days of the BSSP. One of her most remembered proclamations rang out during a lull in the conversation at a BSSP reception: "Yes, sewage will keep Chelsea going for some time."







Fig. 54 John Darbyshire. Fig. 55 Colin Curds. Fig. 56 Bland Finlay.

by mathematical modelling.

In 1972 Curds moved to the Natural History Museum to expand protozoological studies there in a Protozoa and Mathematics group. The emphasis of the work was naturally centred on taxonomy, although the work on sewage ciliates continued and expanded into the newly introduced sewage treatment processes. These included, in North America, Rotating Biological Contactors, in which the film of microorganisms resides on discs that rotate in and out of a flow of sewage at axle depth to increase aeration, and, in the UK, reed beds where sewage trickles through the roots of the reeds and microorganisms in the rhizosphere do the clarifying for small rural communities. Curds published a key to sewage ciliates and with Dave Roberts and Michael Gates two volumes of the Linnean Society's Synopsis of the British Fauna Series on freshwater ciliates.[13] More recently he has published a book on the role of protozoa in used water treatment.[14]

Ecological studies in the English lakes

The only extensive study of the occurrence and distribution of Protozoa in specific habitats in Britain is the almost unbroken study of freshwater protozoa, especially

[13] Work is currently progressing on the production of a CDRom (Curds, Roberts and Warren) which will enable untrained personel to identify ciliates in sewage-treatment processes with the aid of digitised video images, to predict effluent quality from a knowledge of the ciliate species present and continually to increase the accuracy of their predictions by sharing their findings with others in the field via the Internet.

[14] Curds, C.R. (1992) Protozoa in the Water Industry. Cambridge University Press.

ciliates, in the English Lake District over the past 40 years, starting with Marjorie Webb's study of eutrophic Esthwaite Water (1961) and continuing through R. Goulder's researches on Esthwaite and the hypereutrophic Priest's Pot in the 70s to Bland Finlay [Fig 56] and colleagues' studies especially on the latter in the 80s and 90s. The picture that emerges is not only that protozoa play a fundamental part in microbial food webs but also that species richness and the abundance of individuals interact in ways that are not observed in larger organisms.[15] These protozoa live in vast populations, that are readily dispersed and may be cosmopolitan in their distribution, in which extinction is improbable and allopatric speciation (the principal mode of species formation in animals) is a rare event. Many species may be observed in a small natural sample and though the global number of species may be relatively small (about 3000 for free living ciliates) the global number of individuals is unimaginably high. This scenario suggests different evolutionary mechanisms for the creation of biodiversity - an exciting prospect which will be returned to in the last chapter.

The Culture Collection of Algae and Protozoa

An institute of considerable interest to all who work on free-living protozoa is the Culture Collection of Algae and Protozoa (CCAP). The foundation for the collection was the cultures isolated by Professor Ernst Georg Pringsheim in the Botanical Institute of the German University of Prague in the 1920s. When, during World War 2 Pringsheim fled to Queen Mary College, London (then evacuated to Cambridge) he brought some of his isolates with him and these were taken over by Eric George in the Botany School at Cambridge in 1947. In 1970 the expanded culture collection formed the basis of the culture Centre of Algae and Protozoa at Storeys Way, Cambridge, financed by the Natural Environment Research Council (NERC), and staffed with experts - Hilary Belcher, Erica Swale, David Hibberd and Fred Page under the Directorship of John Baker. In 1986, however, the Centre was disbanded and the freshwater algae and all protozoa were transferred to the Institute of Freshwater Ecology, Windermere, and the marine algae to the Dunstaffnage Marine Laboratory at Oban. The Windermere collection is now housed alongside active research groups in protozoan and algal ecology.

[15] See Finlay B.J., Esteban G.F. & Fenchel T. (1996) Global diversity and body size. *Nature* 383: 132-133.

CHAPTER 9

A CHANGE OF EMPHASIS

"The central theme in zoological thought has been Evolution and, whatever be the mechanisms whereby one species gives rise to others, we may be quite sure that the processes involved are essentially of a dynamic nature; the potentialities of the organism and the nature of its environment have operated together to produce new and varied forms of life."

James Gray, 1931

"In 1917.... British Zoology was far gone in that decline from which a small group of 'comparative physiologists' was to rescue it in the mid-twenties, in due course ... to impose on it a hegemony of their own."

P.B. Medawar: The Art of the Soluble, 1967

One of the most striking revolutions in British Zoology was the turn against comparative anatomy as the central discipline, which prevailed, in the post-Darwinian era, and its replacement by the comparative study of function. The transition involved a major change of approach from the evolutionist view of the living world which interprets the phenomena of life in evolutionary terms to the reductionist view which is more aligned with the physical sciences and essentially seeks explanations in terms of their laws. This change took place in the University of Cambridge and was set in train by one man - Sir James Gray FRS [Fig. 57].

James Gray and Experimental Biology

Gray could foresee many more generations of scientists being kept occupied "as sedate taxonomic filing clerks by painstaking description and comparison of structures", but this sort of existence was not for him. It lacked the excitement of discovery and was not likely to make the mechanisms underlying the process of evolution more plausible. He concluded that a change of emphasis was needed in biological research from form to function and like the biometrician W.F.R. Weldon before him he believed that the concept of evolution would remain vague and indefinite until we have established units of measurement which will enable us to orientate the facts to one another on a quantitative basis.

Gray's initial interests were in cell biology and he published seminal books on two subjects relevant to the interests of protozoologists - *Ciliary Movement* (1928) and *Experimental Cytology* (1931). After that he became preoccupied with mechanical problems of animal locomotion. At no stage did he work with protozoa, but his

intellectual progeny did. Essential to his revolution was the establishment of the *Journal of Experimental Biology* as a national scientific journal of repute. In time it replaced the QJMS as a vehicle for cutting edge zoology. The word "experimental" eclipsed "comparative" as the vogue adjective in British Biological science[1], in much the same way that the epithet "molecular" became *de rigeur* in the 1980s. Gray, strangely, saw no particular virtue in experiment as such. "The crucial point," he said, "is whether or not we feel that an analytical study is more useful for the time being than the inductive morphology of the past century (Gray, 1931).

Ciliary and flagellar movement

Since his student days, Gray had had an interest in cell mechanics. He believed that a proper understanding of the processes of fertilisation, cell division and growth, movement and the effects of environmental electrolytes would help to clarify many of life's mysteries. He insisted that the properties of living matter should be studied against a background of first principles of physics and chemistry; the second law of thermodynamics and Newton's laws figure prominently in his writings. It is his fascination with ciliary movement that inspired protozoologists, as he was one of the first to make extensive use of cinematography and the strobe flash in cytological research.

Shortly after he had summarised existing knowledge in his textbook *Experimental Cytology*, and persuaded the University of Cambridge to put up a modern building for experimental zoology, Gray realised that progress at the cell level was slowing down, largely on account of technical limitations. He decided to shelve cytological problems and from then on he became more interested in the relation of locomotion to size in animals. Reynolds' number figured prominently in his papers on propulsion of aquatic animals. Flagellates and ciliates swim at low Reynolds' numbers, i.e. viscous forces dominate over inertial forces and movement occurs only in response to generated force.

Gray may not have studied protozoa himself but his intellectual descendants did. He returned to flagella in 1955 with G.J. Hancock, in a study of the hydrodynamics of sea urchin spermatozoa and developed-resistive force theory. Here the forces exerted by each small element of flagellum are determined and then summed to give the total force. The method was used extensively for analysing propulsion by both planar and helical flagellar waves and by cilia of protozoa by Michael Sleigh [Fig. 58] and Michael Holwill in particular in the UK in the 1960s and 1970s. Sleigh was put onto

[1] Even in the late 1960s, in applying to the Nuffield Foundation for funds to set up a protozoology research unit I was advised to slip the word "experimental" into the title!

ciliary movement in the 1950s by John Harris, Professor of Zoology at Bristol University and a protégé of Gray's. He went on to demonstrate the mechanical basis of the metachronal co-ordination of cilia and produced the first accurate descriptions of ciliary beat patterns. These provided data for collaboration with physicists on the viscous and elastic components of the energetics of ciliary movement and on the low Reynolds' number fluid mechanics associated with ciliary propulsion and co-ordination. Holwill started in Sir John Randall's Physics Department at King's College, London (see Chapter 11) and worked initially on flagellar beat reversal in the trypanosomatid *Crithidia oncopelti*. He and Sleigh later studied the reversal of flagellar beat effected by the tubular mastigonemes (flagellar hairs) on the locomotory flagellum of *Ochromonas*.

Amoeboid movement

Gray's fascination with cell motility also infected his student Carl Pantin (1899-1967) [Fig. 59] who, after moving from Cambridge to the Plymouth Laboratory of the Marine Biological Association, took up the study of amoeboid movement. The concept that the motive force for this movement derives from contractile events was already widely accepted. He chose a marine amoeba of the *limax* type (not until the publication of F. Page's monograph on marine Gymnamoebae in 1980 would it have been possible to identify it further!). Pantin's work, published in eight papers between 1923 and 1931, extended further the hypotheses of (non-Brits) Wallich, Jennings, Rhumbler and Hyman to give the following picture: As the pseudopodium advances, new ectoplasm is being formed by gelation. As water is extracted from the posterior end of the ectoplasmic tube, its contraction drives the fluid endoplasm forward. Continuous forward movement results from constant transformation of the fluid endoplasm at the front into gelated ectoplasm and the transformation of gelated ectoplasm at the rear into fluid endoplasm.

Pantin's investigations formed a prelude to the more detailed studies of the American S.O. Mast (1926 onwards). He observed the effects on amoeboid movement of temperature, oxygen supply, pH, calcium and other salts present in seawater - all of which were known to affect the activity of heart muscle or cilia. Mast worked with *Amoeba proteus* and came to essentially the same conclusions as Pantin but whereas Pantin thought that the affinity of ectoplasm for water was determined by pH. Mast, and later Polack, produced evidence that the conversion back and forth of ectoplasm into endoplasm depended on variations in calcium ion concentrations - a crucial advance in relation to future interpretation of amoeboid movement as based upon an actomyosin sliding filament system.

The nucleus, known to be essential for amoeboid movement (as the nucleated half of







Fig. 57 Sir James Gray FRS. Fig. 58 Michael Sleigh. Fig. 59 C.F.A. Pantin FRS.

a bisected amoeba can carry on moving whereas the anucleate half cannot), did not feature in theories of amoeboid movement until 1950 when R.J. Goldacre [Fig. 60] and J. Lorch Chester Beatty Institute of Cancer Research, London) revived the Mast ectoplasmic tube contraction theory. Contraction of the ectoplasmic *gel* tube at the "tail" of the amoeba drove the fluid endoplasm forward, this contraction was dependent on ATP and localised injection of ATP they found could induce tail formation anywhere on the body. They postulated the existence of a "tail organiser" that produces ATP and that this organiser gradually gets used up causing the amoeba to round up and go into division. In the moving amoebas isolated cytoplasm streams over the nucleus it appeared to become altered in some way so that it is able to *gel* anterior to the nucleus. The nucleus, they suggested collects breakdown products of tail organiser and ATP and re-synthesises new tail organiser, which it releases in division. Controversy over the merits of the tail contraction theory of Goldacre and Lorch and the subsequent anterior pseudopod tip ("fountain zone") contraction theory of R.D. Allen (1961) in the USA lasted for over twenty years until A. Grebecki in Poland in the 1980s showed that the whole cortex provides the motive force for movement.

Jack Kitching and protozoan physiology

Pantin's work on amoeboid movement ceased in 1929, after which he returned to Cambridge and devoted himself to invertebrate physiology, the sea anemone nervous system in particular. But initially he made a brief excursion into the field of osmoregulation which was of particular significance to British protozoology - not because he worked with protozoa (he in fact turned to the turbellarian *Procerodes*)

but because he sparked off an interest in osmoregulation and the contractile vacuole system in a student who was to become an outstanding physiological protozoologist, J. A. Kitching. Kitching was one of the surprisingly few apostles of the Cambridge School to apply their thinking to protozoa.

After graduating from Cambridge in 1931, Jack Kitching (1908-1996) [Fig. 61] accepted a lectureship at Birkbeck College, London. Pantin (who had taught him at Cambridge) suggested that he might explore the hypothesis that the contractile vacuole controls the osmotic pressure of the cell cytoplasm in the face of changes in osmotic pressure of the surrounding medium. Kitching wisely chose to work with sedentary ciliates such as peritrichs and suctorians whose shape was more easily measured than that of motile forms, His researches showed that contractile vacuoles counter the entry of water in food vacuoles and through the surface by osmosis. Water is pumped out by the contractile vacuole but changes in body volume may occur when influx and output become temporarily imbalanced. Accumulation of fluid in the vacuole is energy-dependent (as it is reversibly poisoned by cyanide) and involves an active process of secretion that is somehow sensitive to small changes in body volume, but is apparently uninfluenced by hydrostatic pressure. Pulsation of the vacuole was deduced to involve contraction of the surrounding cytoplasm by an independent rhythmicity. This rhythm is disturbed by temperature change, but is reset to a new level by changes in the rate of filling by the vacuole. Kitching speculated that leakage of salts to adjust cytoplasmic tonicity may also be part of the response of protozoa to changes in osmotic pressure. Later work by others (see Patterson, 1980[2]) has added knowledge about the nature of such changes in tonicity but has not altered our basic understanding of the physiology of contractile vacuoles. Kitching pursued his research on protozoan physiology briefly in Edinburgh and then from 1937-63 in Bristol University interrupted by a year in Princeton and war service in Canada. In 1939 while in Princeton he embarked on research on the effects of high hydrostatic pressure on cell physiology. This interest in the effects of pressure on organisms was perhaps an offshoot of a student passion for diving that persisted throughout his life. It was put to good use in his marine ecological studies - those on Lough Ine in Southern Ireland continuing for over 40 years, this ecological career paralleling his protozoological one.

Kitching's first experiments subjecting cells to high hydrostatic pressure (HHP) were performed in Princeton with Daniel Pease (well known to protozoologists for his later monograph on the ciliate *Blepharisma*), but on mussel gill cilia rather than protozoan. They demonstrated an immediate increase in beat frequency in response

[2] Contractile vacuoles and associated structures: their organisation and function. *Biological Reviews* 55: 1-46.

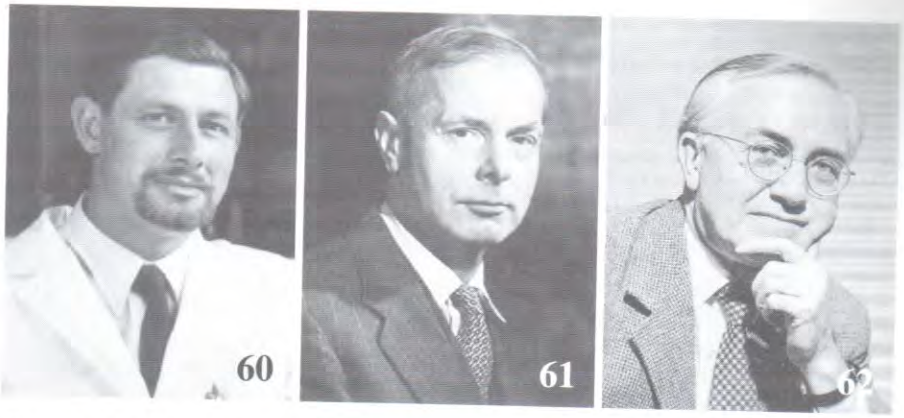


Fig 60 R.J. Goldacre. Fig. 61 J.A. Kitching FRS. Fig. 62 James Danielli FRS

to a sudden increase in pressure (70-350 atmospheres) but if held at 350 atm. the beat rate fell and the cilia showed irreversible damage. The two investigators later showed that the prehensile tentacles of the suctorian *Ephelota* liquefied after exposure for a few seconds to HHP. Later work on the effect of HHP on the axopodia of the heliozoan *Actinophrys* demonstrated their collapse at 300 atm. at 15-20°C but at half this pressure at 5-10°C. These and other studies on the effects of pressure on the contractile vacuole of *Discophrya*, growth of *Acanthamoeba castellanii* and the amoeba-flagellate transformation of *Naegleria gruberi* can now all be interpreted in terms of depolymerisation of microtubular structures induced by HHP or cold. This interpretation had to wait for the experimental ultrastructural work of L. Tilney, K.R. Porter and colleagues in the USA in the 1960s, though Kitching and Macdonald demonstrated the complex array of microtubules in the heliozoan axopod in 1964.

Through his interests in effects of high pressure and his experiences as a diver, Kitching knew that inert gases (e.g. nitrogen, helium, argon) have anaesthetic effect at elevated pressures and his demonstration of the effects of these gases on heliozoan axopod dissolution and swimming speed and beat reversal in the ciliate *Spirostomum* evoked experiments on the effects of inhalational anaesthetics such as halothane on axopodia disassembly and helped the formulation of theories on how inhalational anaesthetics might exert their effects on the brain. Kitching's work illustrates beautifully the value of a broad knowledge of protozoa in selecting suitable experimental organisms for the study of fundamental biological issues.

With the vigorous Society for Experimental Biology serving as the chief biological talking shop and a determined Cambridge Mafia filling vacant chairs of zoology

throughout Britain with their disciples, comparative physiology had no difficulty in ousting evolutionary morphology as the central discipline of the subject in UK universities. But a different kind of experimental biology began to emerge in the 1950s with the controversial appointment of J.F. Danielli to the Chair of Zoology at King's College, London in 1948 on retiral of the protozoologist Doris Mackinnon. He had no formal training in the subject whatsoever.

J.F. Danielli and nucleocytoplasmic relations in amoebae

With a background in physical chemistry, James Danielli [Fig. 62] had entered biology via cell pharmacology at UCL and made a provocative contribution to cell biology with the Davson-Danielli model of the cell membrane - the lipid bilayer in a protein sandwich, as it was often described to students. At King's, however, he pursued a different tack: he became a champion of holistic biology of the cell. Through it he attempted to bring development, inheritance and evolution back into mainstream biology by focusing on the relationship between nucleus and cytoplasm in determining the character of the cell. The material he chose to work with was the large free-living amoebae, *Amoeba proteus* and *A. discoides* (as supplied by Sr Monica Taylor!) and his principal technique was nuclear transplantation by microsurgery.

The robust, lattice-reinforced, nucleus of these large amoebae is readily pushed out of one cell and replaced with the nucleus of another. As material for the study of nuclear control over cytoplasmic activity, and vice-versa, amoebae have the advantage over other cell systems (the large unicellular alga *Acetabularia*, the amphibian egg, fused tissue cells or coalesced slime mould plasmodia) in that the nucleus can be transferred without accompanying cytoplasm. Danielli envisaged that this system could be used to evaluate the respective roles of nucleus and cytoplasm in cell heredity, to estimate the comparative sensitivity of nucleus and cytoplasm to various damaging agents (drugs, radiation) and to investigate transplantation incompatibility. He developed amoeba strains that were relatively easy to grow for extended spells in culture and that were sufficiently different in measurable characters to assess whether these characters came from host or donor in a nuclear transfer experiment.

Danielli and his collaborator Joan Lorch were able to show that a number of characters such as the distribution of nuclear diameters, the amoeba's shape while moving and its shape when inhibited by antiserum, were all determined partly by the nucleus and partly by the cytoplasm, whereas other characters such as the nature of the surface antigens and the composition of the amino acid pools were wholly nucleus-determined. But after that it became difficult to push the analysis further. The characters utilised were often far removed from an assayable gene product. They could be quantified but after the relative contributions of nucleus and cytoplasm had

been apportioned, what then? It was not clear what could be done with the findings.

Nevertheless some intriguing findings were made. Their long cell cycle (48h) and the relative ease with which stages in division of amoebae can be recognised and hence nuclei transferred at a particular stage in the cell cycle without use of stress-inducing stimuli, enabled Muriel Ord (1961, 1971, 1973) to demonstrate the autonomous role of the nucleus in maintenance and termination of DNA synthesis. With Audrey Muggleton, Danielli found that amoebae could be made to undergo an ageing behaviour comparable to that of mammalian cells in culture and that this ageing could be studied by methods of nuclear transfer.

In nuclear transfer experiments, only very few heterotransfers (between strains) gave successful clones, suggesting that some lethal factor was present in the recipient's cytoplasm. In later studies it was realised that the cytoplasm of *Amoeba proteus* contains a veritable zoo of self-duplicating prokaryote symbionts and parasites and that these might well play a part in the success of nuclear transfers. Shirley Hawkins in the 1960s showed that cytoplasmic transfers by injection could lead to stable transformations suggesting the presence of genetic determinants in the cytoplasm. In 1965 Danielli decamped from King's to the State University of New York at Buffalo where he became Director of the Center for Theoretical Biology. He took most of his team with him, though Muriel Ord and Gerry Bell moved to Southampton University. The culmination of the amoeba nuclear transplantation studies was the announcement of the synthesis of a cell! The nucleus of one amoeba was introduced into the cytoplasm of a second amoebae surrounded by the membrane of a nuclear third.

There is no doubt that the line of work that flowed from the transplantation experiments in amphibia (especially those of John Gurdon and colleagues at Cambridge) seems today to be more fruitful than that based on amoebae. But Danielli was no mean prophet. He was among the first to suggest that obligate symbiosis involved gene transfer from symbiont to nucleus and that host nuclear genes might control symbiont activity. From his work on clones, which showed that amoebae grown in the same container move down a trajectory in which the rate of change is sometimes slow and sometime sharply discontinuous, he deduced that the amoebae must be in communication with one another - an outrageous suggestion a the time, but one now amply borne out by the work of Christensen (1997; see chapter 5) and others on various unicellular organisms. And from his work in general he did show that there is more to inheritance than the genes in the nucleus.

CHAPTER 10

VARIATION AND INHERITANCE

"Since the late nineteenth century, everyone had realised that a much better understanding of heritable variation - the great void in Darwin's theory -was needed. Following the rediscovery of Gregor Mendel's work in 1900, many hoped that the new science of genetics with its laws of inheritance would provide the answers to the great controversies over evolution...but this hope was soon disappointed."

Ernst Mayr. Systematics and the Origin of Species. 1999 reprint.

"It is often asked 'What is the significance or meaning of conjugation?' This question is, I believe, meaningless. As well might one enquire the meaning of the moon."

C. C. Dobell, 1914. A commentary on the genetics of the ciliated protozoa[1]

Darwin believed that evolution was the result of Natural Selection acting on abundant variation, though the nature of that variation eluded him. By the early 1930s, evolution had been redefined by Fisher, Haldane and Sewall Wright as the changes in gene frequencies of a population brought about by gradual natural selection of small random nuclear mutations. Recombination of mutations was effected through meiosis and syngamy so that novel genotypes were proffered for Natural Selection to act upon. How far all this applied to protozoa, which often lack an obvious sexual process, was uncertain. Do protozoa have other ways of achieving recombination than through sex? Is there more to variation and its inheritance in protozoa than nuclear genes? Is there more to evolution than Natural Selection? These are fundamental biological questions.

Ciliate genetics challenges the monopoly of the nucleus in inheritance

J.F. Danielli (Chapter 9) was not alone in challenging the monopoly of the nucleus in inheritance. A substantial jolt to the Mendelian geneticist's view of inheritance was delivered by the study of the genetics of ciliates in the hands of Tracy M Sonneborn (1905-81) of Indiana University and his British disciple, Geoffrey Beale (1913-) [Fig. 63]. The process of conjugation in ciliates constitutes a natural experiment in nuclear transplantation. Ciliates have two kinds of nuclei - a diploid non-transcriptive micronucleus and a polygenomic transcriptive macronucleus. The conjugants exchange genetically identical haploid gamete nuclei derived from the

[1] Journal of Genetics 6: 132-190 (1914)

micronucleus so that when the diploid zygote nuclei are formed in each conjugant they are genetically identical but genetically different from the parent micronucleus that gave rise to them. New micronuclei and macronuclei are formed from the zygote nucleus. The cytoplasmic bodies of the two conjugants, however, may be of different character so cytoplasmic effects on nuclear gene expression can be studied. Likewise, in autogamy, the zygote nucleus being formed from fusion of two identical haploid nuclei results in a change in nuclear genetic constitution in the same cytoplasm.

In 1937 Sonneborn had revolutionised microbial genetics with his discovery of mating types in *Paramecium aurelia* and hence an ability to induce mating at will and conduct hybridisation experiments. A morphological species such as *P. aurelia* was shown to consist of several isolated gene pools ("syngens") or sibling species. In 1943 he reported that killer trait in *P. aurelia* depended on cytoplasmic *kappa* particles whose loss by a ciliate abolished its ability to kill off sensitive paramecia that lacked these particles. Prolonged mating, which resulted in some cytoplasmic transfer, also transferred *kappa* and killing ability On inducing autogamy in *kappa*-bearing paramecia, half the progeny were shown to have lost their *kappa* particles due to elimination of a dominant nuclear gene essential for their maintenance. The concept of hereditary determinants (plasmagenes) in the cytoplasm was born. The concept of plasmagenes had taken hold in biology by the early 1950s when in France Ephrussi (1949) demonstrated that the mitochondria of yeast behaved like plasmagenes.

Impact of protozoan genetics on protozoology in Britain

Most significant for British protozoology was Geoffrey Beale's work in Sonneborn's laboratory (1947-48), in which he showed that paramecia could change their surface (immobilisation) antigens with changes in temperature of the surrounding water. The variable antigens were the products of genes at different loci but it was the cytoplasm that exercised control over their expression.

Beale's monograph on *The Genetics of Paramecium aurelia* (1954) and well-attended public lectures given by Sonneborn in London in 1955 raised the profile of protozoology among those sitting on research council committees. They could not help noticing that the subject was not well represented in British universities and that something should be done to remedy this situation! Shortly afterwards lecturers in the subject were appointed at University College London (K. Vickerman, 1958 [Fig. 64]) and King's College London (F.E.G. Cox [Fig. 65]).

Cytoplasmic genetics of ciliates

On his return from the USA in 1948, Beale was able to set up a strong protozoan



Fig. 63 G.H. Beale FRS. Fig. 64 Keith Vickerman. Fig. 65 F.E.G. Cox.

genetics group in Edinburgh. With Ian Gibson[2] he investigated the control of mate-killer (Mu) symbionts by nuclear genes. The inducible surface antigen system of *Paramecium* was pursued further with studies on the nature and location of the antigens by John Sommerville and Robert Sinden respectively. The significance of this antigenic change in the life of the non-parasitic *Paramecium* was a complete mystery, but it had plausible significance in relation to the reported but not well-studied antigenic variation in parasitic protozoa especially Trypanosomes, however, appeared to lack a sexual cycle and so could not be studied by genetic techniques.

Although in 1946 John Preer in the USA showed that *kappa* particles were visible and contained DNA as shown by the Feulgen reaction, Sonneborn refused to concede that *kappa* particles were bacterial symbionts, on account of his inability to culture them outside the ciliate.[3] Not until the 1970's, by which time electron microscopy had confirmed their bacterial nature, did he concede the argument. In fact paramecia are riddled with different bacterial symbionts and Beale with A. Jurand and J.R. Preer in 1969 published a classic paper illustrating the different classes of symbiont as revealed by electron microscopy.

In Edinburgh, Beale's group had continued to study not only the inheritance of symbiotic bacteria such as the *mu* particle, but also mitochondrial genetics in

[2] A candidate for the Heron-Allen (Chapter 7) medal as one time football player for Queen of the South and now an MP in the Westminster Parliament!

[3] At his public lectures on the subject in London in 1955, he was soundly berated by a belligerent Muriel Robertson for not trying hard enough!

Paramecium. In the early 1960s, the widespread occurrence of small amounts of DNA in mitochondria had been demonstrated by electron microscopy by M.M.K. and S. Nass[4]. By the early 1970s, actual circular (or in the case of ciliates, linear) molecules resembling bacterial DNA had been identified. But before that, Beale in the 1960s had found mutants of *P. aurelia* resistant to antibiotics such as mikkamycin and erythromycin, and resistance was shown to be inherited cytoplasmically. In 1972, with Jonathan Knowles and Andrew Tate, Beale was able to show that this resistance could be transferred by microinjection of mitochondria into the cytoplasm of paramecia that lacked the mutation. Such transfer was even possible between paramecia belonging to different gene pools (syngens, sibling species); the resistant donor mitochondria eventually replaced the non-resistant host mitochondria. But transferred back to the cytoplasm of the original syngen lacking resistance, the resistant mitochondria did not survive, suggesting acquisition of recipient nuclear gene dependency.

H.S. Jennings in the USA initiated studies on the genetics of ciliates, at the beginning of the century. Clifford Dobell (see quotation above and Chapter 5) poured scorn on them, but under Sonneborn's leadership ciliates pioneered microbial genetics. That bacterial and fungal genetics have now contributed more to the established corpus of genetic theory does not detract from their significance. The work on inheritance of symbionts and mitochondria[5] contributed significantly to the endosymbiont theory of the evolution of mitochondria and plastids from bacteria revived by Hans Ris in the USA in the early 60s and, as a life's mission, by his graduate student Lynn Margulis in 1970. The widespread occurrence of symbiotic intracellular prokaryotes (also other eukaryotes) in protozoa since then has paved the way for the present view of these symbionts as important gene donors in evolution (see Chapter 12).

Genetics of malaria parasites

By mid-century, investigation of the genetics of parasitic protozoa was long overdue. In truth the schools of tropical medicine had done a grand job capitalising on their Edwardian successes in relation to disease control, but by then they seemed to have become almost impenetrably deaf to recent advances in fundamental biology - especially genetics. The need for the application of genetics to the problem of drug resistance in malaria and other protozoan parasites had been obvious for years but

[4] Before this, the kinetoplast of trypanosomes, known since the early 1920s to be a mass of DNA, had been shown to be part of the mitochondrial system of trypanosomes (see Chapter 11).

[5] Reviewed in Beale G. and Knowles J. (1978) Extranuclear Genetics. London: Edward Arnold.



Fig. 66. Edinburgh group, including John Sommerville, Andy Tait, Richard Carter, David Walliker and visitors (about 1968).

nothing had been done about it. Selection of forms of *Plasmodium gallinaceum* resistant to proguanil and pyrimethamine in the laboratory suggested to Ann Bishop (1962) that mutational events were involved. Beale's group began to study parasites with a programme of research on the genetics of *Plasmodium* in 1967. This programme has been implemented largely by David Walliker and Richard Carter. The use of electrophoretic variants of metabolic enzymes (isozymes) as genetic markers had been pioneered for *Paramecium* by Andrew Tait (1968) in Beale's lab and were first applied to the rodent malaria's (*Plasmodium vinckei, P. vinckei, P. yoelii, P. chabaudi*) by Richard Carter there (1973-78). During the 70s these markers were used by a variety of workers to define parasite populations and study transmission patterns even in the absence of genetic studies, e.g. in human *Entamoeba* infections *by* Peter Sargeant (LSHTM), African trypanosomes by David Godfrey and associates (Lister Institute, London), *Trypanosoma cruzi* by Michael Miles (LSHTM), leishmanias by Michael Chance and colleagues (LivSTM) and coccidians by David Rollinson & Martin Shirley (Animal Health Laboratory, Compton, Berks). The concept of the zymodeme (a population characterised by a particular isoenzyme repertoire) became useful in studying the epidemiology of parasitic protozoa. Thus

in a study of rodent malaria parasites in the Central African Republic, Carter and Walliker using cloning and enzyme typing were able to identify individual pockets of genetically-isolated breeding populations which would qualify as separate species within which considerable random mating (panmixia) was probably taking place.[6] In contrast the human malaria parasite, *P. falciparum* appeared to behave as a single panmictic population across Africa, even the world.

As sexual fusion plays a necessary part in the life-cycle of the malaria parasite, the possibility of undertaking hybridisation experiments was obvious. Gametocytes of two different lines could be mixed, fed to mosquitoes to allow cross-fertilisation to occur, and the resulting sporozoites used to initiate clone infections in new hosts. Controls consisting of individual parental lines only transmitted in this way did not exhibit recombinants in the progeny, so genetic exchange occurs only after cross fertilisation of gametes in mosquitoes. Genetic work on the inheritance of iso-enzymes in *Plasmodium chabaudi* by Walliker (1975) established that blood forms were haploid and in 1985 Bob Sinden (with R.H. Hartley, after moving from Edinburgh to Imperial College, London) detected synaptonemal complexes characteristic of chromosomes in meiosis during early division of zygotes in the mosquito gut wall, suggesting that the ookinete is the only diploid phase in the *Plasmodium* life cycle.[7] The cytological difficulties of determining the number of chromosomes were resolved with the introduction of pulsed field gradient gel electrophoresis; for *P. falciparum* 14 large fragments/chromosomes were identified, with considerable variation in size of homologous chromosomes. The *Plasmodium falciparum* genome project (http://www.sanger.ac.uk/Projects/P_falciparum) is now in full swing.

The genetics of *Plasmodium* has come up with few great surprises, but has refined the important concept of drug resistance considerably. Before the Edinburgh programme, malaria parasites were considered a collection of distinct "strains" and it was customary to consider the spread of drug resistance in *P. falciparum* as the replacement of sensitive by resistant strains. This concept has now been replaced by that of a population of parasites in which random mating of gametes in mosquitoes occurs at high frequency resulting in the production of new gene combinations. The spread of drug resistance should therefore be seen as the spread of resistance genes rather than of resistant strains. Different combinations of genes that affect the resistance character determine variations in the level of resistance. For example

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[6] This work on the rodent malaria parasites was greatly facilitated by expertise on the systematics and natural history of these parasites, resident in the UK. See Killick-Kendrick, R & Peters W (eds) (1978) *Rodent malaria.* London: Academic Press.

[7] Dobell's conclusions (Chapter 5) on ploidy in the apicomplexan life cycle were thus confirmed using different techniques.

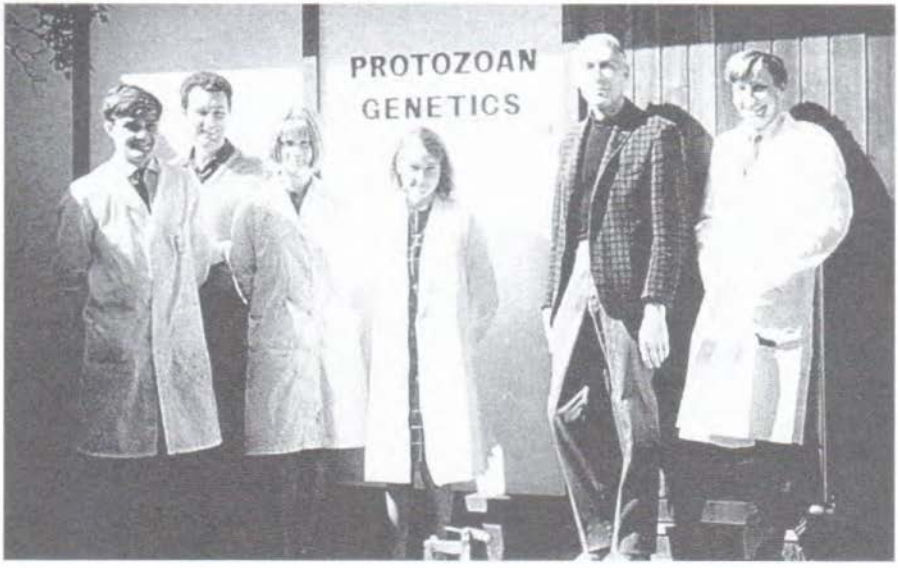


Fig. 67 Edinburgh group, including Bob Sindon (left) and Geoffrey Beale (in jacket).

Walliker (1975) and Knowles' (1981) groups have shown that in *P. chabaudi* and *P. yoelii*, genetic crosses with pyrimethamine resistant and sensitive lines suggest a pattern of inheritance of resistance typical for a single gene, whereas similar crosses between chloroquine-resistant and sensitive *P. chabaudi* by Rosario (1976) and Padua (1981) showed that high level resistance was due to a number of mutations in different genes.

Carter and an international team of investigators have recently demonstrated cytoplasmic inheritance of mitochondrial and relict plastid genes (see Chapter 11).

A considerable number of *P. falciparum* isolates possess more than one form of a given iso-enzyme indicating that human infections may consist of a mixture of clones. The possibility that some of these mixtures consist of clones that have a reciprocal dependency on one another, i.e. exist in symbiotic relationship with one another, is an intriguing one!

The problem of drug resistance in *P. falciparum* is one of increasing importance globally - even in the UK for some 2000 British travellers a year contract malaria and of these at least ten will die as a result. The seriousness of the problem has led to

an all out international effort to produce a vaccine against the parasite. The search for antigens that will confer protective immunity is a major research industry. While much effort has been put into an antisporozoite vaccine (as the sporozoite is the infecting stage in the life cycle), in the 90s some attention is being given to the induction of transmission-blocking immunity i.e. immunity which will prevent gametes which differentiate in the mosquito's gut from effecting syngamy and hence developing further there. In the UK, Richard Carter in Edinburgh, together with NIH colleagues, and Geoffrey Targett at the LSHTM have been prominent in this particular endeavour.

Sex and alternative forms of genetic recombination

Most evolutionary biologists insist that sex is part and parcel of the eukaryote condition as it provides a mechanism for defeating "Müller's ratchet" - the progressive accumulation of deleterious mutations that can be eliminated through the periodic recombination that meiosis and syngamy provide in addition to providing new recombinants for natural selection to act upon. The fact remains, however, that whereas sexual processes are a necessary part of the life-cycle of some protozoa (apicomplexans, ciliates, foraminiferans, mycetozoans) they are not yet documented in perhaps the majority. That this dearth of sexual activity may be due to lack of attentiveness on the part of protozoologists is illustrated by the case of the African trypanosomes. Although attempts to demonstrate sexual recombination using drug resistance characters date back to Paul Ehrlich's time, and although through much of this century fanciful accounts of mating between bloodstream forms have been published, it was not until Andrew Tait (1980) demonstrated that the frequency of iso-enzyme variants in natural populations of *Trypanosoma brucei* conformed to the Hardy-Weinberg Equilibrium that the possibility of genetic exchange through mating could be taken seriously. Later (1986) an international team led by Leo Jenni in Basle, and including Tait, successfully produced trypanosome hybrids in the laboratory by co-transmitting two clones of *T. brucei* through tsetse flies. Subsequent studies by Tait and Michael Turner (Glasgow University) and Wendy Gibson and colleagues (Bristol University) have confirmed that mating does occur, probably late in the developmental cycle of the trypanosome in the vector, but it would appear to be a rare happening and not obligatory for continuation of the cycle. Although re-assortment of characters suggests that meiosis and syngamy are involved, the physical basis of mating and its significance in terms of the evolution of new epidemic-generating genotypes are uncertain. Interestingly, *T. evansi*, which has undoubtedly evolved from *T. brucei* by loss of the tsetse developmental stages, must have abandoned sex in the process, yet it is every bit as successful as its cyclically-transmitted counterpart. The message is that having invented sex, protozoa can learn to live without it so that clonality is their natural state. The possibility that they have

discovered other ways of shuffling their genes to provide new recombinants for Natural Selection to work on, however, is worthy of serious consideration in view of what we now know of the basis of antigenic variation in trypanosomes. This is an aspect of protozoology to which UK researchers have made substantial contributions.

The nature of antigenic variation in trypanosomes

Trypanosoma brucei and other salivarian trypanosomes can evade their host's immune response by changing the nature of the antigens that induced that response. The nature of this variation was resolved in the complete absence of mendelian genetics as the sexual process in these trypanosomes was discovered late in the day, and hybridisation studies proved difficult to conduct anyway, yet extraordinary revelations about the organisation of the genome and novel mechanisms of genetic recombination and evolution in these flagellates have been revealed in the process.

The striking fluctuation in numbers of trypanosomes (parasitaemia) in the blood of infected cattle was noted in Bruce's 1895 report. In the first decade of the 20th century experimental work to determine possible reasons for this was undertaken in the laboratories of Paul Ehrlich and Alphonse Laveran. In 1907 Massaglia in the latter proposed that the recrudescence of parasitaemia (number of trypanosomes in the blood) after a crisis was due to a few parasites escaping destruction because they have become resistant to trypanolytic antibodies and then multiplying to give rise to the next parasitaemic peak. This explanation was accepted by Ronald Ross and David Thomson (1911) in interpreting the fluctuating parasitaemia in "a strong young Englishman, aged 26, infected in NE Rhodesia near the River Langua in 1909" one of the few cases of sleeping sickness ever admitted to a British hospital;[8] his parasitaemia became the classic graph illustrating antigenic variation as the trypanosome's adaptation to prolonging infection in the mammal.

Although H. Ritz (1914) in Germany showed that antigenic variation could occur in an infection initiated with a single trypanosome and that in that infection at least 22 relapse variants could be distinguished by cross immunity tests, the intrusion of the First World War put further investigations on hold until some time after the second. In 1959, the UK Colonial Office through its trypanosomiasis panel expressed an interest in reconsidering the possibility of vaccination against trypanosomiasis as an alternative to tsetse control and an interest in understanding the basis of antigenic variation - seen as the principal stumbling block in this endeavour - was rekindled. Early work on antigenic variation had suffered from lack of standardisation of test

[8] And the one form which *T. (brucei) rhodesiense* was identified as a separate [sub] species by Stephens and Fantham.




Fig. 68 W.H.R. Lumsden. Fig. 69 Stephen Phillips.

materials. Serum could be frozen but trypanosomes had to be passaged endlessly through mice at two-day intervals to avoid antigenic change and this was not always reliable. The introduction of a satisfactory technique for cryopreservation of trypanosome populations in dry ice or liquid nitrogen by C. Polge and M.A. Soltys in the new Cambridge Veterinary School in 1957 was a major step forward in remedying this defect - and not only in the study of trypanosomes but in all protozoan parasites, and it marked the start of innumerable reference collections of stabilate material in research institutes the world over.

In 1959 the appointment of Russell Lumsden [Fig. 68] as Director of the East African trypanosomiasis Research Organisation in Uganda enabled work to start on freshly-isolated trypanosome strains in Africa. Using stabilate populations as test antigen, Matthew Cunningham and Keith Vickerman showed that a wide range of *T. brucei* stocks from sleeping sickness patients and domestic and game animals produced some variable antigens in common in experimentally-infected rabbits, but the nature of antigenic change was obscure. Was it due to selection of genetic mutants by host antibody or was it the result of phenotypic change on the part of the parasite, possibly induced by host antibody?

In 1964, J.F. Watkins in Oxford showed that the rate at which new variants arose was compatible with genetic mutation rates in old laboratory strains. But a year later, Ross Gray, a British vet working in Nigeria, demonstrated that the variable antigen types of a clone appeared in similar processional sequence in the blood of different animals, and what is more reverted to the same basic antigen after transmission through the tsetse fly. A random mutational basis for antigenic variation therefore seemed unlikely and selection of individual phenotypes from a genotype-specific repertoire more likely. In the 1970s the use of immunofluorescence and immune lysis to identify the variable antigen type (VAT) of individual trypanosomes by Nestor Van Meirvenne and colleagues in Antwerp and Russell Lumsden and John Herbert in the Centre for Tropical Veterinary Medicine, Edinburgh made it clear that an unrelapsed clonal population of *T. brucei* is heterogeneous with respect to VAT, small numbers of trypanosomes belonging to different VATs occurring among the majority displaying the same VAT. Using similar methods, Dominique Le Ray, David Barry, Stephen Hajduk, Laurence Tetley and Keith Vickerman in Glasgow University were able to show that the metacyclic population injected by the tsetse fly does not belong to a single basic antigen but is a mixture of VATs characteristic of that particular genotype (VAT repertoire, serodeme). Hopes that vaccination against trypanosomiasis might be possible using the metacyclic VATs of numerous serodemes have been shattered by the finding by David Barry and Michael Turner not only that the m-VAT repertoire might be as high as 25 in number (the bloodstream repertoire may be over 1000) but also that the repertoire changes over the course of successive transmissions, i.e. the repertoire evolves to allow for the acquisition of immunity on the part of the host population.

Location and nature of the variable antigen

In 1969 the writer proposed that the variable antigen was located in a 12nm surface coat found in transmission electron micrographs covering bloodstream and metacyclic *T. brucei* but missing from the other stages of development in the tsetse fly. Loss of the coat on entering the fly corresponded with loss of reactivity with VAT-specific antiserum as observed in the early 1960s by Richard Seed in the USA when trypanosomes were put into *in vitro* culture and assumed the tsetse midgut (procyclic) form. The coat serves as a replaceable surface as well as for protecting the trypanosome against non-specific host defences such as macrophage activity and lysis by complement. The trypanosome changes its coat by replacing one variable antigen with another of differing specificity. In 1970, these hypotheses were tested by the writer and Tony Luckins by examining binding of VAT-specific ferritin conjugated antibody to coated trypanosomes and those from which the coat had been removed by pronase digestion.

The 1970s saw a major revolution in our understanding of surface membrane structure and the relation of protein components to the lipid bilayer in particular: The Davson-Danielli model was replaced by the fluid mosaic model of Singer-Nicolson (1972). The study of the variable antigen composing the surface coat was taken up by George Cross and Mervyn Turner in Bruce Newton's MRC Unit for Parasite Biochemistry at the Molteno Institute in Cambridge. In 1975, Cross using radiolabelling of surface protein showed that the coat was made up of a single 60kDa variant-specific glycoprotein (VSG). Turner that the soluble VSG (exoantigen) is created by phospholipase digestion of the membrane-bound form and this led to the discovery by Michael Ferguson, now at Dundee University, of the glycolipid (glycosylphosphatidylinositol) anchor through which the VSG is inserted into the lipid bilayer.

Interestingly, in France Yvonne De Capdeville and colleagues have shown that the variable immobilisation antigens of *Paramecium aurelia*, studied by Beale, are 200-300kDa proteins with GPI anchors. The regulation of their expression also involves intergenic and interallelic exclusion mechanisms which can be triggered by changes in temperature, pH or salt concentration. In contrast, what triggers antigenic switching in trypanosomes is unknown and it is certainly not antibodies which simply play a selective role

Genetic basis of antigenic variation

Elucidation of the way in which one VSG is replaced by another at the molecular level in order to achieve antigenic variation has been an international effort; the teams of Piet Borst in Amsterdam, Etienne Pays in Brussels, George Cross (now in New York) and David Barry in Glasgow have been most active. Briefly, each VSG is encoded by a separate gene, of which there are up to about 1000 in the trypanosome's nuclear genome, located at the telomeres and in arrays on the parasite's larger chromosomes and at the telomeres of ~100 minichromosomes. In order to be transcribed a gene has to be copied to an expression site at the telomere of one of the large chromosomes. There are about 20 expression sites and only one can be active at any one time. Expression of a new VSG gene involves silencing of a gene at an expression site or its replacement. Replacement involves a recombination event which may be complete, sometimes resulting in loss of the old gene from the genome, or partial so that new recombinant genes are produced. The expression system therefore contains the seeds of genomic change and hence the repertoire is evolving continuously, independent of any sexual process. Particularly important is the evolution of the metacyclic VAT repertoire as indicated above.

Antigenic variation in malaria parasites

Parasitaemias of some species of malaria parasites show recudescences (upsurges after crashes, as distinct from relapses due to emergence of hypnozoites) and these may be due to antigenic variation on the part of the parasite, its antigens being displayed on the surface of the infected red cell. Antigenic variation in primate malaria was first demonstrated by Neil and Ivor Brown at the NIMR, London, (1965) in *Plasmodium knowlesi* of rhesus monkeys. Before this (1962) there had been indirect evidence from Herbert Cox (USA) that AV could occur in *P. berghei* of rodents. Stephen Phillips [Fig. 69] and colleagues (Glasgow University) showed that AV occurs in *P. chabaudi* (1982) in mice. Antigenic variation in *P. falciparum* was first shown by Alastair Voller (LSHTM) (1981). Since then it has been extensively investigated outside the UK and shown to be dependent on ~50 *var* genes scattered over many chromosomes. As in trypanosomes, expression is monoallelic but there is no single active expression site and allelic exclusion is achieved by allele selection at the transcriptional level.

Despite spectacular advances in some areas, it is obvious that few of the questions about variation posed at the opening of this chapter have been answered. As to whether there is more to evolution than Natural Selection one only has to raise the question of the evolution of the facultatively pathogenic amoebae to realise that this is not an unreasonable question. It is difficult to see how adaptations for invasiveness on the part of say *Naegleria fowleri* could have been selected for if once it becomes invasive it can never return to its free-living existence and simply dies with its host!

CHAPTER 11

RENAISSANCE

"Treasure your exceptions. Keep them always uncovered and in sight. Exceptions are like the rough brickwork of a growing building which tells that there is more to come and shows where the next construction is to be."

William Bateson (Inaugural Lecture, Chair of Genetics, Cambridge University, 1912

Victorian naturalists owning microscopes felt privileged to envisage for the first time works of the creator so small that the eyes of their fellow men could not observe them. Up to the late 1950s the great frustration of studying protozoa had been the limited resolving power of the light microscopes. The transmission electron microscope with its infinitely superior resolution put an end to all that. The first electron micrograph appeared in *Nature* in 1933 (with a resolution of 1mm!) but the machines to take them with did not become widely available for another two decades. By the time the First International Congress on Protozoology was held in 1961 papers on electron microscopy were becoming commonplace.

Electron microscopy opened up a new era of discovery at the level of the cell and protozoologists suddenly found they had an exciting brand new world to explore. They could feel what it was like to be Leeuwenhoek in the 17th century all over again. A veritable renaissance in the subject followed - perhaps the nearest protozoology has come to a "big bang". One of the most remarkable features of this renaissance was the breakdown of those old disciplinary barriers, which had long divided the subject. Phycologists suddenly realised they had much in common with protozoologists, and parasitologists that they needed to know more about free-living protozoa and vice-versa. The barricades that Lankester reinforced and Wenyon deplored were silently removed through a common interest in those wondrous creatures that are both organism and cell.

The death of protoplasm

The electron microscope transformed our concept of not only the cell but of the entire physical basis of life. The concept of a colloidal substance called "protoplasm" mystically-endowed with the properties of life was killed stone dead by the revelation that both cellular organelles and the matrix in which they were suspended are highly structured and compartmentalised. The development of cell fractionation techniques in conjunction with increasingly sophisticated cytochemistry and electron microscopy

enabled compartmentalism of the cytoplasm in terms of metabolism to be studied in depth. At the level of resolution of the electron microscope the anatomical merged with the molecular. This was nowhere more obvious than in the development of studies on the elaborate cytoskeleton composed of different classes of "filaments" (microtubules, microfilaments, intermediate filaments) later identified as structural proteins (tubulins, actins, spasmins and so on). The relation of the cytoskeleton wiped out the valiant attempts by D'Arcy Wentworth Thompson in his classic *On Growth and Form* (1917, 1942) to explain the shape and behaviour of protozoa and other cells in terms of droplets and surface tension, though much remains to be admired about that extraordinary book. Of course the bar on the study of living material imposed by electron microscopy meant that parallel study of living protozoa continued to be essential and developments in light microscopy (especially differential interference contrast and confocal microscopy, and video techniques) remained as important as ever in protozoological investigations, as did continued guard against the study of artifacts induced by fixation and embedding

The lament of protozoologists of yore that protozoa exhibit little in the way of obvious morphological adaptation compared with higher organisms proved groundless: at the ultrastructural level adaptations were staring us in the face. A symposium *Function and Fine Structure in Protista*[1] organised by the Linnean Society in March 1962, chaired by C.F.A. Pantin with presentations by Irene Manton (Leeds), Maurice Black (Cambridge), Sir John Randall (KCL), Keith Vickerman (UCL) and A.V. Grimstone (Cambridge) gave a good impression of British work on protozoa at the beginning of the sixties as well as themes that were to be developed later.

Form, function and systematics in phytoflagellates

Among the most successful of enterprises was the study of the fine structure of pigmented flagellates by Irene Manton, Professor of Botany at Leeds University [Fig. 70], and her numerous disciples. Leeds has a tradition of pioneering ultrastructural studies going back to the thirties and Astbury's X-ray diffraction photomicrographs of feathers and hairs, revealing their crystalline regularity of structure. Originally a fern cytologist with an interest in chromosome behaviour, Irene Manton was initially diverted into looking at fern spermatozoa and the fine structure of flagella in general which often disintegrated to show internal components in her metal-shadowed specimens. She expanded her studies on the flagella of algae in relation to algal classification. Up to the mid 1950s phycologists had largely been obsessed with the pigments and storage compounds of algae.

[1] Published (1963) *Proceedings of the Linnean Society*, 174: 31-52



Fig. 70 Irene Manton FRS. Fig. 71 Mary Parke FRS. Fig. 72 Gordon Leedale.

Although Manton dismissed the "Phytomastigophorea" (the dustbin Class into which protozoologists dumped the pigmental/algal flagellates) as something that only existedon blackboards in Zoology Departments, her work and that of her disciples - many from the Maud Godward School of algal cytology at Queen Mary College, London - did much to heal the longstanding rift between University botany and zoology departments which in turn depended on the divide between the reductionist and evolutionist interpretations of biological phenomena. Within protozoology at the international level, however, this divide had already been breached to some extent by developments in cultivation and nutrition of protists as can be seen by glancing at the volumes edited by Seymour Hutner and Andre Lwoff on the *Biochemistry and Physiology of Protozoa* (1951 etc) in which studies on phytoflagellates were prominent.

One of the most exciting aspects of the work of Manton and colleagues was on the production of the surface scales and spines of many pigmented flagellates, especially those of the Prasinophyceae, Prymnesiophyceae and Chrysophyceae, and the part played by the Golgi apparatus (GA) in synthesis, packaging and sorting of scales [Fig. 73]. In 1954 the cytochemist John Randal Baker of Oxford[2] declared the GA an artifact of silver impregnation. He had been unable to uncover common cytochemical properties in the GA of different cells. For years he had been slanging it out with J. Bronte Gatenby of Trinity College Dublin who believed that the GA had a role in secretion and, in protozoa, in contractile vacuole formation. About the

[2] Not to be confused with the parasitologist John R Baker of the LSHTM, Molteno Institute and CCAP, Cambridge (see Chapter 5)

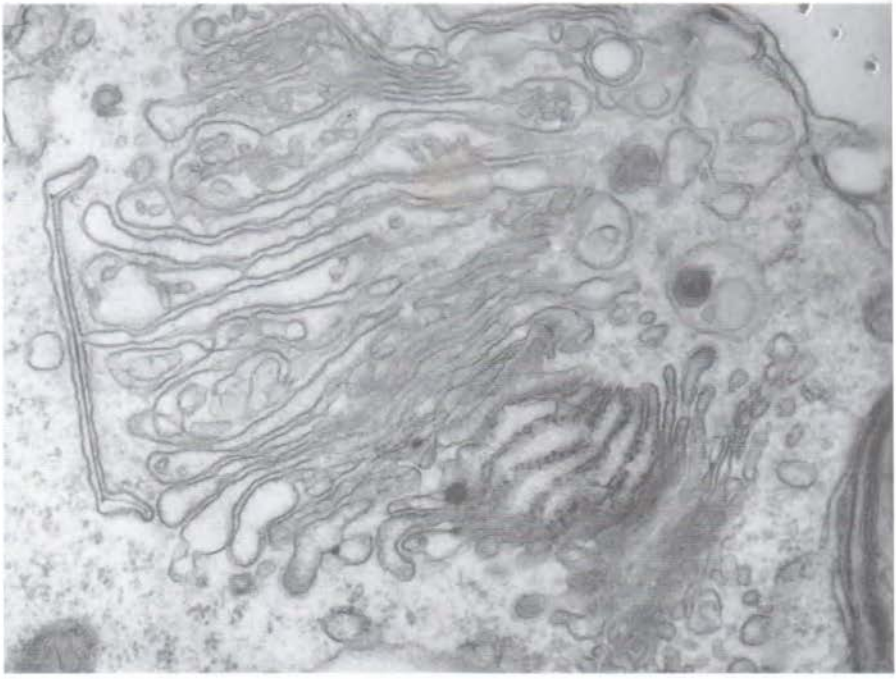


Fig. 73 Golgi apparatus of *Chrysocromulina chiton*.

same time, however, the Americans Dalton and Felix showed that with the aid of transmission electron microscopy the GA has a constant form in all cells - stacked membranous cisternae with peripheral vesicles and tubules in attendance. No wonder Baker hated the electron microscope ever after! The intricately patterned surface scales of flagellates (and similar ones were later revealed in many amoebae) may be present on both body and flagella. In her illustrated lectures, Manton was adept at conjuring up appropriate metaphors to described these surface adornments ("waste paper baskets from Woolworths", "dressing table mats crochetted by Grandma"). Many of these scales become reinforced with $CaCO_3$ or silica. Even the most ardent Darwinian is hard-pressed to imagine the selective forces that moulded them. The precise segregation of the different types of scale on the surface of the body and on the flagella are miracles of microbial architecture. Studies on scale production, led by Manton, provided compelling visual evidence for the 'cisternal progression school', i.e. the cisternae with their contents move down the stack as the secretion matures, as opposed to the 'vesicle shuttling school' who envisage transport of the secretion from one stationary cisterna to the next by the peripheral vesicles. The scales of the

coccolithophorid (prymnesiophyte) flagellates are, of course, the principal component of chalk rock and at the Linnean meeting, the palaeontologist Maurice Black demonstrated the relationship of calcite crystals to the scales of fossil coccoliths. The cellular aspect of biomineralisation in phytoflagellates formed a major avenue of exploration in years to come as can be seen from the Systematics Association Symposia edited by Barry Leadbeater and John Green, both substantial contributors to the subject themselves.

The UK boasts several distinguished pioneers of phytoflagellate form and function in addition to Manton. Mary Parke [Fig. 71] of the Plymouth Laboratory was her principal associate on the prasinophyte work which drew heavily on the collection of marine flagellates assembled by R.W. Butcher of the Fisheries Laboratory, Burnham on Crouch. Gordon Leedale (Leeds) [Fig. 72] made a comprehensive study of the cellular organisation of the euglenoid flagellates, and published a monograph on the group. John Dodge (Birkbeck and Royal Holloway Colleges) [Fig. 74], brought the attention of cell biologists to the extraordinary dinoflagellates, especially their weird chromosomal structure and nuclear division and authored a textbook on *The Fine structure of Algal Cells* in which he synthesised much that was known up to 1973. With the expansion of the CCAP at Cambridge when it was taken over by the NERC in 1970, Hilary Belcher and Erica Swale (who moved there from Windermere) and David Hibberd (who moved from the Natural History Museum, London) added abundantly to the literature on a the taxonomy and ultrastructure of a wide variety of algal and colourless flagellates with the recognition of several new taxa such as the widespread scale-bearing non-flagellate genus *Luffisphaera* and the phyla Chlorarachniophyceae and Eustigmatophyceae. After working on a variety of pigmented flagellate groups, Barry Leadbeater (Birmingham) [Fig. 75] eventually settled on the choanoflagellates, especially those that secrete cages composed of silica spicules and worked out precisely how they did it in relation to the division cycle.

Flagella, cilia and contractile organelles

Among the most striking images to emerge from early transmission electron microscopy, were those of sections of the flagella of the giant flagellate *Trichonympha* published in 1960 by Ian Gibbons and A Victor Grimstone of Cambridge University.[1] Grimstone was attracted to protozoa on account of their possession of organelles of unusual number, structure and function on Bateson's "cherish your exceptions" principle (see head of Chapter). He found the complex flagellate symbionts of termites

[1] Gibbons, I.R. & Grimstone, A.V. (1960) On flagellar structure in certain flagellates. *Journal of Biochemical and Biophysical Cytology* **7**:697-718.

and wood-eating roaches (*Cryptocercus*), extensively studied in the USA by L.R. Cleveland at the light microscope level, especially for their division processes, ideal in this respect. With its 70 Golgi bodies and 15,000 flagella *Trichonympha* clearly had potential. In it the intricate details of the flagellar axoneme (doublet arms, radial cross links) were exposed for the first time. Grimstone gave serious thought to the principles of comparative anatomy at the ultrastructural level and the correlation of resemblances in structure with resemblances in function. He pointed out that the characteristic morphology of an organelle results from the interplay of functional requirements imposed by Natural Selection and the innate structure-building properties of biological macromolecules. He compared the problem of ciliary bending to that of the propulsive bending of the massive ribbon-like axostyles present in *Saccinobaculus* and other oxymonad flagellates found in the hindgut of *Cryptocercus:* these axostyles are composed of layer upon layer of microtubules. This idea proved seminal for indeed, later, Peter Satir [Fig. 79] and Robert Bloodgood in the USA were to show that a sliding filament mechanism is responsible for contractility of both types of structure.

Grimstone and Cleveland co-operated in an ultrastructural study of the Australian termite symbiont, *Mixotricha paradoxa.* This extraordinarily complex trichomonad flagellate has an investment of galley-slave spirochaetes substituting for flagella in propelling it through the hindgut contents of the host; each spirochaete has a special attachment structure anchoring it to the flagellate's surface. This unusual organism received much publicity through Lynn Margulis' attempts to convince the world that flagella and cilia arose during eukaryote evolution from attached symbiotic prokaryotes.

In 1966, that stamping ground of so many British protozoologists since the time of Ray Lankester, the *Quarterly Journal of Microscopical Science,* underwent a sea change. The Cambridge-based Company of Biologists, long responsible for its publication, decided that a new image was called for, emphasising the burgeoning broader field of cell biology. So the QJMS became the *Journal of Cell Science* (the American *Journal of Biochemical and Biophysical Cytology* had already changed its name to the *Journal of Cell Biology*) and the new editor was A.V. Grimstone who emphasised the journal's continuing commitment to the cell biology of unicellular organisms. This commitment has continued with successive editors and the journal has played a valuable part in broadcasting the general interest of protozoa to cell biology at large.

Problems of morphogenesis

One of the first investigators of protozoan fine structure in Britain was Sir John Randall (1905-1984) [Fig. 76], an outstanding physicist who, after World War 2 (in which he had made valuable contributions to the development of radar), was keen to apply the physical sciences to biology. He persuaded the Medical Research Council to set him up in a Biophysics Unit at King's College London where he held the Chair of Physics. His Unit included Murice Wilkins, Nobel Laureate for his X-ray diffraction studies on the structure of DNA and Jean Hanson who with H.E. Huxley was architect of the sliding filament theory of muscle contraction. Randall was attracted to ciliates whose highly ordered surface structures and contractility systems (cilia, myonemes) seemed to offer alternative approaches to fundamental biophysical problems than more standard material beloved of biophysicists (e.g. plant cell walls, collagen, muscle). His EM studies were largely on contractile forms - *Spirostomum ambiguum*, *Stentor coeruleus* (with Sylvia Fitton-Jackson) and the contractile-stalked peritrichs (with John Hopkins), but he also set up a group including Maurice Watson and John Alexander who successfully isolated the cilia of *Tetrahymena* for studies on protein assembly. This pioneering work set the stage for more detailed studies on cortical organisation and myoneme contractility in *Stentor* by Lawrence Bannister at Guy's Hospital, and on the peritrich spasmoneme - a unique contractile system in that it requires ATP for relaxation rather than contraction - by Brad Amos in Cambridge.

Randall became particularly fascinated with the replication of the basal bodies of cilia and whether these structures have their own DNA. The pioneering light microscope work on ciliate morphogenesis by Edouard Chatton and Andre Lwoff in France (summarised by Lwoff in his book *Problems of Morphogenesis in Ciliates*, 1980) envisaged basal bodies (kinetosomes) as dividing organelles, but Randall's group showed that they replicated by induction rather than division. Randall and colleagues found fluorescent staining of DNA at basal body sites in ghosts of *Tetrahymena* but the consensus of re-interpretation was that it represented adsorbed macronuclear DNA released during preparation of the ghosts.

Organelle continuity and activation: the life-cycle

The question of the function of extranuclear DNA and its relation to organelle continuity and activation was one that attracted the writer to trypanosomes in which the kinetoplast represents a mass of such material as demonstrated in the nineteen twenties by Muriel Robertson among others. Around 1960 several electron microscopists found that in trypanosomatids the kinetoplast forms part of the mitochondrial system: my own studies in the early sixties showed that in these

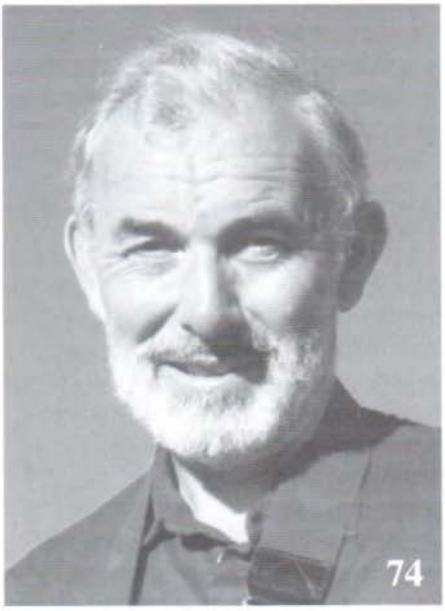








Fig. 74 John Dodge. Fig. 75 Barry Leadbeater. Fig. 76 Sir John Randall. Fig. 77 Elizabeth Canning.

organisms there is just one mitochondrion per flagellate, extending from one end of the body to the other and that this mitochondrion divides along with the kinetoplast before nuclear division in the cell cycle. Moreover, in *Trypanosoma brucei*, drawing on the excellent earlier respiratory studies of T. von Brand and E. Johnson Tobie in the USA, P.T. Grant & J.R. Sargent in Aberdeen University and John F. Ryley at Imperial Chemical Industries, plus my own cytochemical and substrate ultilisation experiments, I was able to show that this mitochondrion undergoes cyclical changes in structure and function during the course of the life-cycle. In the bloodstream, the mitochondrion is repressed, in the vector active, with preliminary activation of mitochondrial oxidase systems in the stumpy bloodstream forms. These findings explained Muriel Robertson's earlier observations on the ability of stumpy forms to infect the tsetse fly - an ability lost in old laboratory-passaged strains and dyskinetoplastic strains where the kinetoplast has undergone irreparable mutation condemning the parasites to mechanical transfer instead of cyclical transmission ever after.

The significance of the slight morphological changes - e.g. back and forth movement of the kinetoplast in trypanosomes - exhibited by protozoan parasites at the light microscope level as they passed through the life cycle had not hitherto been obvious. It was now clear that these slight changes were linked to more profound ones at the ultrastructural, biochemical and molecular level, many of which could be seen to confer distinct adaptive advantages, in the case of mitochondrial activation and repression in *T. brucei* the ability to switch from ultilisation of glucose as respiratory substrate in the mammal to utilisation of proline in the vector - this amino acid being the principal source of energy for flight in the tsetse fly. The metabolic changes in the trypanosome switch were explored in greater detail by Ramsay Bowman and Iain Flynn in Edinburgh in the late 60s, by David Evans, Robert Brown and myself in Glasgow after my move there in 1968, and outside the UK especially by Fred Opperdoes' group in Belgium who identified the glycosome as the organelle that houses the enzymes of the glycolytic chain in kinetoplast-bearing protozoa. The nature of the kinetoplast (kDNA) - the DNA maxi- and minicircles that compose it and the relation of this DNA to the process of editing of kDNA transcripts were major preoccupations of molecular biologists at the international level over the last thirty years of the 20th century.

The cytoskeleton - a protozoan speciality

The recognition of the major components of the cytoskeleton in eukaryotic cells owed much to protozoan studies - especially Porter and Tilney's study (in the USA) of heliozoan axopodia in relation to microtubule assembly and disassembly and the concept of microtubule organising centres (MTOCs). Ciliates in particular present

extraordinary complex cytoskeletons and, as indicated above, were among the first objects of study by electron microscopists. In the UK, John Tucker (St Andrews) used the prey-capturing tentacles of suctorians to illustrate the dynamics of microtubules in tentacle construction and feeding and of MTOCs in the course of a life cycle involving dramatic change in form. Ron Butler and his associates in Manchester have used the diversity of form in suctorians to shed further light on these processes.

One of the most complex of protozoan cytoskeletons is that supporting the adhesive disc of *Giardia* - the means by which this parasite hangs on to its host's intestinal villus. In the 1970s and 80s David Holberton at Hull and Nottingham Universities showed how the disc was reinforced by a broad spiral of micotubules, each microtubule itself reinforced by a ribbon of tubulins and giardins - intermediate filaments of a novel structure, this class of cytoskeletal proteins being rare in protozoa. Holberton also developed a hydrodynamic model of adhesion that James Gray would have approved of. Other cytoskeletal components involved in attachment have less extensively explored, for example the prominent filaments which appear to convert the flagellum of trypanosomatids into an organ of attachment. The importance of these attachments in the relation to development in the vector, and especially the differentiation of the infective metacyclic stage have been pointed out by David Molyneux and Bob Killick Kendrick for the leishmanias in particular. Attachments of a different kind - the focal attachments of moving amoebae to the substratum were shown to be an essential component of forward progression by Terry Preston and Conrad King at UCL [Fig. 78]. They utilised reflection interference microscopy to demonstrate continual formation of these contacts in *Naegleria* and *Acanthamoeba* and by TEM showed dense aggregation of actin filaments in association with the plaques. In the study of amoeboid movement post-Goldacre, so much attention had been given to locating the site of contraction and later to demonstrating the role of an actomyosin system in contraction that the requirement for attachment had been overlooked.

Molecular aspects of trypanosome morphogenesis especially relationships between flagella, mitochondrion and cytoskeleton during the division and life-cycles of trypanosomes were taken up by Keith Gull and co-workers at Manchester University in the 1990s with considerable success. They have revealed a novel mechanism of microtubule genesis in the tight microtubule corset of trypanosomes - lateral nucleation on existing microtubules.



78



79

Fig. 78 Conrad King. Fig. 79 Peter Satir. (drawings by Lawrence Bannister)

Intracellular parasites and mechanisms of cell entry

A topic not covered in the Linnean Society's 1962 symposium was the exciting new work on the ultrastructure of the motile stages of malaria parasites initiated by Cyril Garnham at the LSHTM. Between 1960 and 1969 with Dick Bird, John Baker and others, Garnham published several unique papers, the first four of which preceded any others to be published on the subject. In the elongate sporozoites, merozoites and ookinetes, homologous structures were recognised - in particular an assembly of organelles converging on the anterior tip. This apical complex consisted of concentric apical rings from which the cortical palisade of microtubules originate, and rhoptries (paired organelles of Garnham) and micronemes, both of which with real foresight Garnham believed to be secretory and involved in cell penetration. Other constant features were a three-membraned (alveolate) pellicle and a mid-body "micropore" later shown to function as a cytostome in some stages. Similar structures were later found in motile stages of coccidians (including *Toxoplasma*), piroplasms and all other organisms now included in the Apicomplexa - Norman Levine's refinement of the old Class Sporozoa. Garnham's group eventually described all stages in the *Plasmodium* life-cycle, including exoerythrocytic forms, though ironically the hypnozoite (the dormant stage that permits *P. vivax* and *P. ovale* to span mosquito transmission seasons, see Chapter 6) was the only life-cycle stage he did not describe.

Mechanisms of entry of parasites into cells have attracted several British protozoologists. Entry of *Plasmodium* merozoites into red cells has been investigated by Laurence Bannister and Graham Mitchell (Guy's Hospital) with special reference

to parasite secretory events, by Geoffrey Pasvol (Oxford) in relation to the interaction of red cell receptors and merozoites and Iain Wilson and colleagues with respect to the redistribution of red cell surface proteins on merozoite entry. In the early 70s, Jim Alexander in Glasgow was among the first to demonstrate the dependency of *Leishmania* parasites on phagocytosis by the host macrophage and fusion of lysosomes with the parasitophorous vacuole in contrast to the finding of lack of such fusion in macrophage uptake by *Toxoplasma* as demonstrated by James Hirsch in the USA. Subsequent work by Alexander and David Russell (now in the USA) on the interrelationship of leishmania parasites and the host cell at the molecular level in relation to the host's cell-mediated immune response is among the finest recent explorations of host-parasite relations among protozoa.

The extraordinary mode of entry of microsporidians from their spores into the host cell via an extrusible filament along which the minute sporoplasm migrates is but one of the bizarre features of this group of minute parasites, which for over 40 years Elizabeth Canning [Fig. 77] at Imperial College has made her own and on which she is the recognised world authority. Their minute size (sometimes no bigger than 1mm!) and controversial apparent lack of eukaryote organelles makes electron microscopy essential for unravelling their life-cycles and relationship with the host cell. In the last half century they have been lumped in with Myxozoa (also studied by Canning) in a Class "Cnidosporidia", regarded as the most primitive of eukaryotes on early SSUmRNA sequence phylogenetic studies and finally on protein sequence studies expelled from the Protozoa and attached to the fungi. The Myxozoa have suffered a similar fate having been shown to be of metazoan origin. Despite these shocking exposures I am certain that both groups will continue to be studied by protozoologists.

Scanning electron microscopy

In 1970, the great French protozoologist E Fauré-Fremiet remarked to me that the scanning electron microscope has contributed nothing but pretty pictures to protozoology. That may have been true then, but since that time the pictures have become more informative. This is nowhere more true than in the case of the shelled protozoa. Colin Ogden and Ronald Hedley's *An Atlas of Freshwater Testate Amoebae*[4] (1980) opened up a new chapter in the identification of these organisms.

Previous British students of the testate amoebae include J.S. Dunkerly of Manchester University between the wars, and Bill Heal of the Institute of Terrestrial Ecology's Merlewood Research Station in the 60s to 80s; both studied in particular those of

[4] Published by the British Museum (Natural History) and Oxford University Press.

soil and *Sphagnum* moss. All these studies in large measure inspired Marjorie Hingley's *Microscopic Life* in *Sphagnum*[5] one of the few Naturalist's Handbooks aimed at Sixth Formers that deal with protozoa. Ogden's transmission EM studies of the mode of secretion of the shell in testates and Hedley's more detailed studies of shell structure and secretion in forminiferans were also quite unique contributions to protozoology. Wakefield and Hedley's exquisite reconstruction of the honeycomb membrane lining the shell of *Gromia oviformis* adorns the cover of this book.

Mystery life-cycle

The sudden expansion in protozoological studies included more than just electron microscopy, however. The great age of life cycle discoveries, to which Britain had contributed so much, lived on in the 1960s. One of its most spectacular achievements concerned one of human parasitology's long-standing enigmas - *Toxoplasma*. Despite its broad host range, both its life cycle and its relationship to other apicomplexans was unknown until William Hutchinson at Strathclyde University demonstrated that it was a coccidian parasite of cats undergoing the usual developmental cycle in their small intestine, culminating in production of oocysts which are passed in the faeces. Should these oocysts be ingested by a mouse they undergo asexual reproduction first rapidly in macrophages producing tachyzoites and later in the brain producing bradyzoites inside a "cyst." If the infected mouse is then ingested by a cat the bradyzoites initiate a new coccidian cycle. But if cat-derived oocysts are ingested by other mammals, including humans, an infection terminating in the production of cysts full of bradyzoites in the brain may result. This type of two host life cycle alternating between predator and prey was later shown to be widespread among other enigmatic apicomplexans - *Sarcocystis*, *Neospora* and so on. Hutchinson's dramatic discovery was rewarded with the prestigious Koch medal from Germany, but like many other epoch-making discoveries there were many others who claimed they had got there first and that Hutchinson had jumped the gun by taking advantage of the British Medical Journal's willingness to publish in a month what they consider really important. It was like Ross and Grassi all over again, but at least Ross only had the Italians to contend with!

Effect of host responses on parasitic protozoa

The 1960s showed a dramatic increase in interest in the host's acquired immune response to parasitic protozoa, correlating with rapid developments in our understanding of the immune system and cellular immunology in particular. In the

[5] Naturalist's Handbooks No.20. Richmond Publishing Co. 1994.

1970s many erstwhile parasitologists went over to the other side, so to speak, and became so engrossed in T cell subsets and cytokines they soon came to regard the parasite solely as a bundle of candidate vaccine antigens. Others retained an interest in the consequences of host responses for the parasite, immune evasion and parasite survival mechanisms. In the 60s and 70s, Frank Cox (King's College, London) was particularly interested in intercurrent infections of protozoan parasites and how manipulation of the host's immune response by one parasite could indirectly affect the other, for example by possession of cross-reacting antigens, by induction of immunodepression or by non-immune stimulation of the mononuclear phagocyte system.[6] Mouse oncogenic viruses, for example, could prolong infections of mice with *Babesia microti* as well as enhancing parasitaemia, thus increasing the chances of tick transmission of the piroplasm. Rickettsial infections on the other hand by inducing anaemia and reticulocytosis could reduce the number of circulating mature red cells preferred by *B. microti* and *P. chabaudi* and ameliorate parasitaemias accordingly. For *P. yoelii*, which prefers reticulocytes, the effect was the reverse.

The advent of the AIDS (human inmmunodeficiency virus) pandemic over the last twenty years of the century had a profound effect on protozoology. Novel protozoa such as *Enterocytozoon* were discovered in highly immunodepressed hosts and research on such protozoan parasites as *Cryptosporidium* and *Toxoplasma* which gave rise to florid infections in AIDS patients suddenly became more fundable. In particular a previously relatively obscure parasite *Pneumocystis carinii* was passed off as a protozoon and, it is rumoured, the *Journal of Protozoology* changed its name to the *Journal of Eukaryotic Microbiology* in order to accommodate it after phylogenetic analysis confirmed our suspicion that the miserable creature was a fungus. The bringing to the fore of opportunistic protozoan infections, however, did not have quite the impact in the UK that it did in the USA.

Protozoan Biochemistry

The other important aspect of the protozoological Renaissance was the growth of protozoan biochemistry. The extraordinary metabolic versatility of the bacteria compared with animal cells has long been known and protozoa have long been suspected of being somewhere in between, but the longstanding problem of cultivating protozoa *in vitro* has denied these organisms the investigation they deserve. The importance of many parasitic protozoa as causative agents of human or animal disease, however, has demanded curative or prophylactic drugs. Rational chemotherapy - treatment designed to block some metabolic pathway of the parasite while leaving

[6] See Cox F.E.G. (1975) Factors affecting infections of mammals with intraerythrocytic protozoa. Sym.Soc.Exp.Biol. No XXIX pp. 429-451.



Fig. 80 Group of protozoologists at First Congress of Protozoology, 1961. Left to right: Elizabeth Canning, Nonilla Adams, Frank Cox, Kieth Vickerman, Valerie Cox and Gordon Leedale.

the host unharmed - has since Ehrlich's time been the dream driving most research on protozoan metabolism in research institutes and universities if not in many pharmaceutical companies which prefer the old empirical approach.

Relatively few Universities have encouraged research on protozoan biochemistry - or very few biochemists have decided to commit themselves to protozoa! Notable and long-lived research groups developed: in the sixties in Aberdeen under Pat Grant, with an offshoot in Edinburgh under Ramsay Bowman (trypanosomes), in Cardiff under David Lloyd (phytoflagellates and anaerobes), in Kent under Win Gutteridge (*Plasmodium, Trypanosoma cruzi, Pneumocystis*) and at the Molteno Institute, Cambridge under Bruce Newton; in the seventies in Glasgow under Graham Coombs (*Leishmania*, anaerobes, coccidia) and later in Dundee under Michael Ferguson and Alan Fairlamb (trypanosomatids).

British workers have contributed substantially to our ideas on compartmentalisation of metabolic activities and in this energy metabolism has been to the fore. The work of Pat Grant on the glycerophosphate oxidase system of African trypanosomes at Aberdeen University in the early sixties has already been mentioned as playing an important part in development of the concept of the glycosome. The demonstration 1963 of the glyoxylate cycle in *Tetrahymena pyriformis* by J.F. Hogg and Sir Hans Kornberg (Leicester) was of great interest as it explained the synthesis of succinate from acetate, an essential step in the conversion of fat to carbohydrate in this ciliate, as well as in many phytoflagellates and plants. In addition, it also provided data on synthesis of key enzymes of the cycle in response to environmental stimuli and explained the need for these enzymes to be incorporated into an organised cellular structure - the glyoxysome - if they are to be functional. Falling oxygen tension coinciding with the waning of light and a reduction in photosynthesis by aquatic plant life stimulate the build-up of glycogen reserves to sustain the ciliate in the almost anaerobic environment prevailing during the night.

One of the great successes of co-operative work in the UK has been the research on anaerobic protozoa, especially in revealing the hydrogenosome as a modified mitochondrion.[7] Hydrogenosomes are unusual energy-generating organelles characterised by possession of hydrogenase and pyruvate-ferredoxin oxidoreductase. They appear to have evolved several times in different groups of organisms - trichomonads, some amoeboflagellates, chytrid fungi and at least three different ciliate groups. The last of these include free-living ciliates and rumen ciliates, both with methanogenic bacteria as endosymbionts that utilise hydrogen formed in the

[7] See Fenchel T & Finlay BJ (1995) Ecology and Evolution in anoxic worlds. Oxford: The university Press.

hydrogenosome to generate methane. The research groups of Bland Finlay (IFE, Windermere), Martin Embley (NHM), Alan Williams (Hannah Institute, Ayr) and those of Lloyd and Coombs have cooperated in this work. The UK has a long tradition of research on rumen ciliates extending back to the 1950s with contributions from Margaret Eadie (Rowett RI, Aberdeen), Brenda Nisbet (Aberdeen), G S Coleman (Babraham RI, Cambridge) and Alan Williams. The applied interest of this work revolves around the question are these ciliates true (mutualistic) symbionts or parasite, in other words would the host be better off "defaunated" and without them? Defaunation increases ruminant productivity and decreases methane production - the latter being no mean consideration in the face of global warming.[8]

A protozoan organelle or compartment quite different from the above is the megasome of *Leishmania mexicana* studied by Graham Coombs, Laurence Tetley and associates since the early 1980s in Glasgow. This prominent feature of the intracellular amastigote stage has been shown to contain multiple high activity cysteine proteases believed to play a key role in enabling the parasite to survive and multiply in the macrophage host cell. Such proteases have come under some scrutiny as potential drug targets in recent years.[9] Other targets for rational chemotherapy include the polyamine conjugate trypanothione which with the enzyme trypanothione reductase plays a pivotal role in the maintenance of the correct intracellular thiol redox potential in trypanosomatids. In addition, some of the antoxidant defences of these flagellates appear to depend on trypanothione. This unique system, which replaces the mammalian glutathione-glutathione reductase system, has been under study by Alan Fairlamb's group since the late 1980s.

Finally, of great importance to our conception of the host-parasite interface have been the studies on the surface of trypanosomatids that followed on from those made in the Molteno Institute in relation to antigenic variation (see Chapter 10). Michael Ferguson's studies in Dundee University on the different glycolipid-anchored glycoconjugates of not only *Trypanosoma brucei* but also *T. cruzi* and the leishmanias in different phases of the life cycle of these protozoa have added considerably to our understanding of their infectivity and their survival strategies. The reason for the extensive use of glycosylated phosphatidylinositols as membrane anchors in the protozoa while they are rare in "higher eukaryotes" (apologies to Clifford Dobell for use of this term) is still mystifying, however!

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[8] See Williams A.G. & Coleman G.S. (1991) The Rumen Protozoa. Springer Verlag.
[9] See Coombs, G.H. & North M.J. (1991) Biochemical Protozoology, London: Taylor and Francis.

CHAPTER 12

FULL CIRCLE: BIODIVERSITY AND PHYLOGENY

A major change in the biological sciences this century has been the realignment of loyalties on the part of biologists and this became reflected in the names of university departments, even in those of learned societies. Loyalties to the old vertical divisions of biology - Botany, Zoology and Microbiology have been replaced by loyalties to particular levels of investigation - molecular, cellular, organismal, population, all the way up to ecosystem. The great revival of protozoology in the 1960s was part of an explosion of interest in biology at the cellular level which moved on rapidly to the molecular level, as in journals the electron micrograph gave way to the gel.

Protozoology being essentially a vertical division would seem to be in danger of fragmentation - even disappearance. By the 1980s in Britain, the devotees of parasitic and free-living protozoa seemed to be going their separate ways, the parasitologists to the molecular end of the biological spectrum, the free-livers to the ecosystem end. The view of protozoa as whole organisms whose study might throw up novel systems for biologists to work on was receding. Yet at the end of the 20th century encouraging signs of re-unification and a wider appreciation of protozoa in biology were emerging: these signs can be summed up in two words - biodiversity and phylogeny.

Biodiversity

The enormous diversity of protozoa is part of their appeal for many who call themselves protozoologists but for those who do not it begets a feeling of being overwhelmed by names, in those trying to make a start even a feeling of despair. The appeal factor was evident among light microscopists in the Edwardian hey-day, but for much of this century zoology undergraduates have been told that protozoa are like the insects - you either do them in enough detail to make some sense or you leave them well alone. Most universities for want of expertise still ignore them, and most graduates in the biological sciences these days are barely aware of their existence

In the last decade of the 20th century, however, "biodiversity" became a buzz-word among biologists and among a conservation and environment-minded public - popularised by authors like Edward Wilson in such books as *The Diversity of Life* (1992) - which did actually mention protozoa. What does it mean? According to Ernst Mayr the question is better phrased as "how many species are there on earth and how did diversification into species occur?" As founder of the biological species concept, what Mayr is really asking is how many gene pools are there, for a species is essentially a gene pool. To the protozoologist the answer to this question is muddied

in the first place by the existence of sibling species such as those that make up the *Paramecium aurelia* and *Tetrahymena pyriformis* complexes in ciliates (Sonneborn's "syngens", later given species names). Members of either of these complexes have a common morphology (they belong to the same "morphospecies") but are separated by mating barriers. Even more significantly, the evidence for a sexual process involving mating is just not there for most protozoa; the widespread assumption is that they exist as clones in the wild. But for ecologists the morphospecies is a good starting point for looking at biodiversity, and on this basis alone further interesting questions are beginning to emerge. One concerns species richness in habitats, the other concerns species distribution.

An impression of enormous species richness in aquatic environments (to which protozoa are confined) prevails. This has been bolstered in recent years by the discovery that heterotrophic flagellates are highly important consumers of bacteria in aquatic ecosystems and that their diversity has been poorly explored. In soil, for example, there seems to be no end to novel flagellate genera, let alone species. Valiant attempts have been made to remedy this deficiency by David (Paddy) Patterson [Fig. 81, 84] and his students both before and after he left the UK for Sydney, Australia, but the number working in this field remains small. The work of Bland Finlay and colleagues at IFE, Windermere, presents a different picture for ciliates, however. All the indications for these readily-identifiable organisms are that species numbers all told are limited to about 3000, what is more their distribution would appear to be cosmopolitan. Biodiversity in this world of an infinite number of individuals widely spread is clearly going to have a different basis from that operating among animals and plants, and unless ecologists are prepared to settle for a one-sided view of the ecosystem they must agree that these questions have to be looked into. This situation in free-living protozoa contrasts strongly with that which prevails among parasites where, as we saw in the case of the rodent malarias, geographical distribution of the host imposes barriers that encourage allopatric speciation.

Developments in protocols for filtering, preserving and staining with fluorochromes the smallest components of the plankton (nano and picoplankton) have lead to an outpouring of freshwater and marine ecological studies pioneered by Johanna Laybourn-Parry (Nottingham University), Bland Finlay (Windermere), Ray Leakey (Dunstaffnage Laboratory), Helen Butler (British Antarctic Survey) and Michael Sleigh's group in Southampton.

Phylogeny

We started this century of protozoology with Haeckel's views on phylogeny dominating zoological thinking and it is interesting that 100 years later we appear



Fig. 81 David (Paddy) Patterson. Fig. 82 Tom Cavalier-Smith. Fig. 83 John Corliss.

to have come full circle, and returned to phylogenetic tree construction. But the new phylogeny is based upon measurable differences rather than intuitive guesswork and untestable hypotheses. The biometrician W.F.R. Weldon would have been pleased! When he succeeded Lankester at Oxford, he complained to his predecessor that neither his students nor his colleagues were in the slightest bit interested in quantifying variation which he believed was the next step forward in the study of evolution. Lankester responded by telling him not to bother with such things and return to describing interesting organisms for the delight of the faithful.

The return to an interest in phylogeny started in the 70s and 80s with the development of objective methods for phylogenetic inference and the availability of computer hardware and software that was up to the job of applying these new methods to new data from molecular biology. Especially important were the now readily available gene sequences which were believed to contain a record of the organism's evolutionary history. The landmark paper of M.L. Sogin, H.J. Elwood and J.H. Gunderson in 1986 on the "Evolutionary diversity of eukaryotic small subunit ribosomal RNA genes" based on nine protist species set the frame of the eukaryotic tree for years to come. The molecular diversity among protists was seen to be enormous, far exceeding that found between animals and green plants. Controversy is now rampant about the order of branching of the major protozoan groups and clearly there is much to be done to reconcile phylogenetic hypotheses based on protozoan ultrastructure with those based on molecular sequence comparisons.[1] Martin Embley at the NHM and

[1] See Coombs G.H., Vickerman K., Sleigh M.A. & Warren A. (eds) (1998) Evolutionary relationships among Protozoa. Dordrecht: Kluwer Academic Publishers.



Fig. 84 Paddy Patterson (drawing by Lawrence Bannister)

Tom Cavalier-Smith [Fig. 82], recently back in the UK at Oxford after several years in Canada, have contributed extensively to the debate. Cavalier-Smith has for many years been attempting to build a comprehensive picture of the history of eukaryotic cells and has now added to his objectives a comprehensive natural classification of the protists. He has made striking contributions to the recognition of novel phyla such as the Euglenozoa (uniting euglenids and kinetoplastids) and the Alveolata (uniting dinoflagellates, Apicomplexa and ciliates). His ideas have even led to the recognition of a new Kingdom of life - the Chromista - which even Ernst Mayr approves of. One of the most fascinating aspects of protist evolution to emerge from phylogenetic studies is the widespread genetic input of symbionts into the host's genome and not necessarily always in the context of organelle evolution. Another is the disparity in genetic diversity within a single protozoan genus compared with that in a genus of animals or plants. Cavalier Smith's finding that genetic diversity within the genus *Cercomonas* (several morphospecies of which occur in most soils) is greater than that within the green plants leaves one gasping!

So interest in protozoan phylogeny is running high as we pass into the new millennium. It is still important for protozoan phylogeny to be made accessible to

other biologists, however, and this can only be achieved if an intelligible systematic base is provided. Natural classifications are a fine ideal, but it may be some time before this goal is achieved for protozoa and just so that students can acquire some understanding of the diversity of protists a "user-friendly" classification similar to the one published in 1994 by John Corliss[2] [Fig. 83] that bear some relation to traditional textbook schemes may serve the subject better than attempts to impose overnight idiosyncratic novel classifications that will probably require revision before they are published anyway.

The internationalisation of effort in science (which was obvious in the last few decades of the 20th Century), and the break up of the United Kingdom (which now seems almost inevitable) will make another "Century of Protozoology in Britain" in the year 2100 unlikely. But there seems to be so much left to explore in Protozoology that surely the subject itself must continue beyond then.

[2] Corliss JO (1994) An interim utilitarian (user-friendly) hierarchical classification and characterization of the Protists. Acta Protozoologica 33: 1-51.v

PART 3

CHAPTER 13

INTERNATIONAL CONGRESSES AND THE INTERNATIONAL COMMISSION ON PROTOZOOLOGY

Planning for the First International Congress of Protozoology appears to have begun as early as 1958 (Corliss, 1998) as a joint initiative between the Czechoslovak Academy of Sciences and the Society of Protozoologists. However, the original idea was apparently conceived earlier. The period of cultural re-awakening and academic expansion following the 1939-45 war saw the formation of the Society of Protozoologists in the USA in 1947, and increases in contacts between protozoologists in other countries, many of whom were 'foreign' members of the Society. Among these were protozoologists in Eastern Europe, notably Professor Poljansky [Fig. 85] in Leningrad, Professor Raabe in Warsaw and Professor Jirovec in Prague, who saw the benefits gained from attendance at meetings by members of the Society, and began to think about creating opportunities for comparable meetings, preferably on an international scale. The initiative was taken by the Czechs, who sought the support of the Society of Protozoologists to plan a viable International Conference. An International Committee was set up comprised of three U.S. members, three Russians and 9 Czech protozoologists, under the chairmanship of Professor O. Jirovec. In the political climate of those days it was not easy to arrange meetings, and the Minutes of the Annual Business Meeting of the Society of Protozoologists for 1959 record that unsuccessful attempts had been made to bring Professor Poljansky and Professor Jirovec to that meeting. However, Dr J. Weiser, the Secretary of the Organising Committee for the Prague Congress, was able to visit the University of Illinois to discuss plans for the Congress with Drs Corliss and Levine, two U.S. members of the Committee, later that year. The planning came to a successful conclusion and the Congress took place in Prague from 22 to 31 August 1961. More than 200 participants from some 23 countries attended this Congress and 18 papers by authors from Britain were published, among others, in the volume of Proceedings (Ludvik *et al.*, 1963). At this Congress the British participants were asked if they would be willing to host the Second Congress in London in 1965, and Professor P.C.C. Garnham is understood to have accepted the challenge on behalf of British protozoologists.

Following discussions at the Annual Meeting of the Society of Protozoologists at Corvallis in August 1962, Professor Jirovec, acting on behalf of the members of the International Organising Committee for the First Congress, formally designated Professor Garnham as Chairman of the International Advisory Committee for the

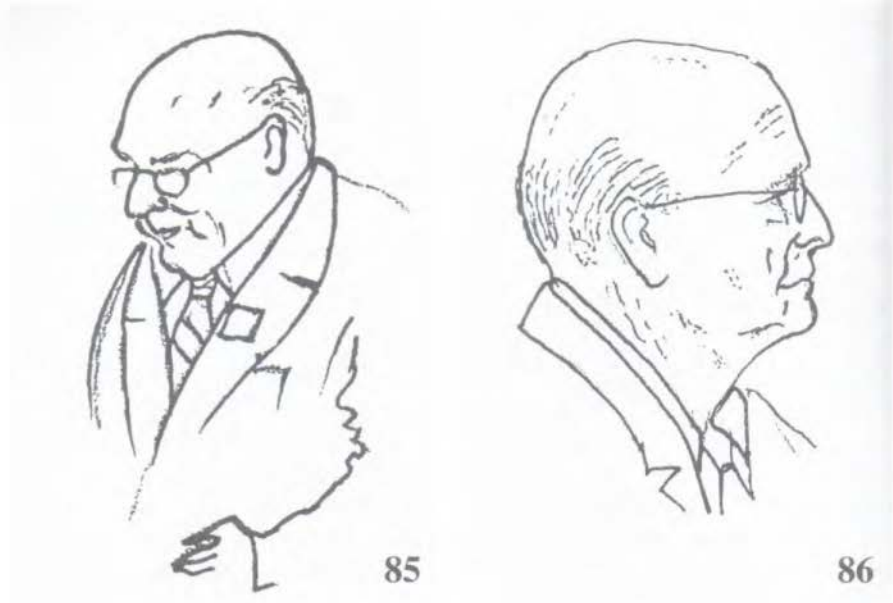


Fig. 85 G.U. Poljansky. Fig. 86 Cyril Garnham. (drawings by Lawrence Bannister).

Second International Conference. He was also empowered to appoint such members to this Committee as would be needed to carry this Conference to a successful conclusion, with due consideration for its international character. The new International Committee was drawn largely from that which planned the Prague Congress, with the addition of a second member from Britain and one from Germany. It is not clear why the title "Conference" was preferred to "Congress" in this instance – all subsequent meetings in the series have been called congresses.

The stimulus given to many protozoologists from Britain by their participation in this Congress (or the realisation of what they had missed), and the need to build a foundation upon which the organisation of the International Conference in London could be based, provided the impetus for the formation of the British Section of the Society of Protozoologists (BSSP) in October 1962, as described in Chapter 2. At the second meeting of the BSSP in April 1963 plans were made to form a National Committee to plan and organise the Second International Conference of Protozoology, due to be held in London in July-August 1965. This Committee commenced its planning at meetings under the chairmanship of Professor Garnham and elected Dr C.A. Hoare as Vice-Chairman, Dr R.S. Bray as Secretary and Dr A.J. Duggan as Treasurer. They were joined by the following other members of the National

Organising Committee:- Drs K.M.G. Adam, G.H. Beale, E.M. Brown, R.E. Burge, E.U. Canning, C.R. Curds, M.R. Droop [Fig. 92], O.W. Heal, R.H. Hedley, S.B. Kendall, R.A. Neal, J.F. Ryley, H. Sandon and K. Vickerman. Dr Bray was able to report at the third annual meeting of the BSSP in March 1964 that arrangements for the London Conference were proceeding satisfactorily, and this was subsequently proved by the abundance of scientific interchange and smooth running of the Conference itself.

The Conference was centred at Imperial College in South Kensington, and used the meeting hall of the Royal Geographical Society for its principal sessions, with parallel sessions in lecture rooms of the Imperial College Physics Department, and with simultaneous translation between English, French and Russian. H.R.H. the Duke of Edinburgh accepted the position of Patron of the Conference, and Professor Emmanuel Fauré-Fremiet [Fig. 87], the father figure of 20th Century ciliatology in Europe, the position of Honorary President of the Conference. The Organising Committee put together a programme in 30 sessions covering a full range of topics on parasitic and free-living Protozoa, plus 5 film sessions. The Programme lists a total of 386 contributions by speakers from 38 countries, British protozoologists being responsible for 54 of these contributions. A Publications Sub-Committee, led by Dr R.A. Neal, prepared a Conference Book (Anon, 1965) containing 357abstracts of papers and 7 abstracts describing films accepted for presentation at the Conference. A copy of this book was given to each participant at Registration, and there was no other publication of the Conference. A Social Sub-Committee, led by Dr E.U. Canning, arranged an extensive programme, including a Reception by the Minister of State for Education and Science, Lord Bowden, the possibility to attend a Promenade Conference at the Albert Hall, a Conference Dinner at the Zoological Society's Gardens, an evening river trip by steamer from Hammersmith to Westminster (with dancing to a band on board), and a Reception by the Vice-Chancellor of the University of London at Senate House. Accompanying ladies were invited to join (on different days) coach tours of London, the City and Tower of London, Hampton Court and Windsor Castle, a fashion show by Norman Hartnell, a steamer trip to Greenwich, and a visit to London Silver Vaults. The Conference was underpinned by the work of a Finance Sub-Committee, led by Dr A.J. Duggan, which secured sponsorship from some 25 organisations to assist in meeting the expenses of organisation, and which was able to leave a modest surplus of funds for use in later protozoological meetings.

The Resolutions Committee of the Society of Protozoologists, meeting at the end of the Conference, warmly commended the efforts of the organisers of the Conference, and passed the following resolution:

"That the Resolutions Committee, being aware of the great expenditure of energy by



Fig. 87 Emmanuel Fauré-Fremiet.

all who helped make this 2nd Conference a success in William Shakespeare's country, suggests that these resolutions be concluded with the following excerpt from Shakespeare's **The Tempest**

> *You sunburned sicklemen, of August weary,*
> *Come hither from the furrow, and be merry:*
> *Make holiday;*"

Meanwhile, discussions were proceeding about ways in which international interests and activities of protozoologists might best be sustained and advanced. A proposal received from the Groupement des Protistologues de Langue Française for the formation of an International Union of Protistologists had been discussed at the third meeting of the BSSP in March 1964. It appeared that this would require the formation of independent national societies of protozoologists, which would then associate to form the International Union. At the suggestion of Dr Bray, it was agreed that, although the BSSP looked favourably on the idea of the formation of an international body, formal discussion should be delayed until the Second International Conference, when there could be full consideration in the presence of representatives of many countries. However, by the time of the fourth meeting of the BSSP in April 1965, it was clear that further thought had been given to the question of international co-ordination. Professor Garnham, the Chairman, explained that he thought that it would be valuable to have an International Committee whose responsibilities would include the organisation of International Conferences (=Congresses) and investigation of potential problems such as type collections and classification, and which could relate to such international bodies as the International Union of Biological Sciences

(IUBS). Dr Bray had prepared the following proposals concerning such an International Committee, which, he suggested, might be discussed at the Second International Conference.

An International Committee is required for the following purposes:

1. To consider matters referred to it by the International Conferences.
2. To consider matters referred to it by its constituent societies or groups.
3. To consider matters of international significance, e.g. the Biological Year, relations with IUBS, UNESCO, etc.
4. To produce an internationally agreed system of classification of the Protozoa.
5. To co-operate with National Organising Committees in planning International Conferences and act as bankers in the interim between International Conferences for any funds available to International Conferences.
6. To maintain an international register of and encourage centres for types and the preservation of strains.

Specifically excluded were:

a. Suggestion of an International Society
b. Responsibility for a Journal
c. Fees of any sort.

It is also proposed that such an International Committee of Protozoologists should have the following composition:

1. Two representatives from any properly constituted society or group of protozoologists or protistologists with an international membership, to serve in the interim between International Conferences.
2. One representative from any properly constituted society group or section of protozoologists or protistologists with a purely national membership, to serve in the interim between International Conferences.
3. The President and Secretary of the immediate past and immediate future International Conferences of Protozoology.

The President and Secretary of the International Committee to be the President and Secretary of the immediate future International Conference of Protozoology.

Members of the BSSP were generally in favour of these proposals. They recognised the need for an International Committee, of different character from the Society of Protozoologists, but which accepted Sections of that Society as representing national

groups of protozoologists. Members of the BSSP were happy with the implication that the Section should continue in its present form as a Section of the Society of Protozoologists, accepting and encouraging the international character of the parent Society, and should not set itself up as an independent society.

The proposals were carried forward for discussion by national representatives during the Second International Conference in London, including discussions at an open meeting held on Saturday 31st July 1965. As a result the following resolution was presented at the end of the Conference on 5 August 1965.

*FORMATION OF AN INTERNATIONAL COMMISSION ON PROTOZOOLOGY**

Footnote * In the broadest sense; e.g., the autosynthetic flagellates are included

Recognising the practical need for the formation of a supra-national body for uniting the different groups of protozoologists of all countries in the world, the undersigned wish to present the following resolutions for adoption by the 2nd International Conference on Protozoology:-

1. *That an INTERNATIONAL COMMISSION ON PROTOZOOLOGY be formed before 1 January 1966 and that its membership meet annually, if possible, or at least once between International Conferences.*
2. *That such a COMMISSION work toward realisation of the following four objectives:-*
   a. *To be active in planning future International Conferences: to decide on sites and dates; to collaborate with National Organising Committees at the appropriate time; to act as banker, for any funds available, in the interim between Conferences; and to fulfil any other obligations related to such Conferences.*
   b. *To study the question of the creation of an International Union, to draft the constitution for such an organisation, and to present it to all groups for definitive decision before the 3rd International Conference on Protozoology.*
   c. *To explore means of establishing close relationships with international biological or other organisations, such as IUBS, FAO, UNESCO, and WHO. To promote, encourage, and maintain co-operation among protozoologists of all countries by serving as a clearing house – probably by establishment of a number of special committees generally chaired by a member of the COMMISSION – for consideration of important matters of an international nature: such as worldwide register of protozoologists and of type-specimen and culture collections; study of the feasibility of centrally located*

bibliographic files and specimen-identification centres; endorsement of worldwide protozoological abstracting services; promotion of revisions, as needed, of systems of classification of Protozoa; strengthening the role of protozoology and the participation of protozoologists in the International Biological Programme.

3. *That the composition of the COMMISSION be as follows:-*
   a. *One representative from each duly constituted society, group, section or "associated society" of protozoologists which has a membership of 21-100 persons.*
   b. *Two representatives from any group with a membership between 100 and 500; and three representatives from any group with a greater number.*
   c. *The President and Secretary of the immediate past International Conference on Protozoology, as the representatives of their society; and the President and Secretary of the immediate future Conference. The President and Secretary of the immediate future Conference shall serve as President and Secretary of the COMMISSION, as soon as their identity is known.*

T.H. Abe, J.O. Corliss, P.C.C. Garnham, K.G. Grell, G.I. Poljansky, P. de Puytorac, Z. Raabe, B.R. Sesachar, J. Weiser, A. Zuckerman.

The essence of this resolution appears to have been adopted, and an International Commission on Protozoology was formed with the following membership:-

Belgium – J. Jadin; Czechoslovakia – O. Jirovec, J. Weiser; Denmark – E. Zeuthen; France – P.-P. Grasse, P. de Puytorac; Germany - K.G. Grell; India – B.R. Sesachar; Israel – A. Zuckerman; Italy – T. Crippa-Franchesci; Japan – S. Inoki; Poland – Z. Raabe; U.K. - P.C.C. Garnham, R.S. Bray; U.S.A. – B.M. Honigberg, R.W. Hull, R.F. Nigrelli; U.S.S.R. – G.I. Poljansky, I.B. Raikov. The final meeting of the London Conference also agreed that the Third International Conference should be held in Leningrad, in the U.S.S.R. in 1969. The International Commission met in Leningrad in July 1967 with the Soviet National Organising Committee for the 1969 Congress in order to discuss plans for the Leningrad Congress.

An International Commission on Protozoology has been in existence since that time, and became affiliated to the International Union of Biological Sciences, within the Zoological Section of that body, in 1967. The Commission appears to have settled down to a pattern of three meetings every four years: an interim meeting with the local organising committee approximately midway between congresses, to consider plans for the timing and tentative programme for the next congress, one meeting near the start of each congress and another meeting near the end of each congress. The venue for the subsequent congress would be decided by majority vote at the

second meeting of each congress. A later paper on the Constitution of the Commission gave its aims as follows:- to promote the exchange of ideas among protozoologists throughout the world and aid in arranging periodic International Congresses of Protozoology. Other possible functions of the Commission discussed at its inception appear not to have developed. It seems likely that the problem of how to cover costs may have prevented this body from taking on wider functions. Certainly the principal duty of ensuring the continuity of Congresses has been faithfully followed through, and Congresses have been held every four years under the auspices of the Commission, at the following cities (from the first):-

I	Prague, Czechoslovakia, 22 – 31 August, 1961
II	London, United Kingdom, 29 July – 5 August, 1965
III	Leningrad, U.S.S.R., 2 – 10 July, 1969
IV	Clermont-Ferrand, France, 2 – 10 September, 1973
V	New York, U.S.A., 26 June – 2 July, 1977
VI	Warsaw, Poland, 5 – 11 June, 1981
VII	Nairobi, Kenya, 22 – 29 June, 1985
VIII	Tsukuba, Japan, 10 – 17 July, 1989
IX	Berlin, Germany, 25 July – 1 August, 1993
X	Sydney, Australia, 21 – 25 July, 1997
XI	Jerusalem, Israel, planned for 22 – 27 July, 2001

Delegates from the BSSP were actively involved in all of these Congresses, although few members from academic institutions were able to attend the Nairobi meeting after the late change in date from September to late June, which coincided with the hectic period of degree examination marking at UK universities. Senior members of the BSSP regularly sought block funding, usually from the Royal Society and the Wellcome Trust, to support the travel costs of members to attend the Congresses.

Membership of the International Commission on Protozoology evolved somewhat, in that two categories of membership became recognised: Honorary and Regular members. The Presiding Official of a past Congress could be elected as an Honorary Member if nominated by their national organisation. Regular members are appointed by their national organisation, one from groups with 20 to 99 members, 2 from groups with 100 to 199 members and 3 from larger groups; groups with less than 20can send a non-voting observer. When an Honorary member is also a regular member representing his group he shall have a vote; otherwise he has no vote and does not count against the entitlement of regular representatives from his group. The first British members of the Commission were, as noted above, Professor P.C.C. Garnham and Dr R.S. Bray. At the Leningrad Congress in 1969, Dr B.A. Newton replaced Dr Bray. After an enquiry from the membership of the BSSP in 1983, it



Fig. 88 A group of Protozoologists. Left to right; John Corliss, Harold Sandon, Emmanuel Fauré-Fremiet, Michael Pittam, Muriel Robertson, Keith Vickerman, Bill Heal and *kneeling* Jacques Berger.

was established from Professor Garnham that he understood that he was a life-time member of the Commission, as were the presiding officials of the other congresses held to that date. Dr Newton stated that he had no information on the normal term of office of members and would be happy to stand down – ideally after the Nairobi Congress, in whose planning he had so far represented the U.K.. In 1985 the BSSP elected Professor K. Vickerman to be its second (nominated) regular member. Although Professor Garnham died in 1994, it appears that he was not replaced by a regular member until after Dr Vickerman resigned his membership in 1997. The two new regular members of the Commission elected by the BSSP in April 1997 were Professor J. Laybourn-Parry and Professor G. Coombs, who are the present U.K. representatives.

CHAPTER 14

ORIGINS AND FORMATION OF THE BRITISH SECTION OF THE SOCIETY OF PROTOZOOLOGISTS

The following hand-written statement appears at the start of the Minute Book of the Section, and illustrates how the enthusiasm of British protozoologists to create a national group was translated into action following the First International Congress in Prague. This and some other early papers will be of particular historical interest to members who joined the Section later, and therefore they are reproduced in full.

Historical Introduction

Following discussion at the First International Conference of Protozoologists, Prague, 1961, on the formation of Sections of the Society of Protozoologists, the Constitution and By-laws of the Society were amended at the next meeting of the Society, held at Denver, Colorado, December 1961.

The amendment allowed for a new class of members, to be known as Corresponding Member, for persons resident outside North America.

In February, 1962, a circular letter and questionnaire was sent to some 150 people in Britain. The response to the questionnaire was so encouraging, that 25 protozoologists, who were attending the meeting of the Parasitology Group of The Institute of Biology at Cambridge in April 1962, met and agreed to establish a British Section of the Society of Protozoologists.

It was agreed that Mrs K.M.G. Adam, Edinburgh University, Dr R.J. Cole, King's College London and Dr K Vickerman, University College London should form a temporary administrative committee to organize the first meeting of the British Section, to be held in London in October, 1962.

It is a pleasure to record gratitude to Dr John O. Corliss, of the University of Illinois, Urbana, who was visiting lecturer at Exeter University during the Session 1961-62, and whose energy and enthusiasm gave impetus to the formation of a British Section. [Figs. 89 and 90 illustrate Kay Adam and John Corliss respectively].

The circular letter referred to was prepared by Mrs Kay Adam [Fig. 89], and is reproduced here [Fig. 92] to show the extremely careful way in which the wording has been prepared; a copy of the list of the prospective members to which it was sent is also added [Fig. 93].



Fig. 89 Kay Adam. Fig. 90 John Corliss. Fig. 91 Michael Droop.

The response of those who promptly answered this circular was positive and particularly strongly encouraged the holding of a full meeting in London in the autumn of 1962 (see the report on the questionnaire [Fig. 94]). It also provided a basis for the discussion at Cambridge on 4 April 1962, at which the largely parasitological group referred to above selected a temporary administrative committee to organise the first meeting in London in the following October. For interest, the page of signatures of the group that met in Cambridge is copied here [Fig. 95]. Incidentally, the meeting at Cambridge at which these protozoologists met was also the meeting at which the British Society for Parasitology was formed.

In preparation for the first meeting Mrs Kay Adam circulated the following paper [Fig. 96] outlining proposals for the administrative organisation and functioning of the Section, which again is admirably succinct, yet comprehensive.

The First Meeting of the BSSP duly took place at University College London on Saturday 20th October 1962. The programme of that foundation meeting is reproduced here [Fig 97]. It is recorded that at least 54 people attended.

From the historical point of view, the conclusions of discussions at the business meeting are the most important part of that first meeting of the Section. The following are the principal outcomes of that meeting.

The recommendation that the British Section be administered by a committee of six members, President, Secretary, Treasurer and three ordinary members, the President,

Dear Colleague,

At the 1st International Conference on Protozoology held in Prague in August, 1961, the question of the formation and exact constitution of Sections of the Society of Protozoologists was discussed in detail. In the recent annual meetings of the Society in Denver, Colorado, the matter was voted upon officially; the important points settled will be discussed below. It appears that there are some 100 persons in Britain with protozoological interests; of these about 35 are already full members of the Society of Protozoologists. It seems, therefore, that the best way to provide an opportunity for protozoologists in Britain to meet would be to form a British Section of the Society.

There has long been a provision in the Constitution of the Society of Protozoologists permitting formation of a Section by "a group of not less than ten members.....[who may] hold local meetings for the presentation of scientific papers,.....elect their own officers," etc. These persons, however, had to be "regular" members of the Society, i.e., had to be paying their $12.00 per year dues. The amendments to both the Constitution and the Bye-Laws recently passed at the Denver meetings are very important because they recognize a new class of membership, persons to be known as "Corresponding Members", whose dues will be only $1.00 a year [= ca. 7/-] but who will have all the rights and privileges of regular membership except for receiving only the annual Supplement to the Journal, not the entire Journal itself. Sectional members, then, need be only Corresponding Members, if they are willing to forsake subscription to the Journal of Protozoology. Every Section having over 20 members may elect a "voting Section Representative" to the Society's Executive Committee. If the Section desires to have Abstracts of papers presented at its own "local" annual meetings, these will be acceptable for publication, without cost to the Section, in the regular Supplement to the Journal.

The value, to the parent Society, of Sections in countries outside North America is to have an increased membership of interested persons, whether "regular" or "corresponding". The value to any Section itself is to aid in bringing together persons interested in the diverse fields of protozoology at a cost which is not prohibitive. Also an opportunity for annual meetings, in order to exchange ideas, present papers, etc., is a stimulating one. Furthermore, the Supplement would then offer an outlet for publication of "local" abstracts, if it is decided to take advantage of such an opportunity. All members of the Section, whether paying $1.00 or $12.00 dues to the Treasurer of the parent Society, would have equal rights in voting for Society offices, being elected to them, etc. In view of/

Fig. 92. Letter from Kay Adam inviting prospective members to complete and return questionnaire.

of the fact that the Prague Congress passed a Resolution to hold the 2nd International Conference in England in about 1965, it may be particularly fitting that an active British Section of the Society of Protozoologists be well organized long before that date.

The foregoing explanatory paragraphs seemed advisable. But the primary purpose of the Circular Letter is to enquire as to your own support and interest in formation of such a Section as that described above. Incidentally, the list for circulation of this letter is appended. If you know of others who might be interested in receiving a copy, would you please let me know?

Although the month of April is not distant, it seems possible that an informal initial "organisational meeting" might well be held in Cambridge during the forthcoming meetings of the Parasitology Group, of which many of you are members. Perhaps it should be emphasized that the protozoological Section, if formed, should not be considered either to replace the Parasitology Group in any way or manner or to overlap its activities. Many aspects of protozoology are not parasitological, of course, and there is no existing organisation which permits such persons to come together independently. The two organisations would be harmoniously complementary in their work and outlook.

Your comments are warmly solicited. And would you please tear off and return the short "Questionnaire" at the bottom of this page?

(Mrs.) K.M.G. Adam,
Department of Zoology,
The University of Edinburgh,
West Mains Road,
EDINBURGH, 9.

February, 1962.

---

(1) Are you in favour of the proposal to form a British Section of the Society of Protozoologists?

YES ☐
NO ☐

(2) If so, would you favour annual meetings, the first full one to convene probably sometime next Autumn?

YES ☐
NO ☐

(3) Are you in favour of a preliminary "organisation meeting" to take place in Cambridge, 3-5 April?

YES ☐
NO ☐

SIGNATURE _____

ADAM, Katherine M.G., Zool. Dept., Edinburgh
ADAMS, M. Ninnila, Bot. Dept., Edinburgh
ALEXANDER, J.B., Biophysics Dept., King's Coll.
ALLEN, M. Ann, Belvedere School, Liverpool
AUGUSTIN, Rose, Liverpool School Tropical Medicine

BAKER, J.R., London School Tropical Medicine
BALLANTINE, Dorothy, Bot. Dept., Bangor
BEALE, G.H., Inst. Animal Genetics, Edinburgh
BEVERLEY, J.K.A., Microbiol. Dept., Sheffield
BIRD, R.G., London School Tropical Medicine
BISHOP, Ann, Molteno Inst., Cambridge.
BLACKLER, M.C.H., Bot. Dept., St. Andrews
BROOK, A.J., Bot. Dept., Edinburgh
BROWN, Eleanor M., Chelsea Coll., London
BROWN, K.N., Nat. Inst. Medical Research, Mill Hill
BURROWS, E.M., Bot. Dept., Liverpool

CANNING, Elizabeth U., Imperial Coll.
CLARKSON, M.J., Liverpool School Tropical Medicine
COLE, R.J., Zool. Dept., King's Coll.
COLEMAN, G.S., Inst. Animal Physiol., Babraham
COWEY, J.B., Zool. Dept., Glasgow
COX, F.E.G., Zool. Dept., King's Coll.

DANIELLI, J.F., Zool. Dept., King's Coll.
DAISLEY, K.W., Nat. Inst. Research in Dairying, Reading
DAVIES, S.F.M., Vet. Lab., Weybridge.
DEE, Jennifer, Zool. Dept., Univ. Coll.
DENYER, H.W., Chertsey, Surrey
DODGE, J.D., Bot. Dept., Birkbeck Coll.
DROOP, M.R., Marine Station, Millport

EADIE, J. Margaret, Rowett Research Inst., Aberdeen
EVANS, J.H., Bot. Dept., Royal Holloway Coll.

FOGG, G.E., Bot. Dept., Westfield Coll.
FREI, E., Bot. Dept., Leeds
FULTON, J.D., Nat. Inst. Medical Research, Mill Hill

GARNHAM, P.C.C., London School Tropical Medicine
GEORGE, E.A., Bot. Dept., Cambridge
GHOSH, T., Zool. Dept., King's Coll.
GOLDACRE, R.J., Chester Beatty Res. Inst.
GOODWIN, L.G., Wellcome Lab. Tropical Medicine
GRANT, P.T., Biochem. Dept., Aberdeen
GRIMSTONE, A.V., Zool. Dept., Cambridge
GUTHRIE, M.G., Zool. Dept., Leicester

HARDY, A.C., Zool. Dept., Oxford
HARRIS, Katherine, Bot. Dept., Reading
HAWES, R.S.J., Zool. Dept., Exeter
HAWKING, F., Nat. Inst. Medical Research, Mill Hill
HAWKINS, S.E., Zool. Dept., King's Coll.
HAYES, A., I.C.I., Macclesfield
HAYES, Catherine, Notre Dame Coll., Glasgow
HEAL, O.W., Nature Conservancy, Merlewood
HEDLEY, R.H., British Museum
HENTSCHEL, C.C., Chelsea Coll.
HERBERT, I.V., Agric. Zool., Bangor
HILL, J., May & Baker, Dagenham
HOARE, C.A., Wellcome Lab. Tropical Medicine
HOPKINS, J.M., Biophysics Dept., King's Coll.
HORTON-SMITH, C., Houghton Poultry Res. Station

IND, M.O., Agric. Zool., Bangor

JANE, F.W., Bot. Dept., Royal Holloway Coll.
JARUMILINTA, R., Liverpool School Tropical Medicine
JEPPS/

Fig. 93. List of names to whom Kay Adam's questionnaire was sent.

JEPPS, Margaret W., Zool. Dept., Cambridge
JOYNER, L.P., Vet. Lab., Weybridge

KABATA, Z., Marine Lab., Aberdeen
KAIN, J.M., Marine Station, Port Erin
KEILIN, D., Molteno Inst., Cambridge
KENDALL, S.B., Vet. Lab., Weybridge
KERKUT, G.A., Biochem. Dept., Southampton
KITCHING, J.A., Zool. Dept., Bristol

LACY, D., Zool. Dept., St. Bartholomew's Coll.
LEEDALE, G.F., Bot. Dept., Leeds
LEITCH, I., Rowett Res. Inst., Aberdeen
LONG, P.L., Houghton Poultry Res. Station

MANNERS, D.J., Chem. Dept., Edinburgh
McCONNACHIE, E.W., Molteno Inst., Cambridge
McFADZEAN, J.A., May & Baker, Dagenham
MARTIN, M., Bot. Dept., Bangor
MERCER, E.H., Chester Beatty Res. Inst.
MILES, H.B., Zool. Dept., Hull
MILLER, J.K., Liverpool School Tropical Medicine

NEAL, R.A., Wellcome Lab. Tropical Medicine
NEWTON, B.A., Biochem. Dept., Cambridge

ORMEROD, W.E., London School Tropical Medicine

PARKE, Mary, Marine Station, Plymouth
PICKEN, L.E.R., Zool. Dept., Cambridge
PITTAM, M.D., Lister Inst.
PIERCE, A.E., Inst. Animal Physiol., Babraham
PERCIVAL, E.E., Chem. Dept., Edinburgh
PORTER, Annie, Zool. Soc., London
POTTAGE, R.H., Gatty Marine Lab., St. Andrews
PRINGLE, C.R., Zool. Dept., Aberdeen

RANDALL, J.T., Biophysics Dept., King's Coll.
RIDDLE, J., Zool. Dept., Bristol
ROBERTSON, D.H.H., Tororo, Uganda
ROBERTSON, Muriel, Lister Inst.
ROSE, M. Elaine, Vet. School, Cambridge
ROSEN, G.D., Pfizer Ltd., Folkestone
RUSSELL, G., Marine Station, Port Erin
RYLEY, J.F., I.C.I., Macclesfield

SANDON, H., London
SHAFFER, B.M., Zool. Dept., Cambridge
SLEIGH, M., Zool. Dept., Exeter
SMITH, Katherine, Bact. Dept., Edinburgh
SOLTYS, M.A., Vet. School, Cambridge
SPENCER, C.P., Marine Biol. Dept., Bangor
STREET, H.G., Bot. Dept., Swansea
SUGDEN, Brenda, Aberdeen

TATE, P., Molteno Inst., Cambridge
TAYLOR, Monica, Notre Dame Coll., Glasgow
TURNBULL, L.P., Bot. Dept., Bedford Coll.

VICKERMAN, K., Zool. Dept., Univ. Coll.

WATSON, M., Biophysics Dept., King's Coll.
WALKER, P.J., Nat. Inst. Medical Research, Mill Hill
WEITZ, B., Lister Inst.

Department of Zoology,
University of Edinburgh,
West Mains Road,
Edinburgh, 9.

6th March, 1962.

Dear Dr. Sleigh

Questionnaire on the formation of a British Section of the Society of Protozoologists.

The response was as follows:

Questionnaires sent	In favour of British Section	Against	No replies to date	In favour of Autumn meeting in London
142	62	10*	70	61

Guide to the interests of those in favour:

Parasitologists	Protozoologists	Phycologists	Others	Total
18	21	7	16	62

The results of the questionnaire would seem to justify further action, namely, that steps be taken to organize a meeting in London before the end of the year. I hope that this suggestion may meet with your approval. Comments would be helpful.

Owing to the very full programme of the forthcoming meeting of Parasitologists at Cambridge, it will not be possible to arrange a special meeting of Protozoologists a this time. Nevertheless, it is hoped that there will be informal discussion.

K.M.G. Adam (Mrs.)

*6 of these were in favour, but unable to join because of other commitments.

Fig. 94. Results of the questionnaire.

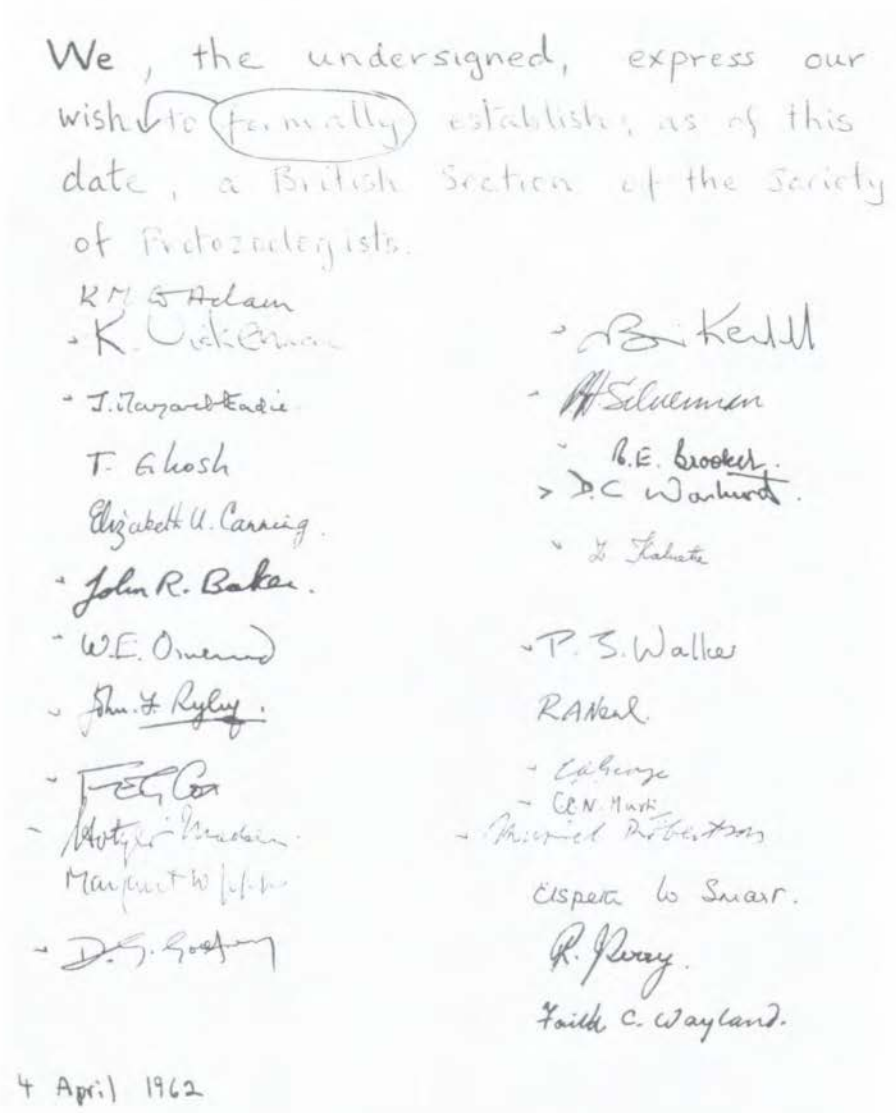


Fig. 95. Signatures of protozoologists who agreed to call the first meeting of the BSSP.

British Section of the Society of Protozoologists

Matters to be discussed at the first meeting of the Section, 20th Oct.

The Section shall be administered by a committee of six members, President, Secretary, Treasurer and three ordinary members, all to hold office for a period of 3 years. The President, Secretary and Treasurer along with one ordinary member to be elected on succeeding years.

The President shall be, automatically, the representative of the Section on the executive committee of the Society of Protozoologists.

The aim of the Section is to provide opportunity for all those in Britain with protistological interests to meet annually for the purpose of presenting papers and demonstrations and for discussion.

Full members and corresponding members shall pay their annual subscriptions to the Treasurer, who shall transfer the dues in a lump sum to the U.S. Treasurer, retaining an agreed proportion for the expenses of the Section.

The Secretary shall be responsible for keeping an up-to-date list of members and their addresses and submitting these to the U.S. Secretary. The Section Secretary shall receive general information from the U.S. Secretary and shall keep Section members informed either at the annual meeting or by circular, if need be.

Minutes of the Section meetings and abstracts of the communications presented at the meetings of the British Section will be published in the Supplement to the Journal of Protozoology. Each member may submit one abstract only of not more than 350 words, including title and references. For publication in the current issue, abstracts must be in the hands of the U.S. Secretary not later than 1st May of each year.

The British Section should work in co-operation with the following Societies: Soc. of general Microbiology, British Soc. for Parasitology. British Phycological Soc., Soc. for experimental Biology, Soc. for comparative Physiology, Royal Microscopical Society.

Joint meetings or meetings in conjunction with the above societies should be considered.

Meetings should be held at different, but appropriate, centres.

One feature of meetings should be demonstrations of techniques, particularly of culture techniques.

To be arranged:

Time and place of next meeting.
Election of Officers.

Fig. 96. Proposals for the agenda of the first business meeting of the BSSP.

PROGRAMME FOR THE FIRST MEETING OF THE BRITISH SECTION OF THE SOCIETY OF PROTOZOOLOGISTS.

To be held at the Zoology Department, University College London on Saturday 20th October, 1962.

10 a.m. HEAL, O.W., Nature Conservancy, Merlewood Research Station.
"Morphological variation in Testacea".

GHOSH, T., Dept. of Zoology, King's College.
"Biology of Entamoeba".

GRANT, P.T., Dept. of Biological Chemistry, Aberdeen.
"The effects of iodacetate, arsenite and melarsen oxide on the metabolism of a cell-free preparation of Trypanosoma rhodesiense".

11 a.m. Coffee.

11.20 a.m. MANNERS, D.J. & RYLEY, J.F., Dept. of Chemistry, Edinburgh and Imperial Chomical Industries, Macclesfield.
"Protozoal polysaccharides".

GIBSON, I., Institute of Animal Genetics, Edinburgh.
"Gene action and cytoplasmic particles in Paramecium aurelia".

12 p.m. WARHURST, D.C., Dept. of Zoology, Leicester.
"The biology of Endolimax blattae, Lucas, an endocommensal of the cockroach".

GEAORGE, E.A., The Botany School, Cambridge.
"The Cambridge collection of algae and protozoa".

ELKAN, E., Watford Pregnancy Diagnostic Centre.
"A Dermocystidium in sticklebacks (Gasterosteus aculeatus L) from Surrey".

2.15 p.m. HAWKINS, Shirley E. & COLE, R.J., Dept. of Zoology, King's College.
"Some preliminary studies on the basis of cytoplasmic inheritance in amoebae".

O'NEILL, C., Dept. of Zoology, King's College.
"The cell membrane of Amoeba proteus".

SLEIGH, M.A., Dept. of Zoology, Exeter.
"Preliminary observations on the evolution of ciliary metachronism in ciliated protozoa".

3.15 p.m. Business meeting.

4 p.m. Tea

Fig. 97. Programme of the first scientific meeting of the BSSP.

Secretary and Treasurer, along with one ordinary member, to be elected in succeeding years, was accepted. The following nominations were approved:

Office	*Elected person*	*Proposer*	*Seconder*
President	Professor P.C.C. Garnham	R.S.J. Hawes	E.U. Canning
Secretary	Mrs K.M.G. Adam	P.C.C. Garnham	E.U. Canning
Treasurer	Dr K. Vickerman	F.E.G. Cox	S.E. Hawkins
Committee Members	Dr M.R. Droop	M. Parke	M.N. Adams
	Dr J.A. Kitching	K.M.G. Adam	K. Vickerman
	Dr H. Sandon	O.W. Heal	M.W. Jepps

For illustrations of founder and early members see: Kay Adam, Fig. 89; Nonilla Adams, Fig. 80; Bill Bray, Fig. 41; Elizabeth Canning, Fig. 77; Frank Cox, Fig. 65; Michael Droop, Fig. 91; Cyril Garnham, Fig. 40; Jack Kitching, Fig. 61; Margaret Jepps, Fig. 27; Mary Parke, Fig. 71; Harold Sandon, Fig. 53; Keith Vickerman, Fig. 64. Also John Corliss, Fig. 90.

It was agreed that the Easter vacation would be the most suitable time to hold the annual meeting of the BSSP, and that the Second Meeting should be held in London in April 1963. Future meetings of the BSSP might be arranged to fit in with meetings of other Societies, in particular, the British Society for Parasitology (BSP) and the Society for General Microbiology (SGM). The hope was expressed that consideration be given to holding some meetings outside London. The suggestion that abstracts of communications might be pre-circulated to Section members was not accepted.

The following rates of subscription, due annually on 1st January, were set:
Full member - £4.10s; Student member - £2.10s; Corresponding member - 10s.

These classes of membership were defined in the Constitution of the Society of Protozoologists as follows:

Full members have full privileges and voting rights and receive the Journal of Protozoology.

Student members also have full privileges and voting rights and receive the Journal of Protozoology they must be undergraduates or graduates studying for a higher degree, and their subscription returns must be accompanied by a certificate of student status from the Supervisor.

Corresponding members have full privileges and voting rights, but must reside outside North America and receive only the Supplement to the Journal of Protozoology.

Although the Executive Committee of the Society of Protozoologists has ruled that

Sections may retain 5% of the subscription money of their members to help cover local expenses, it was realised that this would not provide sufficient funds, and so the above subscription rates were agreed. It was pointed out that since subscriptions would now be paid in sterling, individual members would no longer pay the bank charge for transfer of sterling to dollars, so that the actual increase in the subscription for full members would be only about two shillings.

The planning of the temporary administrative committee turned out to be highly successful. Their proposals were largely implemented, and have continued to provide the basis of the administration of the Section with very little alteration in the subsequent four decades. In particular, this is an opportunity to recognise the indispensable and far-sighted contribution made by Kay Adam to the successful launching of the Section.

Incidentally, the second Section of the Society of Protozoologists, the Israeli Section, held its Founding Meeting on 25 December 1962, and its first Scientific Meeting was held on 3rd April 1963.

CHAPTER 15

SUBSEQUENT ACTIVITIES OF THE BRITISH SECTION OF THE SOCIETY OF PROTOZOOLOGISTS

The second scientific meeting of the BSSP was duly held at the London School of Hygiene and Tropical Medicine on 8th April 1963, and attracted a good attendance, confirming the establishment of the group. Following this meeting the names of 99 members of the BSSP were forwarded to the U.S. Secretary. It is interesting that the parent Society recorded that year the names of 58 full members and 60 corresponding members who had paid dues to the Society, so evidently there were a number of members of the Society resident in Britain who had not joined the Section. Presumably they were full members who were already paying their subscriptions direct to the U.S.A. before the Section was founded. A picture of the growth and fluctuations in membership of the Society can be gained from [Fig. 98]. The fluctuations result from losses following exceptional rises in subscription levels or following the actions of successive treasurers in deleting delinquent members, and growth associated with new initiatives and active recruitment.

Annual scientific meetings have been held regularly in the spring since 1961, with one exception. At first the meetings lasted only one day, but from 1972 these annual meetings have usually lasted one and a half-days, sometimes with an invited lecture on the evening before the first (whole) day to launch the meeting. In recent years the regular Easter meeting has been supplemented by a one-day (usually) autumn meeting. [Fig. 99] gives a full list of these meetings. Many of the meetings have been arranged as joint meetings with other societies; these meetings often lasted for several days and the joint meetings with parasitologists attracted the highest numbers of contributions. Further comments about joint meetings will be found in chapter 17. The abstracts of contributions by members of the Society of Protozoologists to annual meetings of the Section have been published in the Supplement to the Society's Journals, when the author chose to submit them.

The affairs of the BSSP were initially administered by a 6-person committee whose composition was based on that originally proposed when the Section was founded. This Committee has normally met twice a year, once immediately before the start of the annual spring meeting, and once in the autumn. The Committee reports to the Annual Business Meeting of the Section that is held on the main day of the Annual Scientific Meeting. Reports from both Committee and Annual Meetings have often appeared in the Section's Newsletter. The six members of the original Committee retired in rotation, in 1964 the Treasurer and one Committee Member were replaced, then the Secretary and a second Committee Member, and in 1966 the President and

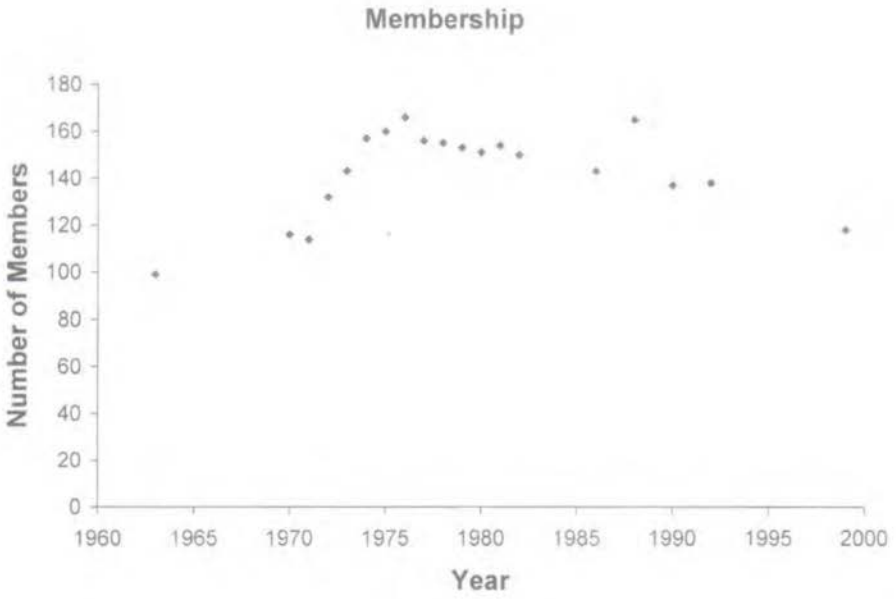


Fig. 98. Membership numbers of the BSSP since its formation in 1962.

the third Committee Member retired. Nominations for membership of the Committee are normally made to the Committee by the time of its spring meeting, so that the Committee can ensure that there are nominations that can be presented to the Annual Meeting the following day. It has only been on rare occasions that ballots were necessary. The office of Vice-President was created in 1971, with the intention that the Vice-President should be the president-elect, thereby ensuring that the incoming president should be informed about current affairs of the Section. In fact, this did not happen in the case of the first Vice-President, and it was necessary to confirm the intention in 1978. A list of the officers and committee members who have served the Section is given in [Fig. 100].

In the early years of its existence the minutes of the Annual Business Meeting of the Section were published along with the abstracts of its members in the Supplement to the Journal of Protozoology, which was circulated to all members of the Society of Protozoologists. After a few years this practice became more erratic, and in any case, a growing number of the members of the Section were not members of the parent Society. In the mid-1970's the Secretary found it necessary to send periodic newsletters to members on specific urgent topics. This practice became more frequent, and in 1980 it was decided that there were many items of business and news connected

Fig. 99 Meetings of the British Section, and some associated meetings involving members

Year	Place	Date	Local Secretary	Notes
1.	University College, London (Zool)	20 Oct. 1962	K. Vickerman	11 papers
2.	London Sch. Hyg. Trop. Med.	8 April 1963		13 papers, 4 demonstrations
3.	Edinburgh University (Zool)	20 March 1964	K.M.G. Adam	14 papers, 7 demonstrations
4.*	King's College, London (Biophys)	8 April 1965	J.B. Alexander	0 papers, 7 demonstrations
5.	Cardiff University (Zoology)	19–21 April 1966		Joint with BSP
6.	University of East Anglia	14 April 1967	I. Gibson	22 papers
7.	University of Bristol	28-29 Mar 1968	M.A. Sleigh	Joint with Soc. Exp. Biol.
8.*	Chelsea College, London	11 April 1969	E.M. Brown	19 papers, 4 demonstrations
9.	Aberdeen University	2 April 1970	B. Nisbet	Joint with BSP
10.	Zoological Society, London	16 April 1971	D.G. Godfrey	21 papers
	Joint meeting of the BSSP with the Linnean Society and BSP (8-9 July 1971)			
11.	Christ's College, Cambridge	7-8 April 1972	B.A. Newton	Joint with the Scandinavian Section and the British Phycological Society – 36 papers
12.*	University of Kent, Canterbury	9-10 April 1973	W. Gutteridge	23 papers
13.	University of Liverpool	18-19 April 1974	D.H. Molyneux	26 papers
14.	University of East Anglia	15-17 April 1975	G. Kearns	Joint with BSP – 69 papers on protozoa
15.	University of Glasgow	24-25 Mar 1976	K. Vickerman	Joint with Br. Phycological Soc.
16.*	University of Edinburgh	4-5 April 1977	K.M.G. Adam	36 papers
17.	University of Southampton	13-14 April 1978	M.A. Sleigh	30 papers, 6 posters
18.	University of York	4-5 April 1979	R. Warr	27 papers, 9 posters
19.	University of Reading	27-28 Mar 1980	A.R. Jones	21 papers, 13 posters
20.*	University of Manchester	7-8 April 1981	R.D. Butler	25 papers, 8 posters
21.	Portsmouth Polytechnic	5-7 April 1982	J. Reader	Joint with BSP – 69 papers and 19 posters on protozoa

22.	New Hall, Cambridge	28-29 Mar 1983	J.R. Baker	34 papers, 9 posters
23.	University of Bristol	3-4 April 1984	D.J. Patterson	Adjacent to BSP
24.*	University of Edinburgh	2-3 April 1985	A. Tait	Coincided with Genetical Society
25.	University of Leicester	3-4 April, 1986	M. Walker	24 papers, 5 posters
26.	University of Glasgow	23-24 Mar 1987	R.S. Phillips	36 papers, 16 posters
	The International Society for Evolutionary Protistology met at Royal Holloway College, 20-24 July 1987			
27.	University of Bristol	18-21 July 1988	D.J. Patterson	With Society of Protozoologists
28.*	University of Cambridge	4-7 April 1989	J.R. Baker	Joint with SGM
	The planned Joint meeting with the British Society for Cell Biology at Manchester in 1990 was abandoned			
29.	University of Liverpool	3-5 April 1991	S. Croft	Joint with BSP
30.	University of Reading	6-10 April 1992	A.R. Jones	First European Congress
	Natural History Museum, London	23 Sept. 1992 Cell Biology and Modern Techniques		
31.*	Charlotte Mason Coll. Ambleside	15-16 April 1993	B.J. Finlay	14 papers, plus poster session
	Natural History Museum	14 Sept. 1993 Modern Microscopy in Protozoology		
32.	University of Lancaster	13-15 April 1994	M. Walton/ J. Eccleston	24 papers plus posters
	Natural History Museum	13 Sept. 1994 Immunological Methods in Protozoology		
33.	University of Liverpool	27-29 Mar 1995	M. Chance	24 papers plus posters
	Second European Congress on Protozoology at Clermont Ferrand, France, 21-26 July 1995			
34.	Imperial College at Silwood Park	10-12 April 1996	H. Jones	30 papers, 15 posters, workshop
	Symposium "Evolutionary Relationships Among Protozoa", with Systematics Ass., Linnean Soc. Sept. 1996			
35.*	University of Manchester	6-8 April 1997	R.D. Butler	
	Linnean Society of London	Sept. 1997	Motility in Protozoa	
36.	Strathclyde University	6-8 April 1998	J. Alexander	
	Symposium on "Heterotrophic Flagellates" Birmingham, 7-11 September 1998.			
37.	University of Reading	29-31 Mar 1999	S.Tong/H.Jones	

*** Years in which International Congresses were held**

Fig. 100 Officers and Members elected to serve on the Committee of the BSSP

(Note. Officers and Committee Members are elected for a (staggered) three-year term, dates are those of election of the President)

Date	President	Vice-President	Secretary	Treasurer	Committee members
1962	P.C.C. Garnham		K.M.G. Adam	K. Vickerman	M.R. Droop, J.A. Kitching, H. Sandon
1966	G.H. Beale		P.J. Walker	J.M. Eadie	R.S. Bray, W.H.R. Lumsden, E.M. Brown
1969	B.A. Newton		E.U. Canning	D.J. Godfrey	J.R. Baker, F.E.G. Cox, C.R. Curds
1972	W. Peters	K.M.G. Adam	R. Killick-Kendrick	W.E. Gutteridge	L.H. Bannister, R.H. Hedley, M.A. Sleigh
1975	R.H. Hedley	K. Vickerman	D.H. Molyneux*	P.I. Trigg	B. Nisbet, F.C. Page, O. Harry
1978	K. Vickerman	M.A. Sleigh	C.R. Curds	G. Coombs	T. Hitchen, T. Preston, R.E. Howells
1981	M.A. Sleigh	E.U. Canning	R.E. Sinden	D. Walliker	R.J.M. Wilson, D.J. Patterson, A.R. Jones
1984	E.U. Canning	J.R. Baker	L.H. Bannister	R.S. Phillips	A. Tait, C.A. King, R.D. Butler
1987	J.R. Baker	R.D. Butler	D.J. Patterson	R.D. Butler	C. Ogden, M. Walker, B. Nisbet, M. Pudney
1991	R.D. Butler	D.J. Patterson*	M. Walker	C. Ogden	P. Carey, S. Croft, K. Gull, G. Coombs
		G. Coombs	A. Warren		T. Preston, A. Rogerson, J. Laybourn-Parry
1994	G. Coombs	B.S.C. Leadbeater	J. Laybourn-Parry	T. Preston	M. Chance, J. Alexander, J. Eccleston-Parry
1997	B.S.C. Leadbeater	J. Alexander	W. Gibson	S. Brown	S. Croft, H. Jones, R.S. Phillips

Note. The editors of the Section Newsletters, who were successively J.R. Baker, P. Carey, H. Smith and G. Novarino, were also invited to attend Committee Meetings.

*In several cases, as when Drs D.H. Molyneux and D.J. Patterson were appointed to positions overseas, elected members were unable to complete their full term of office, so that substitutes were elected; in some other cases elected members were invited to serve for an extra year for some particular reason.

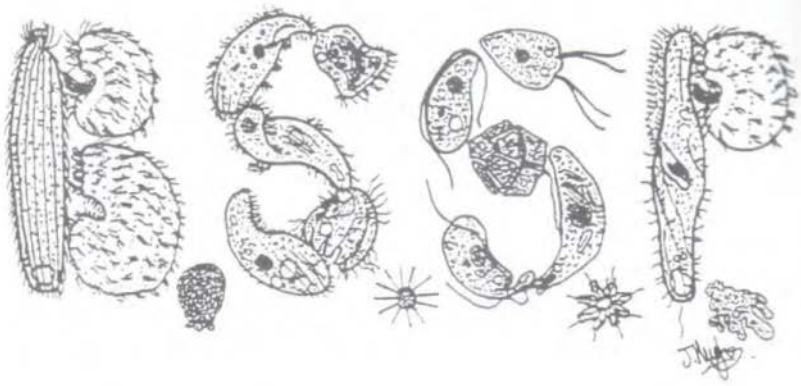


Fig. 101. A logo for the BSSP drawn by John Hughes for the newsletter in 1992.

with the Section which should be communicated to the membership by a regular Newsletter. It was too much to burden the Secretary with this additional task, and John Baker agreed to become the first Newsletter Editor of the Section. He continued to perform this task energetically until lack of clerical support forced him to resign. Thereafter the post joined in the three-year rotation system, although some editors have volunteered to stay longer. Holders of the post have been invited to attend meetings of the Committee in recent years, in order to enhance the circulation of information.

From small beginnings in 1981, the Newsletter grew to its largest size in the late 80's and early 90's. It usually had an editorial, often news of elections and the Minutes of the Section's Annual Meeting, some reports and news of activities of the Section and the Society of Protozoologists, reports on other meetings and book reviews, as well as advertisements of meetings and of books of interest to protozoologists, and even cartoons. Members have been occasionally persuaded to write provocative articles, but such is the natural reticence of most members that the Newsletter Editors have usually had a hard time to extract much from the general membership. One of the editors, Humphrey Smith, persuaded a colleague to produce a protistological cover design, reproduced in [Fig. 101]. With the almost universal use of electronic mail for rapid and informal correspondence, it has been decided to transmit the Newsletter as an e-mail attachment. Sadly some members have difficulties with opening these attachments, and personally I find e-mail reports transient and less easy to read than hard-copy documents, though I appreciate the costs to the Section of circulation in this way are greatly reduced. I have found it very interesting to go back to read copies of the older newsletters, which have the feeling of historical



Fig. 102. The current website and letterhead logo.

documents. After a number of attempts to design a logo for the British Section, the following clever yin-yang of trypanosomes [Fig. 102] has appeared to grace the website of the Section at www.bsspweb.freeserve.co.uk. and the letterhead of the Secretary.

CHAPTER 16

RELATIONS BETWEEN THE BRITISH SECTION AND THE SOCIETY OF PROTOZOOLOGISTS

Provision was made at an early stage in the history of the Society of Protozoologists for the formation of Sections of the Society by groups of members outside North America. At the beginning it was probably intended that these Sections should merely be formed from groups of 'Full' (or 'Regular') and 'Student' members already paying dues to the Society. Not surprisingly, many protozoologists outside North America could not afford to pay the full subscription, and often had not the desire to accumulate personal copies of a journal from North America as well as local journals, so that at first the idea of forming a Section held limited attraction. In 1961 the Society approved the category of 'Corresponding Member', initially for members outside North America, but later also for the spouses of full members. These Corresponding Members would pay a reduced subscription, but receive only the Supplement to the Journal, containing abstracts and minutes of business meetings, not the full Journal. The opportunity to combine membership of the parent Society, either as Full or Corresponding member, with membership of a Section with local organisation and meetings appealed to many protozoologists in Britain, and led to the formation of the British Section, as described in Chapter 14.

Given a nucleus of people interested in protozoology, some of whom were willing to devote time and effort to the organisation of meetings, the initial steps in the formation of the Section appeared straightforward. However, over many years there were persistent problems in the relationship between the British Section and the parent Society, which were only gradually resolved. In explanation, it has to be remembered that the British Section was the first one to be formed, and, as such, it was an experimental creation. Some of the problems which developed may have arisen because the Section did not grow up in the manner that its parent expected, while other problems were the result of outside influences beyond the control or expectation of either party. As so often in fraught relationships, the usual cause of difficulty was money.

The original arrangements agreed between the U.S. (so expressed in the recorded document) Treasurer and Secretary and the Committee of the British Section laid down the following pattern.

British members shall pay their subscriptions in sterling to the Treasurer of the British Section.

Subscriptions are due on 1st January each year.

The Section Treasurer shall remit the proportion of subscription money due to

the U.S. Treasurer by April 1st each year.

The Section Treasurer shall inform the U.S. Treasurer by April 1st of all British Section members who have not yet paid their subscriptions for the current year.

Members of the Society of Protozoologists who do not wish to partake in the activities of the British Section may pay their subscriptions directly to the U.S. Treasurer.

The Secretary of the British Section shall send an up-to-date list of the names and addresses of British Section members to the U.S. Secretary once or twice a year.

The Secretary of the British Section shall undertake to receive the abstracts of papers given at Section meetings and forward these to the U.S. Secretary to arrive not later than May 1st.

The Section Secretary shall also send titles of communications given at Section meetings and brief Minutes of Section Meetings to the U.S. Secretary by May 1st.

Members of the British Section wishing to send an abstract in absentia *for publication in the Supplement to the Journal of Protozoology shall send it directly to the U.S. Secretary.*

Money problems first became serious in 1968 with a devaluation of the pound against the dollar. Members of the British Section were told at their Annual Meeting at the end of March that, as a result of the devaluation, the subscriptions collected on 1st January would not cover the dues that must be paid to the U.S. Treasurer on 1st April. In response to this situation the Meeting agreed to a retrospective increase in the annual subscription to cover the extra costs of paying dues in the more expensive dollars, and all members were requested to instruct their banks to make appropriate changes. Some members did so, but many failed to pass on the instruction to their banks, so that the Treasurer was faced with a complex muddle, with not only three classes of membership but two levels of payment having been made for each – as well as some members who had not paid at all! At the subsequent meeting of the parent Society in the summer of 1968 the U.S. membership agreed to raise subscription levels for all members with effect from 1st January 1969. Although this was discussed at a meeting of the Committee of the British Section in November 1968, it was felt that the new rates could not be levied until the situation had been explained to members at the spring meeting in 1969. The Secretary, Liz Canning, wrote to the Secretary of the parent Society about this, but received no response. At the 1969 Annual Meeting of the British Section members were told of the need to raise subscriptions and change banker's orders for the second time, which would make the Treasurer's task of collecting correct subscriptions even more difficult. As a result it was suggested that the Section should consider whether to secede from the parent Society and form an independent British Society, which would be better able to manage its own finances. After discussion it was agreed to accept the proposal of

John Baker that representatives should meet with officers of the parent Society during the Leningrad Congress in the summer of 1969 to attempt to formulate better financial arrangements.

The results of discussions between representatives of the British Section and U.S. members, including the President of the Society, Dr R.W. Hull, were reported to an informal meeting of members of the British Section held in Leningrad. Two principal issues were raised with the U.S. members:

(a) Difficulties in collection of correct subscriptions due on 1st January after increases have been decided at a business meeting of the parent Society held in the summer or autumn. The next time the British Section can approve an increase is in the following spring, after the increase has come into effect, so that increases have to be back-dated.
(b) British members have no voice in the affairs of the Society because of inability to attend meetings in the U.S.

The first difficulty can be met by sending out notices of increased subscriptions immediately after the U.S. meeting without waiting for approval by the British Section. No easy way round the second problem was evident, although the American members suggested that they would welcome the attendance at meetings of the Society's Executive Committee of any member of the British Section who was present in the U.S. at the appropriate time, as a substitute for the President of the British Section, who is an *ex-officio* member of the Executive Committee. The British representatives were conscious that the Americans were anxious to uphold the international nature of the Society of Protozoologists and preserve the Sections. The most substantial points raised during the discussion among the assembled members of the British Section were:

(1) That the Americans might consider forming themselves into a Section comparable to the European Sections.
(2) That an independent British Society would probably be financially unstable. Some members would wish to continue membership of the Society of Protozoologists in order to receive the Journal and might not be willing to pay an additional subscription to a British Society.
(3) If affiliation of an independent British Society with the Society of Protozoologists were impossible, a section might be arranged within the Society for General Microbiology, which had made an earlier approach (see Chapter 17).

These points were put to the membership of the British Section by mail, together with a form on which they were invited to record their vote to indicate whether or

not they favoured the existing arrangements between the British Section and the Society of Protozoologists. A contributory feature in these deliberations was the fact that discussions were proceeding with a publisher about the possibility of starting a British Journal of Protozoology (see Chapter 20).

The result of the vote, reported to the Annual Meeting of the British Section in 1970, was that a clear majority of the membership of the British Section had voted to remain linked with the Society of Protozoologists. However, the same meeting heard disturbing reports that some members who had paid for the Journal were not receiving it and some corresponding members were receiving the Journal! Any members who were not receiving the correct mailings were asked to write to the British Section Secretary, who would take up the question with the appropriate officer of the parent Society. (In spite of this the same problem was repeatedly reported in subsequent years, although it appeared to have been solved by 1973.) On the contrary, attempts were also being made to improve relationships, and the Society was asked, following an initial discussion between Kay Adam and the President of the Society in Leningrad, whether the parent Society would consider holding its Annual Meeting in the U.K. in 1971, probably in Edinburgh. Sadly, the Executive Committee of the Society decided to hold that meeting in the U.S.A., although the President, Dr William Balamuth, expressed pleasure at the receipt of the invitation and regret that it could not be accepted.

Financial questions continued to interfere with relationships, since, that same summer, the Executive Committee of the Society decided to raise the page charges for publication in the Journal. As a result questions about affiliation to the Society for General Microbiology, and some form of link with their Journal, were again raised at the next meeting of the British Committee. At the same time British members were pleased to learn that the Society might be able to consider holding its annual meeting in Britain in 1974 or 1975. Later the American Secretary (Dr Bovee) wrote to say that the idea would have to be postponed, as it seemed that American members would be unable to get funding to come to Britain for such a meeting.

Another round of unease was aroused at the 1972 Annual Meeting of the British Section with the news that a letter had been circulated by the President of the Society Professor E.R. Noble concerning proposals to modify the section (Article VI) on *Sections and Affiliated Societies* in the Constitution of the Society. What these were and how would they affect the Section was not evident to members because reports of the business meetings of the Society were no longer printed in the Supplement to the Journal. It appeared to many members that while the British members considered themselves to form a Section of the Society, the parent Society now considered that the British membership constituted an Associated Society. The principal concern

was that the British membership had apparently not been consulted about the change. If the problem was a fiscal one, concerned with the taxation status of members of the Society, or some other technical point, this could have been explained to overseas members. The problem continued to be discussed by the Committee of the British Section, and at their meeting in April 1973 they learned by letter from the Society that a Committee to consider the status of Sections and Associated Societies was to be set up.

The 1974 Annual Meeting received a report from Dr J.F. Ryley on the results of a questionnaire to members. Out of 79 replies, three-quarters of respondents were dissatisfied with present relationships with the parent Society. Eighty percent believed that an improvement in organisation would result if an American Section were formed within the Society. Dissatisfaction with the Journal was also expressed, based largely on page charges (rare in Europe) and previous problems with distribution. On this occasion the British Section were fortunate to welcome Dr Honigberg, a former President of the Society and current Editor of the Journal, at their meeting. He was ideally placed to explain the page charges, to report that he felt Allen Press now had distribution problems under control, and to reassure members that British protozoologists were well represented on the Editorial Board. In his view the question of whether the British Section should remain a Section or be re-named an Associated Society was negotiable.

The unresolved problems rumbled on through the mid 1970's, exacerbated once more by inflation, depreciation in the exchange rate between the pound and the dollar and by substantial rises in U.S. postal rates. There was also a case of a lack of communication from the U.S. Treasurer to the British Treasurer concerning a rise in the central subscription rates to the Society decided in 1975. This did nothing to improve relationships, especially since it again immediately followed a rise in British subscription rates to cope with the existing deterioration in exchange rate. The British Committee requested concerted action by the Secretary and Treasurer of the British Section to seek an improvement in the management of the collection of subscriptions and their remittance to the U.S.A. They were instructed by the Committee to write to the President and Secretary of the parent Society to say that it was impossible to maintain a viable Section if information is not communicated in a businesslike manner. Admission by the relevant officer in the parent Society that he had lost the year's batch of abstracts in his office did nothing to improve confidence! Ten members resigned that year, apparently as an immediate result of being subjected to two substantial increases in subscription in the same year.

At the next Annual Meeting of the British Section, the Secretary, Colin Curds, asked the members to consider the situation. He explained that continuing financial

problems had three main causes: the fact that the Section acted as an agent for collecting money for the Journal of Protozoology (the bulk of the subscription funds collected); the difference in time between the business meetings of the parent Society and the British Section; and the problem of changes in the exchange rate between the pound and the dollar. Discussions of the Committee had suggested three obvious possibilities:

1. The Section could remain as it was, but with continuing problems of financial instability.
2. All members could be advised to become Corresponding Members (as was apparently the case for the Israeli Section), a solution urged by the current President of the Society, Franklin Wallace, or
3. The Section could become financially independent of the parent Society.

Members had been canvassed by post before the meeting, and 6 had voted for the *status quo*, 20 had voted for a uniform Corresponding membership, and 31 had voted for independence. After discussion it was agreed that the option of all becoming Corresponding Members was not practicable. There was much sympathy with the suggestion that Section members should pay dues directly to the Society, in spite of the costs of currency change. The Section would, however, still require some income in order to function. Behind the discussion was an uneasy feeling that information exchange with the parent Society left much to be desired, and it was revealed that this was not solely a British problem. Liz Canning stated that, in her capacity as Vice President of the Society, she had met with Cicely Chapman-Andresen of the Scandinavian Section and they had written a joint letter to the parent Society proposing ways by which better communications and understanding between the parent Society and the Sections might be established and maintained. She hoped that, should these proposals be acted upon, the situation might improve and the advantages of remaining a Section would be retained. Kay Adam confirmed that it had always been difficult to obtain information from the officers of the Society. Although there was some feeling that a vote should be postponed, and time given for more discussions with the parent Society at the New York Congress, the President, Ron Hedley, felt that the membership should be given a chance to indicate their views. A motion that the Section should become independent of the parent Society was carried by 27 votes to 6. However, there was no desire to close the door immediately and without time for reflection, so it was agreed, by 20 votes to 12, to defer the date of implementation of independence for one year. The conclusion therefore was that the Section would become independent at the Annual Meeting in 1978, unless new and significant circumstances arose as a result of discussions at the New York Congress.

Discussions about the difficulties of the British Section took place at three meetings

during the 5th International Congress in New York in June-July 1977: an informal meeting between Bob Sinden (the Secretary of the British Section) and Liz Canning (Society Vice-President) from the British side and Franklin Wallace (President), Phyllis Bradbury (President-elect) and Barclay McGhee (Secretary) of the parent Society; the meeting of the Executive Committee of the Society; and a meeting of the Committee on Associated Societies. The outcome was described in detail in a Newsletter prepared by Bob Sinden following the Congress and discussed at the 1978 Annual Meeting of the British Section. The Secretary reported that against the background of difficulties over finance, communication and the status of the Section/ Associated Society, and the vote by the British Section to become independent after one year if no solutions were found, amicable and constructive discussion had taken place. The conclusions reached were that:

a. Finance. Members would be billed directly for their subscriptions to the parent Society (by Allen Press).
b. Communication. The Vice-President of the Society, who usually comes from outside North America, had been given the responsibility for liaison with the c.
c. Sections and Associated Societies. Also an informal newsletter would be circulated twice a year, and international members actively invited to contribute.
d. Status. The Constitution of the Society had been re-written to allow overseas groups to become Sections of the Society of Protozoology, so we could then be what we always thought we were! Apparently it is not possible for the American membership to form a U.S. Section without loss of tax-exempt status.

The Society agreed to cancel debts arising from delayed notification of the rise in subscription in 1975.

Upon receipt of this information the British Section voted on the motion "That significant circumstances have arisen from discussions in New York". This motion was passed by 26 votes to 10 with 2 abstentions. As a result the British Section considered itself re-instated as a Section of the Society of Protozoologists, and so remains to this day. Members of the British Section accepted the need to pay a local subscription for purposes concerned with the organisation and administration of the Section, as well as paying a subscription in dollars for their membership of the parent Society. However, only about half of the members of the British Section appear to have paid subscriptions to the parent Society, via Allen Press, within the first 6 months after the agreement. At its subsequent meeting the Committee of the British Section agreed that all members of the British Section should be expected to be corresponding or full members of the parent Society, but they felt in no position to insist on the latter. One encouragement to members of the British Section to remain members of the parent Society was the receipt of a letter from Jerry Paulin, Secretary

of the Society of Protozoologists, stating that British members would be allowed to pay their annual dues to Allen Press in sterling, and that where desired these dues could be paid in advance. It is not clear that this concession was ever implemented, and indeed a minute from the autumn Committee Meeting of the Section indicated that the matter was to be raised with the parent Society. The result of this was another letter from Secretary Paulin stating that he had arranged for Allen Press to receive payment of British subscriptions in sterling.

Co-operation continued to be a problem, illustrated by the fact that ballot forms for elections in 1979 arrived after the date they were due for return. However, on the positive side, repeated requests for an increase in the number of charge-free pages in the Journal were rewarded by a proposal to increase the number from 4 to 5.

By 1980 only 40 out of a total membership of 151 in the British Section were paying dues to the parent Society, and (in the opinion of this writer) the Section had essentially become an Associated Society! This anomaly became more evident with time, and by 1984, when, it appears, the category of corresponding membership was being reconsidered, it was decided to discuss the anomaly with Secretary Paulin. It was agreed by the Committee of the British Section that the membership should be asked at the 1985 Annual Meeting to propose that, if the present structure is untenable: either all members of the British Section should take out Corresponding Membership, or that the Section establishes itself as a separate society, merely affiliated to the parent Society. However, it was pointed out that opportunities for discussion with officials of the parent Society would be available during the forthcoming International Congress of Protozoology in Nairobi. It was therefore agreed to request that the Secretary and President should seek ways of maintaining close relations with the parent Society in discussions at the Congress with members of the Executive Committee of the Society, and report back to the 1986 Annual Meeting of the Section. A proposed revision of the Constitution of the Society would provide a compromise solution as another alternative. This would allow the British Section to remain as it was, with some members who were members of the parent Society and some who were not, but only those who were members of the parent Society would be able to hold office in the Section, submit abstracts and vote at the Annual Meetings. The membership assembled at the 1986 Annual Meeting of the Section voted overwhelmingly for this solution, with no votes against and three abstentions. They also thanked John Corliss, who had attended the meeting, for his help in resolving the problem and expressed the hope that with this outcome the question of the status of the Section would not be raised again for at least 5 years. In fact the problem did not immediately go away, for the first attempt at revision of the constitution indicated that only groups with more than 30 *regular* members of the parent Society would be permitted to have a voting representative at Executive Committee meetings of the

Society. It was doubtful if any section had such a large number of regular members, so that all sections might be disenfranchised by this change. The solution agreed in 1988 was that sections with more than 30 regular plus corresponding members would be permitted to have a voting representative at Executive Committee meetings, but only those with more than 30 regular members could vote on matters concerning the Journal.

The parent Society canvassed the views of the membership about possible name changes of the Society and its Journal in 1991. As a result a ballot was held seeking approval of the retention of the name Society of Protozoologists, but a change in the name of the Journal to the Journal of Eukaryote Microbiology. The membership of the Society accepted these suggestions, although there were some misgivings in Britain over the change in name of the Journal, which, it was thought, could lead to misunderstandings about its scope.

Although this history of administrative problems between the British Section and the officers of the Society may suggest that the growing offspring was continually arguing with its parent, there were numerous two-way interactions that were positive. Preferential access of Section members to the Journal, both as contributors and subscribers, was balanced by the contributions of many members of the British Section to the Board of Reviewers of the Journal. A series of members of the British Section (Geoffrey Beale, 1971; Keith Vickerman; Liz Canning, 1976; John Baker, 1979; Michael Sleigh, 1986; 'Paddy' Patterson, 1995; Bland Finlay, 1997 and probably more) have served as Vice-Presidents of the Society. This typically involved contributing (often after wide canvassing) the views of non-Americans in the deliberations of the Executive Committee of the Society, and also delivering a special address at the Annual Meeting. The efforts of Michael Sleigh to consult other sections and associated societies about Society matters resulted in him being persuaded to accept chairmanship of the Society's Committee on International Relations in 1990. However, he found that the functions of this Committee were not exactly clear, and, like the editors of the Newsletters of both the parent Society and the British Section, he found it difficult to extract meaningful contributions from the constituent members. Members of the parent Society, including (on several occasions) its President, have attended meetings of the British Section, and once (in 1988) the Society held its Annual Meeting in Britain. In the other direction, several British members are usually able to attend, and enjoy, meetings of the parent Society in North America.

Although it has been pointed out on many occasions that the Society of Protozoologists cannot expect to be accepted as truly international until a member of any nation can be elected as President, it is not reasonable to expect the large membership in North America to give up tax exempt status on their subscriptions to make this possible. In

spite of this criticism, the relationship between the British Section and the parent Society now seems to have settled down to a reasonably amicable working pattern, and British members feel themselves almost equal members of a scientific society that makes genuine attempts to satisfy its international membership.

CHAPTER 17

RELATIONSHIPS WITH OTHER ORGANISATIONS

Overtures to join with other groups and Societies were received as early as the First Meeting of the Section, at which Kay Adam reported that she had received a letter from the President of the Society for General Microbiology (SGM) inviting protozoologists in Britain to form a group within that Society. The SGM President pointed out that it had always been the aim of that Society to include protozoological papers in their journal and at their meetings. Associate members of the SGM were at that time paying a subscription of 10s. per annum. Since British protozoologists had just agreed to form a Section of the Society of Protozoologists, no further action was taken.

The question of a relationship with the SGM was again raised in 1970 when a new schedule of page charges had been issued by the Journal of Protozoology. On this occasion Bruce Newton, who was then President of the Section suggested that a linkage with the microbiologists at the same time as remaining a Section of the Society of Protozoologists, might provide a route for support of a protozoological journal in Britain. Subsequent consideration of this matter led to the conclusion at the next meeting that simultaneous affiliation to both the SGM and the Society of Protozoologists might be unacceptable. There was a further mention of affiliation to the SGM by the Secretary of that Society after a joint meeting in Cambridge in 1989, when another crisis with the Society of Protozoologists was under discussion. By the time there was an opportunity to discuss this within the BSSP, the situation in the Society of Protozoologists had been resolved.

The subject interests of members of the BSSP have common ground with the interests of a number of other scientific societies in Britain. In addition to invitations by the BSSP to speakers from these other societies to speak at our meetings, and invitations from others for protozoologists to speak at their meetings, there have been numerous joint meetings between societies, indicated in the list of meetings in Table I, above. It is not surprising that the largest number of joint meetings (at least 7) have involved the BSP, since a substantial proportion of protozoa are parasites. There has always been extensive common membership between the BSSP and the BSP, and swings of allegiance of some individual members between the two groups, whilst others remained faithfully active members of both. Although there is a common, and ill-defined, boundary between the interests of protozoologists and phycologists, we have only succeeded in organising two joint meetings involving the British Phycological Society; perhaps the interests of many of their members in multicellular algae discourage the exploration of common interests. Other joint meetings, for example

with the Society for Experimental Biology, the Linnean Society and the Systematics Association have probably come about because members of the Committee of the Section have also been officers of these other societies, and have seen opportunities to explore common ground in joint meetings. A particularly significant recent example was the Symposium on "Evolutionary Relationships Among Protozoa", jointly sponsored by the Section with the Linnean Society and the Systematics Association at the Linnean Society's rooms in September 1996, which resulted in the publication of an important volume (Coombs et al., 1998). Attempts to arrange joint meetings with the British Society for Cell Biology and the Genetical Society have met with less success.

A number of British Protozoologists have been active members of the International Society for Evolutionary Protistology (ISEP). Although the foundation membership of this group was largely North American, meetings of the Society are held in many different countries. A successful meeting of ISEP involving many members of the British Section was held at Royal Holloway College in July 1987 (see BioSystems vol. 21, pp. 177-426). A less formal international group has held three meetings in Europe devoted to the biology of flagellates, which have attracted participation by many members of the British Section. The first meeting, held at Helsingør in Denmark in 1990, and the second, in St Petersburg in 1994, were specifically concerned with free-living heterotrophic flagellates, and the third (in place the autumn meeting of the Section), in Birmingham in 1998, was concerned with a wider range of flagellates. Papers from all of these meetings have been, or will be, published (Patterson and Larsen, 1991; *Cytology* vol. 37, 1995, pp. 951-1096; Leadbeater and Green, 2000, respectively).

For many years representatives of most biological societies in Britain met together as a body called the Biological Council. The BSSP became affiliated to the Biological Council in 1968. This focus group levied a modest subscription and in return produced an annual booklet containing a calendar of the scheduled meetings of the constituent societies, together with contact addresses for their officers and information on their publications. The Council also provided a forum for discussion of matters of common biological interest, sponsored occasional special meetings and publications, and submitted evidence or comments on biological matters of public interest to government bodies or newspapers. In 1991 the Biological Council was wound up and amalgamated with the Institute of Biology. In consequence of the amalgamation an invitation was received to affiliate with the Institute of Biology at an initial cost of £25. In return for this fee the Section would gain mention on joint professional registers, access to educational activities, access to Institute of Biology office accommodation and services in the Centre for Biology, participation in the annual meeting of representatives of learned societies, in the IOB link group and in IOB conferences and symposia, as

well as entries on the Societies page in the Institute's Journal (Biologist) and in the re-launched annual handbook. The Committee agreed that the Section would affiliate with the Institute at the current subscription rate, but would review the situation if the fee increased substantially. It is not clear whether this decision was carried forward, since a similar decision was made the next year, on the assumption that the subscription had risen to £27. However, when the Committee was informed in the autumn of 1993 that the subscription required was now £75, it was decided not to seek affiliation. (Many members of the BSSP are individual Members or Fellows of the Institute.) There is some doubt as to whether the annual handbook was ever published again.

Co-ordination on another scale was provided by a system of National Committees, comprised of representatives of societies relevant to the discipline, operating under the umbrella of the Royal Society. The principal function of these committees, such as the British National Committee for Biology, was to take an interest in international affairs related to their discipline. In particular they were to provide channels of communication between U.K. scientists and international unions – in the case of Biology with the International Union of Biological Sciences (IUBS). An informal meeting in 1971 attended by the Section's President, Bruce Newton, was called to discuss the representation of microbiologists on sub-committees of the British National Committee for Biology. It was felt by the Committee of the British Section that protozoologists had interests in both the Zoology and Microbiology sub-committees. These proposals were accepted by the Royal Society; representatives were appointed to both sub-committees and nominations renewed at 3-year intervals, as required. These sub-committees met erratically – in some 3-year cycles representatives were not called to meetings at all, although they received circulated information.

The British Section had also been persuaded during the 1970's to take out membership of the International Association of Microbiological Sciences (IAMS), but in 1979 the Committee received advice that it was no longer appropriate to pay membership dues to that Association. Although this opinion was reiterated the next year, there were still doubts in 1981, when it was learned from Terry Preston, the Section's representative on IAMS, that this body had been reorganised as the International Union of Microbiological Sciences (IUMS). It was decided to allow some time to see whether this body would be of more value than its predecessor. By 1983 a decision had been taken at national level that the appropriate route for representation of societies in Britain would be through a British National Committee for Microbiology, now that the IUMS had taken over microbiological interests from the IUBS. The British Section were invited to nominate a member of this British National Committee, and agreed that they would informally represent parasitological interests too, since the BSP did not have a member on this Committee. The new British National

Committee for Microbiology proved to be more active than its predecessor, at least to the extent of holding meetings. The Section was still expected to contribute a subscription to the IUMS, although societies affiliated to the IUBS were not required to make any subscriptions to that Union.

A new body, the U.K. Forum for Microbiology, developed in the early 1990's and began to meet annually. At its meeting in July 1993 the Forum proposed that member societies should form a loose federation in order to present a national voice, and planned a series of meetings ("Microbiology 2000") to be held during 1994 to discuss issues associated with this proposal. In particular the meetings would attempt to recognise common interests, promote better understanding about microbiology, protect teaching programmes in Microbiology, consider professional qualifications for microbiologists and discuss the possibility of creating a single umbrella organisation for all microbiologists without damaging existing societies. The principal outcome was the formation of a U.K. National Committee for Microbiology, which would also act as a new Microbiology Division of the Institute of Biology. This body was intended to promote the interests of microbiologists and give microbiology a clear national voice. Membership required a subscription.

A related matter was the question of hazards associated with handling micro-organisms. As early as 1979, when the Health and Safety at Work Act was in its early days, questions were raised by the membership about the way in which certain protozoa were being classified into pathogenic or non-pathogenic categories. The Committee agreed that the President should set up appropriate *ad hoc* committees to respond to technical questions in this area. One concern was that, as a result of incorrect classifications, valuable cultures in national collections might be unnecessarily destroyed. In 1981 the Royal Society set up a Microbiological Consultative Committee to consider microbiological safety, and invited the Section to nominate a member to attend its meetings; Iain Wilson was subsequently nominated. Initially this Committee discussed little of relevance to protozoologists. However, later the Committee received a document on recommendations to place pathogens (including various protozoa) in categories, according to risks associated with containment, that had been prepared by the Health and Safety Executive; the deep disappointment voiced by the Consultative Committee was echoed by the Committee of the British protozoologists. This had little effect, and when the Advisory Committee on Dangerous Pathogens produced its report, there was still widespread dissatisfaction with the categorisation of protozoan pathogens. Liz Canning consulted experts about the appropriate categorisation of various protozoan pathogens and reported the results. A proposal to change the categorisation of various protozoan pathogens was received in 1994, and, in response to representations from the President of the Section, the Health and Safety Executive agreed to reverse the changes by the

end of the year.

A national collection of cultures, drawn extensively from the Pringsheim and other collections maintained by Eric George in the Botany Department at Cambridge, as well as from other university collections and individuals, was set up by the Natural Environment Research Council. This was established at the Culture Centre for Algae and Protozoa (CCAP) in Cambridge, and was placed under the control of the Director of the Institute of Terrestrial Ecology (ITE). Although the prime purpose of the CCAP was to maintain a collection of cultures for use of scientists in research and teaching, the staff also pursued research on protozoa, particularly on methods of culture and preservation of strains, including cryopreservation, as well as on taxonomic topics. In 1980 John Baker was appointed to head the Centre, following the retirement of Eric George. As finances became squeezed the CCAP raised the costs of supplying cultures, and in 1983 the President of the Section wrote to the Director of ITE to emphasise the value of the cultures to the scientific community and the concern that the raised costs would restrict access to the material. This concern was echoed by Barbara Kirsop, President of the U.K. Federation of Culture Collections, who pointed out that restriction of access to cultures was contrary to the aims of the Interdepartmental Committee on Biotechnology. The situation of CCAP worsened by 1985, with threats of closure. It was decided to write again, this time to both the Secretary of NERC and the Chairman of the Inter-departmental Committee on Biotechnology. Later that year news came that the CCAP in Cambridge was to close in September 1986. It was also reported that the British National Committee for Microbiology had set up a working party chaired by Professor John Postgate to investigate the funding and stability of culture centres. By the next spring it had been decided that, although the Culture Centre at Cambridge would close, the cultures of freshwater and marine protozoa together with non-marine cultures of algae of the CCAP would be moved to the Freshwater Biological Association's Station at Ambleside on Lake Windermere. Marine algal cultures would go to the Scottish Marine Biological Association's laboratory at Oban. Meanwhile the recommendations of Professor Postgate's working party would be presented to the Royal Society. The CCAP settled down on a smaller scale at Ambleside, and has continued to serve the biological community ever since. A positive response to the problem of the high cost of obtaining cultures for teaching was made by selecting a range of cultures used in teaching, and by developing "teaching packs"; the Section made a donation of £100 towards this development.

CHAPTER 18

EUROPEAN LINKS

A number of protozoologists in many countries in Europe were members of the Society of Protozoologists before the British Section was formed in 1962, and already had contacts through the Society. (By 1963 there were 118 members of the Society in Britain, 90 in other countries of Western Europe and 16 in Eastern Europe. Many other contacts between European protozoologists were made or reinforced at the First International Congress in Prague, and later at the Second International Conference in London. In the same year as the formation of the BSSP, the Groupement des Protistologues de Langue Française (GPLF) was formed in France. Several British protozoologists joined the French Society, probably more to obtain the journal Protistologica at an advantageous price than to attend the meetings of the GPLF, but they did gain contacts with and information about protozoological activities in France. A formal contact between the British Section and the GPLF took place in 1964 over discussions about the formation of an International Union of Protistologists, as mentioned in Chapter 13. At an individual level protozoologists from European countries were invited to speak at meetings of the BSSP, and people from Britain were invited as speakers at meetings of the GPLF. It was still difficult to engage in constructive activities with countries in Eastern Europe, although many contacts established at the Third Congress in Leningrad led to sustained correspondence.

For a decade or so, contacts were largely at an individual level, reinforced by meetings at International Congresses. In some areas there were additional opportunities to meet, for example at the European Congresses on Parasitology and through the establishment of a group of workers on ciliate genetics who began to meet at regular intervals in France, Italy, Germany and Britain. In 1972 members of the Scandinavian Section accepted an invitation to join with the British Section at a meeting in Cambridge, but attempts to arrange a return joint meeting in Odense in 1976 foundered because few British members could find the necessary funds to travel there. Other meetings provided opportunities to meet, or maintain contact with, protozoologists in Eastern Europe. Some members of the Section visited Poland to celebrate the 50th Anniversary of the foundation of the Nencki Institute for Experimental Biology in Warsaw in 1968, and to attend an International Symposium on Motile Systems of Cells in Cracow in 1971 (see Symposium proceedings in *Acta Protozoologica* vols. 7 and 11). Hungarian protozoologists invited members to attend an international meeting in Budapest in September 1985 to celebrate the centenary of the birth of Josef Gelei and a second meeting in August 1991 on the Ecology of Protozoa at the field station in Tihany, on Lake Balaton.

In 1977 Bob Sinden, the Secretary of the BSSP, reported to the Committee an informal discussion with Professors Vivier and Schrevel of the GPLF. The French protozoologists had expressed interest in the formation of a European Society of Protistology. This would hold biennial meetings alternating with the International Congresses of Protozoology, and could expect that material from meetings might be published in *Protistologica*. The Committee agreed that they could support an informal grouping analogous to the European Society of Parasitology, but would not welcome any unnecessary and cumbersome increase in bureaucracy. Further they agreed that such a grouping, if formed, should complement and not conflict with the international role of the International Commission on Protozoology and the international status of the Society of Protozoologists. There is no further comment on this discussion in the minutes of the Society; maybe the BSSP at that time were too involved with interactions with the parent Society to consider additional questions.

Opportunities for improved contacts increased all the time, for example with the formation of the German Society of Protozoologists in 1981. Although there were now more societies inviting individuals from other countries to speak at their meetings, the number of contacts remained rather small.

The organisers of the meetings on ciliate genetics made an important change in policy by inviting workers on other aspects of ciliate biology to take part in the 4th ciliate meeting they were planning in Camerino (Italy) in 1979. This series of meetings continued to grow, through meetings in Geneva (5th) in 1983 (see summaries of main sessions published in *Protistologica* vol. 20), Aarhus (Denmark)(6th) in 1987, and Toledo (Spain)(7th) in 1991, with a progressively widening range of themes. At the meeting in Toledo British representatives invited members of the ciliate group to take part in a meeting covering a wider range of protistological topics which was being planned to take place in Britain in the following year.

Renewed suggestions that the time was ripe for the initiation of pan-European meetings on protistology were made at the meeting of the BSSP Committee in 1988. These matured the next year into a definite proposal to hold such a meeting in place of the Section's regular spring meeting in 1992, with Reading as the venue. Contacts were made with societies, sections and national representatives (where no groups were known) throughout Europe, including the British Phycological Society, to seek their views on the value of European Meetings on Protistology, and on the likelihood of their participation in the proposed meeting. Encouraging responses from all major protozoological groups, except the French (who interestingly had earlier suggested the idea), were received by the next meeting of the Section Committee in December 1989, and planning began in earnest. It was agreed that a scientific organising committee should be established, with representation from each participating country,

and that Michael Sleigh be invited to chair this committee. It was also agreed to propose two main workshop titles for the meeting: "Opportunistic protozoan infections" and "Protozoa, pollution and the environment", which would be communicated to European contacts. John Baker, Paddy Patterson and Colin Ogden (Treasurer) agreed to seek funding to support the administration of the meeting.

Planning proceeded steadily over the next year, and foreign contacts became more positive. During this time the Secretary had received a letter from the German Society of Protozoologists proposing the formation of a European Federation, which would tie together existing groups, but not substitute for them. This suggested holding a European Congress of Protistology in a four-year cycle, alternating at two-year intervals with the International Congresses of Protozoology. In an initial reply to the German Society the British Secretary had pointed out that this idea had been in the minds of the British Committee when they first proposed the 1992 meeting. There was unanimous support from the Committee and strong support from the membership at the 1991 Annual Meeting for the proposal of a Federation, and the hope was expressed that the 1992 meeting in Reading might prove to be the inaugural meeting of such a Federation. Several alternative ways in which this Federation could operate were discussed, including the holding of annual meetings, taking different specialist themes, following perhaps the pattern of the ciliate meetings. These perhaps could be combined successively with the annual meetings of different national groups. Questions about financial implications of the formation of a Federation were also discussed. The positive response by the Secretary to Professor Hausmann in Germany did not elicit any further comment from him at this stage.

Some positive responses were received from sponsors willing to give funds to support the meeting, which encouraged the circulation of a first circular about the meeting in the summer of 1991. More than 270 people returned the form indicating their intention to attend and requesting the second circular. This comprised a formal call for papers and a form for registration of attendance, with indications of a provisional programme. It was with great sorrow that the Committee of the Section learned of the death of Colin Ogden, on 19th December 1991, after a short illness. They unanimously decided to dedicate the 1992 European Congress to his memory since it was largely through his initiative that the concept of a European Meeting had developed

Over 170 protozoologists from 19 countries attended the meeting. The abstracts of 162 contributions were printed in the programme of the Congress. Ninety-five papers were scheduled in twelve sessions of spoken contributions, the remaining contributions being presented as posters. Contributors represented the following countries:- Austria, Belgium, Bulgaria, Czechoslovakia, Denmark, Finland, France,

Germany, Holland, Hungary, Italy, Poland, Spain, Sweden, Switzerland, the United Kingdom, the U.S.A. and the U.S.S.R. They were greeted by a "European Community logo" comprised of selected star-shaped protists [Fig. 103], also presented on mugs and tee-shirts sold at the Congress. The Congress was acclaimed as a significant success, in no small measure because of the efforts of Alick Jones and his team of helpers in Reading.

Scheduled in the programme of the Congress was a discussion on the formation of a "European Protozoology Federation". Comment at the Committee of the British Section had confirmed the earlier view that the Federation should not swallow up individual societies or sections, but complement them. It was also emphasised that there was no intention to disturb the relationship between individual groups and the parent Society of Protozoologists. Committee members felt the aim should be to establish an informal federation, which might operate by effective communication between the secretaries of the various groups, and should avoid financial implications. One route would be to establish computer networking. Then there was the question of whether the Federation should restrict itself to promoting the holding of congresses every four years, or whether it might encourage an increased number of smaller meetings – based on the meetings of national groups, but reinforced with special symposia. To encourage this discussion, a paper prepared by Michael Sleigh was circulated to the various national representatives in advance of the meeting.

The discussion on the proposal to form a Federation was led by Michael Sleigh, with the following results:-

1. It was agreed that the initiative to hold a European meeting had proved successful and it was agreed that it should be repeated.
2. It was agreed in principle that it was desirable to set up a European Federation of Protistological Societies. It was felt by some delegates that since at this stage some parties that could be interested had not been approached, the present meeting did not have the authority to establish a *protistological* federation. However, among all the protozoological societies which replied to the letter from the German Society there had been unanimous support for a federation, and there was also majority support from the floor of the meeting. It was appreciated that further groups might wish to join the Federation at a later date, and their participation should be invited.
3. It was agreed unanimously that the Federation should not replace national societies, but strengthen them.
4. Suggested roles for the European Federation would be:
   a. To hold a European Congress every four years, ideally midway between International Protozoology Congresses, by negotiated fusion with the meetings

of European Ciliate Biologists.

b. To provide an information network to enhance contact between constituent societies.

c. To encourage attendance of protistologists at national meetings, including specialist symposia, in other countries.

d. To provide more opportunities for student members to attend international gatherings. International Protozoology Congresses are held anywhere in the world and it might be financially more feasible for students to attend international gatherings within Europe.

e. To co-ordinate multi-national applications for funding of conferences or other activities.

5. Suggestions were made for the operation of the European Federation of Protistological Societies. It was hoped that the administration of the Federation would be informal and would operate in a similar fashion to that of the currently successful ciliate meetings. A national group organising a congress would be responsible for inter-congress continuity. It was anticipated that at one meeting the next would be nucleated – Societies could express their interest in organising the next European Congress, and a final decision concerning the venue for the next Congress could be made at the next intervening International Congress of Protozoology, should there be any problems.

Professor Lom made a provisional offer to organise the Second European Congress in Czechoslovakia in 1995, subject to consultation with his colleagues at home. This offer was gratefully acknowledged and it was agreed that a final decision would be taken at the International Congress in Berlin in 1993. In the interim the Steering Committee for the Reading Congress would be responsible for organisation of European matters until the next group takes up the baton in Berlin.

As far as the timing of European Congresses is concerned, the majority view of the Reading delegates was that early April was the most suitable time to hold meetings. However, it was agreed that there should be a written survey of members of all societies in the Federation to decide the optimal time of year to hold European Congresses.

Professor J. Blum, President of the Society of Protozoologists, attended the Discussion Meeting as an observer and gave his full support to the establishment of a European Federation along the lines proposed.

The First Congress was declared a success both for its scientific content and for its effectiveness in reinforcing old contacts and making new ones. However, the plan to hold the Second Congress in Czechoslovakia ran into problems, because, as reported by Jiri Lom early in 1993, the recent division of the former country into Slovakia and the Czech Republic made funding uncertain. Offers to provide an alternative

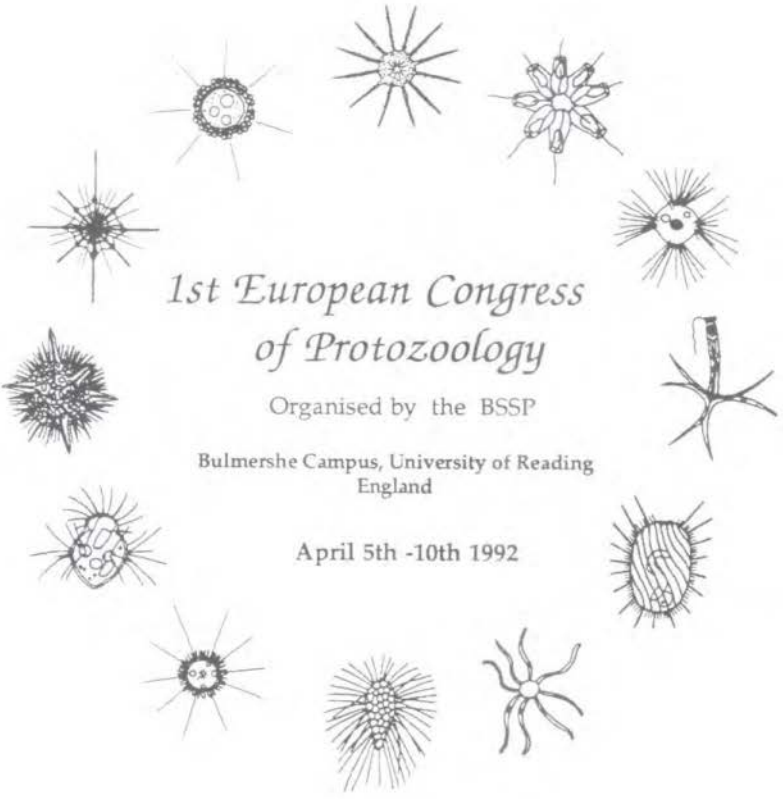


Fig.103 The Reading Congress logo imitating the European Community flag.

venue were received from Poland (Warsaw) and France (Clermont-Ferrand). National representatives were invited to consider their preference so as to make a decision at the Berlin Congress of Protozoology in July 1993. It was felt important to draw the French, whose attendance at Reading had been less than had been hoped (but the timing was not ideal for them), firmly into the Federation. As a result it was formally resolved at the Berlin Congress that the Second European Congress would be held in Clermont-Ferrand in 1995. In addition it was agreed that the meeting in Clermont-Ferrand should be regarded as both the Second European Congress of Protistology and the 8th European Meeting on Ciliate Biology, thereby achieving an amalgamation

and economy of organisational effort. Incidentally, it is interesting that in the autumn of 1992 the British Phycological Society indicated its support for the formation of a Federation of European Phycological Societies, with similarities to that proposed above!

The Second Congress was held in France from 21-26 July 1995, with typical French hospitality. It covered a broad range of themes and attracted around 300 delegates from many countries contributing over 280 presentations. The Plenary Lectures at this Congress, and summaries describing the various symposia, were published in a post-congress volume (Brugerolle and Mignot, 1995). Discussions were held at Clermont-Ferrand to consider mechanisms of future co-operation between national societies in Europe and to ensure continuation of the series of European Congresses. The following report prepared jointly by Michael Sleigh and Jean Grain (Chairman of the Organising Committee for the Clermont-Ferrand meeting) was circulated to representatives of 14 participating countries: Belgium, Bulgaria, Czech Republic, Denmark, Finland, France, Germany, Holland, Hungary, Italy, Poland, Russia, Spain and the U.K.

EUROPEAN COMMITTEE OF PROTISTOLOGISTS

At the first European Congress of Protistology held in Reading, England, in April 1992, there was discussion concerning the possible formation of a European Federation of Protistological Societies. Consultations and discussions have continued since that time, and culminated in the conclusion that for the present the best way forward would be to form a European Committee of Protistologists. This proposal was accepted by representatives of National Committees of Protozoology/Protistology meeting during the second European Congress of Protistology at Clermont-Ferrand, France, in July 1995.

- *The primary purpose of this Committee will be to ensure the future programming of European Congresses of Protistology, which should take place every four years, mid-way between International Congresses of Protozoology.*
- *The membership of the Committee will comprise one representative (the President or his nominee) from each National Society plus a Chairperson (as defined below), who will be responsible for co-ordination of Committee activities.*
- *The duties of the Committee shall be:*
  1. *to determine the venue of the next Congress*
  2. *to propose components of the programme*
  3. *such additional business as the chairperson shall consider appropriate, including particularly the co-ordination of matters of interest to*

protistologists, research networks, satellite meetings or relationships with supra-national organisations.

- *The meetings of the Committee shall be of two types:*
  1. *A meeting will be held during each European Congress with the primary purpose of fulfilling duty (1), and advising on the related question of suitable dates. The Chairperson and Organiser for this meeting shall be the President of the Organising Committee for the Congress then in progress. This chairperson will ensure transfer of responsibility for co-ordinating the European Committee to the President of the Organising Committee for the next Congress, and will pass on a list of addresses of contact persons of the constituent National Societies.*
  2. *A meeting will be held during each International Congress of Protozoology (two years before the next European Congress) to consider practical questions related to the forthcoming European Congress, and advise (but not direct) the Local Organising Committee, through its President, on matters concerned with the scientific programme (e.g. symposia, plenary speakers etc.), domestic arrangements and social programmes. The chairperson and organiser for this meeting shall be the President of the Organising Committee for the Congress being planned.*

Other business of the Committee will be conducted by correspondence between the members in order that no central financial costs be incurred in its administration beyond minimal postage costs.

At the meeting in July 1995 the Committee accepted the offer from Danish Protozoologists to organise the next Congress at Helsingør / Copenhagen in 1999.

Plans for the Third European Congress were confirmed at the Tenth International Congress of Protozoology in Sydney. The Congress was held in June 1999 at Helsingør, and was scientifically productive, although the expense of meeting in Denmark may have kept the attendance lower than it might have been. Plans are in process to hold the Fourth European Congress of Protistology at Camerino in Italy in 2003.

CHAPTER 19

PROTISTOLOGICAL SCHOOLS AND THEMES IN POST-WAR BRITAIN

In this Chapter an attempt has been made to survey the strands of research on protozoa in Britain in the second half of the 20th Century. Many of the individuals involved have gained their interest in protozoa through contacts with, or stimulation by, a limited number of individuals, or their protozoological descendants. The opportunity has been taken to point out the relationships of individuals concerned with the history of the BSSP, and to add information on their interests by mentioning monographs or research volumes that they have written or edited.

The most prominent protozoologist occupying an academic position in Britain after the 1939-45 war was probably Cyril Garnham, at the London School of Hygiene and Tropical Medicine. Garnham's distinguished career commenced with a medical degree followed by a period of medical service in East Africa, where his interests in parasites and their biology were richly rewarded (see Bruce-Chwatt, 1981 and Lainson and Killick-Kendrick, 1997). He worked on many parasites, but his main work was on the organism which formed the subject of his acclaimed book *Malaria Parasites and Other Haemosporidia* (Garnham, 1966). After formal retirement in 1968, Cyril Garnham continued active research for many years as a Senior Research Fellow at the Silwood Park Station of Imperial College. His many colleagues and friends contributed to a festschrift in his honour, edited by Liz Canning (1981).

The influence of Garnham upon protozoology extended far and wide, not only in Britain and the Commonwealth, but also in many countries where his numerous students worked (See also Chapter 6). Well-known among his colleagues at the London School were a number of people who later played significant roles in the BSSP: R. Killick-Kendrick served as Secretary, and both J.R. Baker and R.S. Bray as early members of the Committee; another of their number, Ralph Lainson, was elected to Fellowship of the Royal Society. These scientists worked on a wide range of blood parasites, and are probably better known for their work on kinetoplastids than malarial parasites (e.g. Baker, 1982b). Roger Bray was Secretary of the Organising Committee for the Protozoology Congress in London. John Baker has been very active in publishing works on parasites (Baker, 1969, 1982a, 1982b), as well as being the first editor of the BSSP Newsletter, Head of the Culture Centre in Cambridge, and a President of the BSSP. Amongst the protozoological contemporaries of Garnham at Silwood Park were Liz Canning, working principally on microsporidians (Canning and Lom, 1986), who served the BSSP as both Secretary

and President, and Bob Sinden, working on malaria parasites, who was also a BSSP Secretary.

Meanwhile there were other active centres of research on parasitic protozoa. Cecil Hoare was still involved in research with others at the Wellcome Laboratories of Tropical Medicine, and published a monograph on trypanosomes (Hoare, 1972). Another group was active at the Liverpool School of Tropical Medicine, where Wallace Peters, later to become a President of the BSSP, was also working on various protozoan parasites, including chemotherapy of malaria (Peters, 1970) and leishmaniases (Peters and Killick-Kendrick, 1987). From that same school came David Molyneux, who also worked with trypanosomatids (Molyneux and Ashford, 1983), and was BSSP Secretary until he moved to a position in Africa. Ann Bishop was at the Molteno Institute in Cambridge, later to be joined by Bruce Newton, who became the third President of the BSSP. Other teams were working on parasites of veterinary importance, for example at the Central Veterinary Laboratory at Weybridge, from which Davies, Joyner and Kendall (1963) published a monograph on coccidiosis. W.H.R. Lumsden, who published on kinetoplastid flagellates (Lumsden and Evans, 1976), worked at the Veterinary Station at Easter Bush in Midlothian (at which time he was on the BSSP Committee) before moving to the London School of Hygiene and Tropical Medicine.

Individuals and smaller groups were working in other university departments. At Exeter University the lamentably short career of Julian Hawes was cut short by his early death, but under his guidance Keith Vickerman studied for his PhD, and Frank Cox gained an undergraduate interest in protozoa (see also Chapters 10, 11). Keith went on to University College, London, where his work on kinetoplastids and other flagellates flourished, and gained him a Chair at Glasgow, and in time election to Fellowship of the Royal Society as well as to the Presidency of the BSSP. He was a member of a substantial parasitology group at Glasgow, within which Stephen Phillips and Graham Coombs have flourished (Gutteridge and Coombs, 1977; Coombs and North, 1991); both of them (as well as Win Gutteridge, from the University of Kent) have served the BSSP as Treasurer, and Graham also as President. Frank Cox, went to King's College, London, where his links with protozoologists drew him into BSSP affairs and to membership of the Committee; later he displayed broader parasitological interests in his general text (Cox, 1982) and in secretaryship of the BSP.

There were other protozoological activities at both University College and King's College in London. Terry Preston remained at University College after Keith Vickerman departed; he has worked on the movement of small amoebae among other topics, and has faithfully supported the BSSP through two terms as a Committee Member and as Treasurer. At King's College the legacy of Doris Mackinnon lived

on. In the Zoology Department the growing importance of cell biology, vigorously championed by Jim Danielli, was exemplified in studies on amoebae by Gerry Bell and Shirley Hawkins, and especially by the nuclear transplantation work continued later by Muriel Ord. Research using protozoa was also a feature of the Biophysics Department at King's, both through Sir John Randall, with interests in both ultrastructure of ciliates and in mechanisms of gene functioning, and later through Tom Cavalier-Smith whose interests in cell evolution have led to his present position as an authority on eukaryote phylogeny. Although much of Tom's work was done in Canada, we hope it will continue to thrive now that he has moved to Oxford.

The second President of the BSSP was Geoffrey Beale, of the Institute of Animal Genetics, associated with Michael Swann's Zoology Department at Edinburgh University. Beale's collaboration with Tracy Sonneborn in the U.S.A. had involved him in research on ciliate genetics, especially with *Paramecium aurelia* (Beale, 1954), and to an influential position in studies on protozoan genetics in Europe (see also Chapter 10). He was a founder member of the ciliate genetics group who arranged regular meetings in different European countries. Two of his Edinburgh colleagues published an early electron microscope study of *Paramecium* (Jurand and Selman, 1969). One of Beale's students was Ian Gibson, an early recruit to the University of East Anglia, who has recently taken up a new career as a Member of Parliament and is a spokesman on scientific matters for the current Labour Government. Geoffrey Beale's career has also broadened, with an interest in the genetics of parasites, especially malarial parasites. This interest was taken up by David Walliker (1983), at one time Treasurer of the BSSP, and Andrew Tait, also a BSSP Committee member, subsequently appointed Director of the Wellcome Unit for Molecular Parasitology in Edinburgh. Another important Edinburgh protozoologist, mentioned earlier, was Kay Adam, the indispensable Secretary of the BSSP at its foundation and its first Vice-President, who worked on small amoebae in the Zoology Department.

The promotion of experimental biology at Cambridge by James Gray and his colleagues found several outlets in protozoology, through the use of protozoa as objects for experimental study (see also Chapter 9). At the advice of Carl Pantin, who had himself used protozoa in various studies, Jack Kitching set out on studies of contractile vacuoles of protozoa (see biography by Sleigh, 1997). His career, principally at the Universities of Bristol and East Anglia, led to many publications on water balance of protozoan cells and to research on the effects of high pressure on the physiology of protozoa. Kitching's numerous research students included several who went on to academic posts teaching about protozoa. From Kitching's days in Bristol Roy Sladden went to Birmingham, Arthur Chadwick to Leeds, John Riddle to New Zealand and Alick Jones to Reading– all were sometime members of the BSSP, and Alick Jones a Committee Member, as well as being the author of a

monograph on ciliates (Jones, 1974). Fewer of Kitching's students from East Anglia remained in academia, notably Alister Macdonald, whose research on effects of high pressure on *Tetrahymena* led him to a career at Aberdeen, studying deep-sea animals.

Two other active members of the BSSP learnt their protozoology with Kitching, although they did not number among his PhD students. Lawrie Bannister found a route into protozoology via research and teaching on Anatomy, which led him to a post at Guy's Hospital Medical School, where he made important electron microscope studies on both malarial parasites and ciliates, and also contributed to BSSP affairs as a Committee Member and Secretary. Michael Sleigh was persuaded by John Harris to reinvestigate some of James Gray's studies on cilia. With knowledge of protozoa gained from Kitching (as well as from a technician who had picked up many hints about culturing protozoa from Doris Mackinnon during the period when King's College were evacuated to Bristol during the war), he chose to study ciliary co-ordination in ciliates. From this beginning grew a lifetime interest in protozoa described in many papers and books (e.g. Sleigh, 1973, 1989), and to involvement with the BSSP, leading to the post of President. Paddy Patterson was caught up with a fascination with protozoa in a similar way. As part of his PhD study on contractile vacuoles, supervised by Michael Sleigh at Bristol, he chose to survey the characteristics of contractile vacuoles in as many protozoa as he could find. He has never looked back, having developed skills in diverse forms of microscopy on protozoa of several groups (Patterson and Hedley, 1992), he was led to the specific interest in heterotrophic flagellates for which he is best known. He served the BSSP as Secretary and was elected Vice-President, but emigrated to a chair in Australia before he could transfer to the office of President. He has served the wider interests of protozoology as Co-President of the Tenth International Congress of Protozoology in Sydney, as an active member of the ISEP and as a prime mover of the first international meeting on heterotrophic flagellates (Patterson and Larsen, 1991).

Another product of the Zoology Department at Cambridge was the study of communities of freshwater protozoa by Lawrence Picken. This, and research on protozoa of Hobson's Brook by E.G. Gray, and on brackish water sediments by M. Webb, led the way in systematic ecological studies on protozoa in Britain. Meanwhile, in Scotland, at first in Edinburgh and Aberdeen, and later in Stirling, John Stewart was encouraging students to take up ecological research on protozoa. From that group in Stirling came Johanna Laybourn and Bland Finlay, who worked together on some laboratory studies of ecological energetics of ciliates, and have both gone on to work on lake protozoa. Johanna Laybourn-Parry took the academic route via Universities of Lancaster, La Trobe (Australia) and Nottingham, and lake studies in Scotland and Antarctica, and has recently been Secretary of the BSSP, as well as

writing books (Laybourn-Parry, 1984, 1992). She also collaborated with Andrew Rogerson, another active BSSP committee member, who was at Millport Marine Station for some years before emigrating to the U.S.A. Bland Finlay joined the Freshwater Biological Association at Ambleside, and has enjoyed fruitful collaboration with Tom Fenchel in Denmark on the way to establishing his present high reputation through lake and laboratory researches. Meanwhile, John H. Baker, bacteriologist at the Freshwater Biological Association's River Laboratory in Dorset, where there was no protozoologist, invited the collaboration of Michael Sleigh in studies on micro-organisms of flowing waters which generated a series of papers on river protists. This entry into protozoan ecology led Sleigh on to collaboration with marine biologists, specifically Peter Burkill at Plymouth Marine Laboratory, and a productive period of research on ecology of protists of the open seas. This work helped stimulate co-operation between marine protozoologists through the organisation of a NATO Advanced Study Institute in Plymouth (Reid, Burkill and Turley, 1991).

Ecological researches of different types were going on at two laboratories at Aberdeen. British protozoology had a background in research on soil protozoa since the work of Sandon and Cutler in the 1920's, but it remained a neglected area, with the exception of some studies by O.W. Heal at the Institute of Terrestrial Ecology. John Darbyshire at the Macaulay Institute for Soil Research (near Aberdeen) (see also Chapter 8) ploughed a rather lonely furrow in this field of work, but was a faithful member of the BSSP, and saw his area of research become more productive (Darbyshire, 1994). Humphrey Smith, who served the BSSP as a Newsletter Editor, gained his experience on soil protozoa in the Antarctic. Work on the roles of soil protozoa is being continued by Brian Griffiths at the Scottish Crop Research Institute. At the Rowett Research Institute Margaret Eadie, an early Treasurer of the BSSP, was working on rumen ciliates, following the researches of G.S. Coleman at the Babraham Laboratory in Cambridge. These studies were continued by Alan Williams at the Hannah Research Institute in Ayr (Williams and Coleman, 1991). Alan Williams collaborated with Ron Butler at the University of Manchester in studies on ultrastructure and with David Lloyd in Cardiff in work on the physiology of these anaerobic ciliates. Ron Butler trained as a plant ecologist, but migrated to electron microscopy. He found that a bequest to support research on protozoology at Manchester had lain unused for some years, and was sufficient to support several research studentships. The students he recruited worked on the fine structure and physiology of suctorian and rumen ciliates, and among them Trevor Hitchen served as a Committee member. Ron Butler himself became actively involved in BSSP affairs as Treasurer and later President of the Section. Two other stalwarts of the BSSP whose interests in protozoa were aroused by contacts made during teaching were Brenda Nisbet from Aberdeen, twice elected a member of the Committee and

author of a book on food and feeding of protozoa (Nisbet, 1984), and Muriel Walker from Leicester, who was Secretary of the BSSP at a particularly busy time.

These ecological and structural studies were supported by taxonomic work, concentrated especially at the British Museum (Natural History), now the Natural History Museum (NHM), and at the CCAP. Ron Hedley, who was elected to be President of the BSSP and later appointed Director of the NHM, worked on foraminiferans and testate amoebae. With his assistant Colin Ogden, himself a Treasurer of the BSSP, Hedley produced a book of scanning electron micrographs of highly photogenic testate amoebae (Ogden and Hedley, 1980) (see also Chapter 11). Fred Page, working at the CCAP was a world expert on the naked amoebae, and published a series of valuable keys to these protozoa (Page, 1976, 1983, 1988), as well as being a regular attender and Committee member of the BSSP. Foraminifera have also been of much interest to British geologists, several of whom, like John Murray (Murray 1971) and Andrew Gooday, have been members of the parent Society and spoken at BSSP meetings. After working on ciliates of activated sludge sewage systems at the Water Pollution Research Laboratory Colin Curds moved to the NHM. His key to the ciliates of activated sludge (Curds, 1969) was very useful in microbiological teaching, and the later taxonomic books on freshwater ciliates (Curds, 1982, Curds, Gates and Roberts, 1983) important research aids. Colin served as Treasurer of the BSSP, as did his colleague Alan Warren, whose links with the Systematics Association made him a leading member of the group organising the symposium on Evolutionary Relationships among Protozoa in 1996 (Coombs et al., 1998). A valuable key to the diversity of interstitial ciliates of marine sands was written by Phil Carey, another of the BSSP Newsletter Editors, while he was at the NHM (Carey, 1992).

Some of the modern British research on free-living flagellates can be traced back to that redoubtable early electron microscopist Irene Manton, whose studies at Leeds included groups of interests to both algologists and protozoologists (see also Chapter 11). Among her colleagues at Leeds, Gordon Leedale established his name as an authority on euglenoid flagellates with a systematic account (Leedale, 1967), and a volume of contributed chapters (Leedale, 1971). Comparable expertise on the dinoflagellates was developed by John Dodge (1982, 1985), who also published an early ultrastructural review featuring many flagellate groups (Dodge, 1973). Barry Leadbeater, the current President of BSSP has worked with both John Dodge and Irene Manton; his special interest has been in choanoflagellates, but he has gone on to a broader interest in free-living heterotrophic flagellates. This has been exemplified in the research on flagellate feeding ecology by his students, including Jackie Eccleston- Parry, an active BSSP Committee member in recent years, and by his role in promoting the symposium on *The Flagellates* at Birmingham in 1998 (Leadbeater

and Green, 2000). Heterotrophic flagellates also appear among the haptophytes (Green and Leadbeater, 1994) and the chromophytes (Green, Leadbeater and Diver, 1989), both of which have attracted interest from British protistologists. Cryptophyte flagellates have been a special interest of 'Franco' Novarino at the NHM, the current BSSP Newsletter Editor. Both Keith Vickerman (1998) and Paddy Patterson (Patterson and Larsen, 1991) have been active in research on heterotrophic flagellate species from smaller groups, which have especial interest from the point of view of eukaryote evolution (see also Chapter 12).

Protozoologists associated with the BSSP appear to have contributed a surprisingly large number of books in the last 40 years. With the current pressures to generate publications with a high impact factor to impress panels in research assessments, it seems unlikely that this form of publication will be as popular in the future.

CHAPTER 20

PUBLISHING OF PROTOZOOLOGICAL WORKS

IN POST-WAR BRITAIN

A recurring theme in the earlier history of the BSSP was the question of whether or not the Section could, or should attempt to, support a British protozoological journal. One of the inducements for protozoologists in Britain to form a Section of the Society of Protozoologists was the prospect of publication of abstracts of their meetings in the Journal of Protozoology, and the possibility of publication in that journal at reduced rates. In 1968, at a time when separation from the parent Society was being discussed because of two subscription increases in successive years, a publisher approached British protozoologists for comments about a new journal. Iliffe Science and Technical Publications Ltd. were considering publishing a journal to cover all aspects of Protozoology. The journal would be published quarterly with about 10 papers per part costing about £6-£10 according to circulation. The intention would be to publish papers from any country within 6 months of acceptance. The Committee of the BSSP welcomed the idea, but commented that the proposal of the publishers that their own graduate staff would edit the journal could lead to lack of confidence in editorial standards. At the next meeting it was learned that Iliffe now proposed to include translations of selected Russian papers in the journal.

Negotiations continued; first the publishers offered the editorship to Keith Vickerman, whose view was that the job was too much for one person and would need a team. By the next year Dr J.F. Ryley had been approached to act as editor. He had agreed in principle, but needed support from the BSSP at its Annual Meeting in 1970. The support he sought was a promise of sufficient manuscripts in the ensuing 6 months to fill the first two parts of the proposed journal. He had discussed the arrangements in detail with the publishers, who would provide technical editing and publishing services after acceptance of papers by a panel of protozoological editors, who would also decide editorial policy. The quarterly journal would publish papers in English and abstracts of Russian papers, which Dr Raikov in Leningrad would collect and select. After vigorous discussion among the 34 members present, it was revealed that only 9 members present felt that the journal was really needed, but 20 were prepared to submit articles for it if launched. In view of the under-representation of members working on free-living protozoa at that meeting, it was decided to take a postal vote. This vote revealed that support looked likely to be insufficient, and the publishers withdrew their proposal. In the same year a proposal was made, apparently in conjunction with the Commonwealth Agricultural Bureau, to seek support for an

Abstracting Journal for Protozoology. Although several possible organisations were approached in a search for funds, almost all were unwilling, and even the CAB felt unable to finance it. The information was passed to the parent Society in case resources could be found in the U.S.A.

Discussions in the mid-1980's between Paddy Patterson in Bristol and John Corliss in Maryland about the lack of suitable outlets for reviews on the broad range of "Protists" led to an approach to Frank Round, the proprietor of Biopress Ltd. of Bristol. With the co-operation of Biopress the series *Progress in Protistology* was born, under the editorship of Corliss and Patterson, with the first volume appearing in 1986. Two further volumes appeared in 1987 and 1989. Although the majority of the reviews were on protozoological topics, there was a strong trend towards inclusion of a broader interest in lower eukaryotes. There were also substantial book review sections. Sadly the editors did not feel able to continue their noble efforts beyond the three volumes, but protistologists are grateful for some excellent reviews which might not otherwise have been written. Other editorial activities included the sustained efforts of John Baker with *Advances in Parasitology* and *Transactions of the Royal Society of Tropical Medicine and Hygiene.*

British protozoologists turned out to be considerably more successful at publishing textbooks on Protozoa, as well as the more specific monographs mentioned in the previous chapter. The first comprehensive British text on Protozoa to appear after the 1939-45 war was *An Introduction to the Study of Protozoa* by Doris Mackinnon and Julian Hawes (1961). Professor Mackinnon had started writing the book after she retired from King's College, London, but she was taken ill when she had only worked on three chapters. She approached Dr Hawes in the summer of 1956, seeking his collaboration with her in writing the book, but unfortunately she died in September 1956 before they could meet, leaving Julian Hawes to write the bulk of the book. It was a scholarly volume that concentrated particularly on types that exemplified classes of protozoa, and it remains very valuable in the laboratory for the descriptions of practical techniques and excellent illustrations. The purpose of the slender, large-format, book on *The Protozoa* by Keith Vickerman and Frank Cox (1967) was rather different. It successfully satisfied the need to give modern information and illustrations on the types of protozoa featuring in senior school syllabuses and first-year undergraduate courses. The aim of *The Biology of Protozoa,* by Michael Sleigh (1973) was to relate the new insights into cell ultrastructure and functioning of the previous 2 or 3 decades to the diversity of cellular organisation and physiology of Protozoa of all types. It therefore reviewed current conceptions about the nature of the various groups of Protozoa, as well as providing a guide to recent research on the structure and life processes of Protozoa. This book proved successful in many countries, and appeared in a Spanish translation. It was reprinted several times, and 1989), initially published by Edward Arnold, but later by Cambridge University

Press. Another modern text, whose slightly more limited aim is indicated by the an extensively revised version appeared as *Protozoa and Other Protists* (Sleigh,title, was *A Functional Biology of Free-Living Protozoa*, by Johanna Laybourn-Parry (1984). A particularly valuable practical guide, by virtue of its keys and both colour and line-drawn illustrations, is *Free-Living Freshwater Protozoa: A Colour Guide*, by Paddy Patterson and Stuart Hedley (1992). The colour photographs in this book were of the same high quality as those in a *Taschenatlas* jointly written in German by Klaus Hausmann and Paddy Patterson (1983). Practical information on the collection, identification and culture of protozoa appeared in many of these texts, but valuable books specifically aimed at providing this information for free-living protozoa were written by Page (1981) and Finlay et al. (1988), both from the point of view of the CCAP.

British protozoologists have also been involved in the production of texts on parasitic protozoa. The most prolific author and editor of such texts has been John Baker, writing/editing both on his own (Baker, 1969, 1982a) and in collaboration with Julius Kreier (Kreier and Baker, 1987, 1991etc.). John Baker was also involved in preparation of a book on culturing parasitic protozoa (Taylor and Baker, 1978). Books by protozoological parasitologists with a more general coverage included *Modern Parasitology* by Frank Cox (1982).

Although the widely-used *Illustrated Guide to the Protozoa* (Lee et al. 1985) was published in the U.S.A., 5 of the 22 contributors were written by British authors. The extensively re-written second edition of the *Illustrated Guide* is expected to be published very soon – indeed it has been expected for several years, but held up by accidents involving two of the editors. Two of the four editors, Gordon Leedale and Paddy Patterson we can surely claim as British, and, according to an early list, British authors are making contributions to 18 of 39 chapters.

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