

MICROBIOLOGY TODAY

49:2 October 2022



Protists

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Editorial

Welcome to the October 2022 issue of *Microbiology Today*. I'm writing this editorial on the back of a heatwave (and imminent hosepipe ban) in August – hopefully when you are reading this, we have some cooler and wetter weather coming our way!



In this issue, I am delighted to showcase articles contributed by members of Protistology-UK, a society which has been affiliated with the Microbiology Society since 2018. It has been a pleasure to work with members of the Protistology-UK elected committee to provide you with this fascinating snapshot of research and engagement activities carried out by their members, and hopefully you will have an equally enjoyable experience as you make your way through the issue. To give you some more details on the theme of this issue, I will pass you on to Fiona Henriquez, Sonja Rueckert, and Anastasios Tsaousis, committee members of Protistology-UK (page 68).

For the remainder of my Editorial, I want to highlight some exciting news relating to *Microbiology Today*.

I am very pleased to announce that we are looking for a Deputy Editor of *Microbiology Today*! In this role you will work with me for a year to learn about the editorial process before taking over as Editor and Chair of the Editorial Board in 2024. Editor of *Microbiology Today* has been a great experience for me – not only do you get to hear about the diversity of work being carried out by members of the

Society, but you also get to work with the wonderful and incredibly talented staff at Microbiology Society HQ! If you like the sound of translating the enthusiasm of Society members into print articles, then I urge you to put in an application. Find the full job description and learn how to apply online (microb.io/jobs). Applications close on **1 November**. If you do have any questions about the role, you are more than welcome to contact me directly.

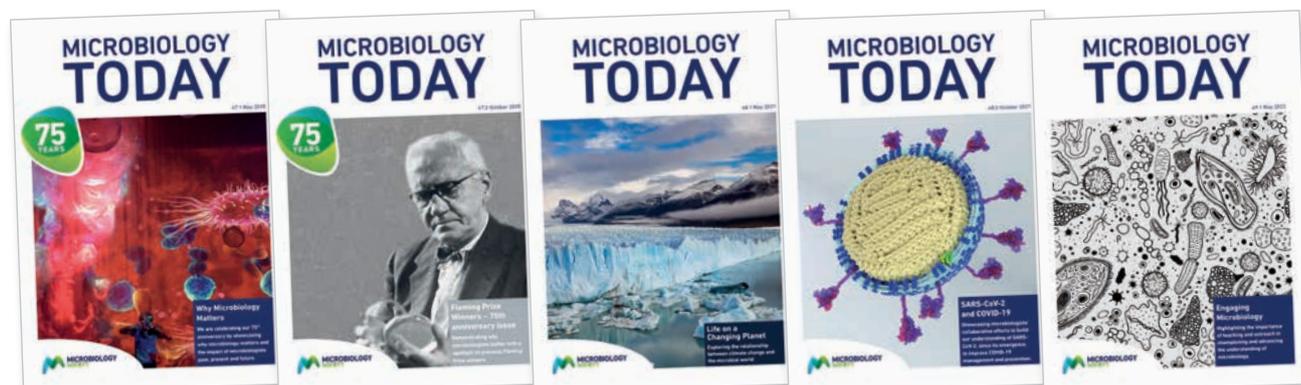
The Editorial Board and Society staff have been working over the past year to define how *Microbiology Today* can best represent the work and interests of all Society members in 2023 and beyond, and we are very keen to hear from you. I am always delighted to be contacted directly with your thoughts, feedback and suggestions for what you would like to see in future issues of *Microbiology Today*.

Chris Randall

Editor

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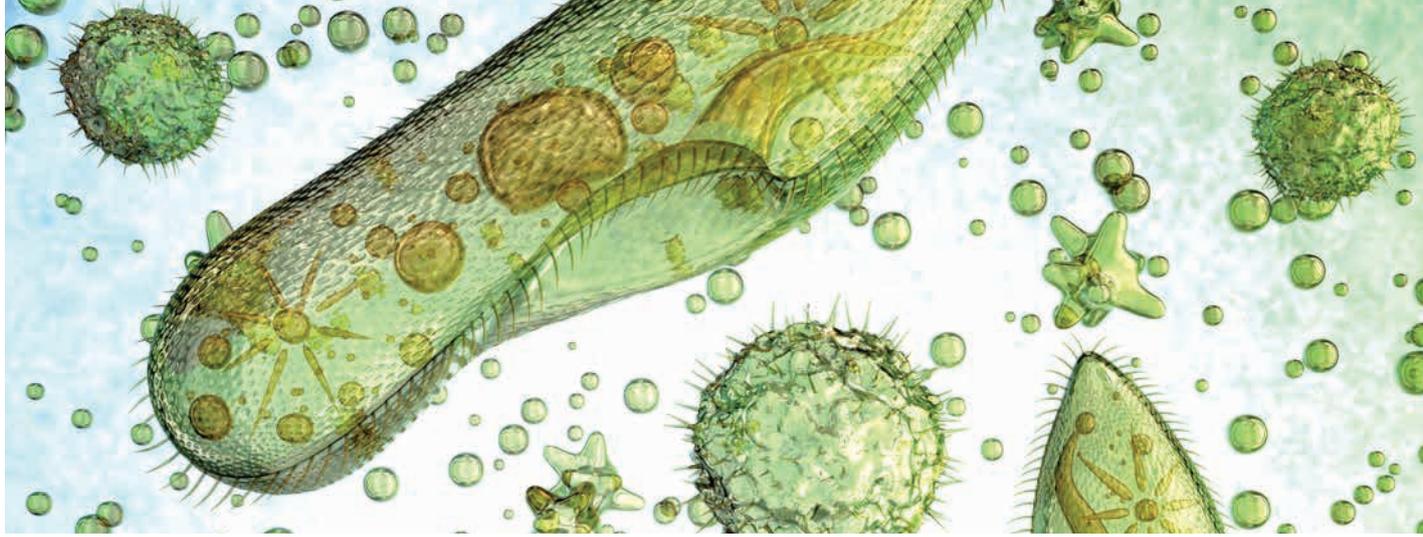
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From the President

Welcome to the October issue of *Microbiology Today*. I want to start by thanking the members of Protistology-UK (protistology.org.uk) who have been heavily involved in the production of this issue. This Learned Society (formerly the British Society for Protist Biology) is a membership organisation for scientists and amateurs interested in all areas of protistology, from ecological to medical and from sub-cellular to population studies.



The Society primarily exists to support and promote protistan research and teaching in the UK, but a key aim is to encourage the development of young scientists.

The organisation hosts two scientific meetings a year and provides bursaries for student attendance together with prizes for student presentations. Membership of Protistology-UK is a benefit of Microbiology Society membership – just head to the 'Update details' section when you log in and select 'I would like to be a member of Protistology UK' under the 'Get involved' tab.

This is the second *Microbiology Today* issue of 2022 and my second issue as President of the Microbiology Society. As we come to the final months of the year, I would like to thank all the members who have participated in Society activities and attended events during 2022 – it has been a great pleasure to meet so many of you in my first year as President, and I look forward to opportunities still to come.

At our Annual General Meeting in September, we launched the Society's ambitious new strategy, which lays out our vision, mission and values and will guide our work. In the five years between 2023 and 2027, the Society's principal goal is to strengthen our culture of being a community-driven Society by amplifying our members' voices, wherever they are in the world, and empowering them to embed the benefits of microbiology within wider society. The period of the strategy will undoubtedly bring new opportunities and great change for the Society. We will gain a better understanding of the diversity of our members; we will harness local knowledge for worldwide impact; and we will recognise global differences in accessing opportunities.

To achieve our ambition, we rely on your ongoing support. In January, our founding journal, *Microbiology*

(mic.microbiologyresearch.org), will transition to fully Open Access, the first of the journals in our portfolio to do so. We are doing this because of the benefits Open Access brings to our membership, all microbiologists and those with an interest in microbiology. The world is entering a new era of open science, challenging the status quo by recognising the value of greater transparency and focusing on reproducibility, data management, collaboration and good scientific citizenship. At the Microbiology Society, we embrace these changes and recognise the positive impact they represent for our community, for the scientific endeavour and for society's understanding of pressing global challenges. We cannot achieve this major change without your support; if you publish one article with us you are benefiting your community. Ask your institution to sign up to our Publish and Read model to give your work a chance to really make a difference – when you publish Open Access with us, your articles will have a greater reach and impact. You can read more about Publish and Read on our journal platform (microbiologyresearch.org/publish-and-read).

As always, we are incredibly grateful to all the members who submit to our journals and to those who give up their time to so enthusiastically get involved in everything we do, by joining Committees, Divisions, Panels, Working Groups and by becoming Champions. Thank you all, and I look forward to meeting and hearing from more of you during the remainder of the year and in 2023.

Gurdyal Besra

President

president@microbiologysociety.org

From the Chief Executive

At the Annual General Meeting in September, the President launched the Microbiology Society's new strategy, which will run from 2023 to 2027. It is the result of months of work by Council members and staff, consultations with various groups of members and assessments of the changing external environment. It would be easy to imagine that all this effort would lead to substantial changes in the strategy, but in the end much of it is unaltered. The changes are focused and important.



As Council members listened to the membership and thought about how the Microbiology Society can have an even greater impact in the future, they honed in on three things that they want to strengthen.

The first is to be ever more inclusive – our values say that we are welcoming to anyone interested in microbes, and the more we can make that a reality, the stronger we will be. Through a better understanding of you, the members, we can better unlock the potential of your broad and deep specialised knowledge.

The second emphasis is on the international dimension of the Society's work. If the last two years have shown us anything, it is that microbes don't respect national boundaries. What the Microbiology Society seeks to do is harness local knowledge, whichever part of the world it comes from, and use it for worldwide impact.

Third, recognising that our strength comes from our membership, Council wants to redouble our efforts to engage with you and to make it easier and ever more rewarding for you to interact with staff and with members of Committees and Editorial Boards so that we can optimise what we do to support and advance your careers in microbiology.

The things that remain the same in the strategy are the things that have been unchanging since the wisdom of our founders originally set out the purpose of the Microbiology Society. Our first President, Sir Alexander Fleming, spoke at the inaugural meeting about "bringing together workers in the various branches of microbiology who might not otherwise meet and who would thus get acquainted and talking together – it is in this way that real advances will be made." Marjory Stephenson, who was offered the founding Presidency before Fleming but modestly turned it down, said "we should make the scope of the Society as wide as possible." They knew that one of the most crucial ways to advance the science of microbiology was to bring together microbiologists and get

them interacting. The world is now very different – technology, travel, funding, social pressures, the list of changes is endless – but the basic principle has been constant throughout.

As we move into the period of the new strategy, one of the most important changes we face is the world of scientific publishing. It is a more competitive, more time-consuming business than it has ever been, and its importance in the lives of researchers has grown relentlessly, as scientists are measured, rewarded and judged more and more on the basis of articles they publish.

From its earliest days, the Society has published important microbiology research – in its 75th year, our flagship journal *Microbiology* has published three papers by historian Peter Collins, detailing its fascinating story. Publishing has always been the main source of income for the Microbiology Society. The financial surplus that our journals generate funds our conferences, prizes, professional development activities and meetings. Rampant inflation makes life tougher for the Society just as it does for family budgets; the reason we have a financial buffer is the historic success of our journals.

If the next five years are to be successful, if Council's aim of a more inclusive Society with ever greater impact is to be realised, the journal titles will be crucial to that success. If you value the Microbiology Society, if you enjoyed Annual Conference or know someone who received a Harry Smith Summer Studentship, if you'd like to be on a Committee or if you think we can help with your professional development, the single easiest thing you could do to help is to submit your next research paper to one of our six journals, which between them provide a home for all microbiology.

Peter Cotgreave

Chief Executive

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Protists on the spot: opening the field of view on protistology

Fiona Henriquez, Sonja Rueckert and Anastasios Tsaousis

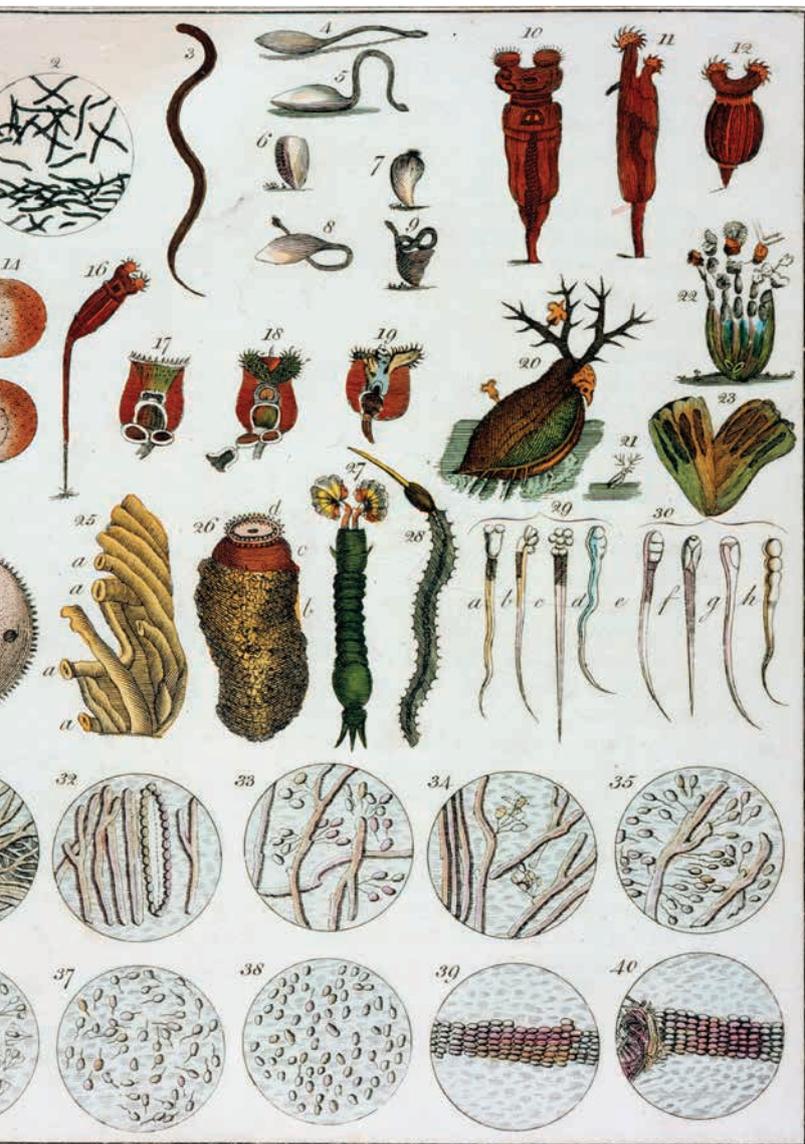
Discovery of protists

When it comes to the natural world, most knowledge, including that of the general public, is focused on animals and plants. Until a few centuries ago, one of the major reasons for this was the lack of technology to make micro-organisms visible. This changed when Antoni van Leeuwenhoek (1632–1723), a trained linen draper and haberdasher, developed a single-lensed microscope out of his own interest to study what lay beyond his eyes. Leeuwenhoek spent a lot of time making lenses to find the perfect one. The range of magnification of these lenses was between 50 and 300 times. Driven by his curiosity, he used these simple microscopes to describe the little critters he discovered in environments that ranged from rainwater to the human intestine, as animalcules. Even though he was not a trained scientist, his thorough observations enabled him to make some fundamental discoveries, which he sent in the form of letters to the Royal Society. In the beginning, his discoveries were often disputed due to his background, but this changed over his lifetime, and his work (~375 contributions) was mostly published in *Philosophical Transactions*. He has been coined as the father of microbiology as his microscopes enabled him to describe bacteria and protists for the first time ever. He was motivated to answer essential questions, some of which we are still trying to answer today: why is there such a diversity (morphology/behaviour) of these organisms and how did it evolve? How can they be distinguished and classified?

Why is protistology important?

Protists or protozoa are a large group of single-celled eukaryotes that have been identified across the eukaryotic tree of life. They are not a monophyletic group, and some species are close relatives of plants, animals and fungi.





They contribute significantly to microbial ecology, soil fertility and water quality. They also have an enormous impact on animal and human health, with many species known as emerging pathogens. Protists interact with other microbes (viruses, archaea, bacteria and fungi) through predatory, mutualistic or symbiotic relationships. This makes the study of protists (protistology) an important node in the different fields of biology, including ecology, infectious diseases and evolution.

Ecology. Protists have been isolated from diverse habitats, including extreme environments, such as polar regions, deserts or deep-sea ocean vents. Advances in protistology reveal new species and ecological interactions with other organisms. Their key roles in environmental niches highlight their importance in influencing environmental health.

Infectious disease. Many human and animal obligate and opportunistic parasites are protists. They use different routes to transmit infections, e.g. through vectors (*Plasmodium*, *Leishmania*, *Trypanosoma*) or the oral-faecal route (*Cryptosporidium*, *Toxoplasma* oocysts, *Eimeria*, *Entamoeba*, *Giardia*). A common challenge with all protist pathogens is the tremendous difficulty in treating and preventing the disease they might cause. In addition to causing infection, some protists are themselves vectors of infectious agents. For example, the opportunistic pathogen *Acanthamoeba* harbours pathogenic bacteria itself, such as *Legionella*. By contrast, some protists are described as key determinants in animal and plant health, due to their ability to phagocytose and therefore remove pathogenic bacteria.

Left: Antoni van Leeuwenhoek. Right: 'Animalcules' observed by Leeuwenhoek, ca 1795. Rijksmuseum (left); Ann Ronan Picture Library (right)/Science Photo Library



Coloured scanning electron micrograph of a single *Dictyostelium discoideum* amoeba with bacteria. Eye of Science/Science Photo Library

Evolutionary biology. Protists are excellent models for understanding evolution. Their genomes often include evidence of lateral gene transfer, in particular from bacteria, archaea or other protists. This is no surprise in view of their intimate relationships with other micro-organisms. Genetic data strongly suggest protist–microbe symbioses, from the first studies identifying mitochondria, plastids and other organelles as products of early endosymbiosis of bacteria. Moreover, several protists, such as choanoflagellates, are used as models to understand the evolution of multicellularity.

Modern technologies

Over the last few decades, there has been an explosion of new technologies that have been used to understand the biology of all lifeforms. These ‘omic’ technologies have also revolutionised protistology research. Scientists have identified novel species at a rapid rate using a combination of single cell genomics, metabolomics and proteomics, and this has also increased knowledge of symbiotic relationships between protists and other microbes. Despite this tremendous progress in the field, the major challenge is to understand how protists survive, develop relationships with other microbes and adapt to new environments in a temporal manner. Traditional protistology includes cell culturing, single-cell isolations, staining and microscopy (from light to advanced electron microscopy), techniques that are slowly being ignored by

researchers due to lack of time and expertise. Whilst modern omics technologies have allowed us to study communities, from molecules via species to the system level, they do not provide deep insights into the basic biology and ecology of protists. The strength of observations, that can be made with even the simplest microscopes like Leeuwenhoek developed and used, are not to be underestimated when it comes to understanding the biology and ecology of protists and should be a valid aspect in combination with new advanced technologies.

With this *Microbiology Today* issue we would like to increase cross-sector awareness of the field of protistology, emphasising the role of protists in ecology, health, disease and evolution and their importance in the environmental and health sectors, including the benefits and challenges associated with their presence in certain niches.

About the authors



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All authors are currently elected committee members of Protistology-UK, a society that aims to promote the study, teaching and dissemination of all aspects of protistology, from ecological to medical and from subcellular to population studies.

We have formed a long-term partnership with the Microbiology Society, which so far has proven successful in bringing together and sharing knowledge between communities for the benefit of our memberships.

More information about the authors, news and events regarding the society can be found on the Protistology-UK website (protistology.org.uk).

What inspired you to get involved in protistology research?

Fiona: During my honours project I started working on *Toxoplasma gondii* and I was fascinated by these tiny eukaryotic cells that could invade mammalian cells. During my PhD and postdoc I met researchers who were amongst the first to characterise protist life cycles and their role in the environment – this consolidated my enthusiasm for such fascinating micro-organisms.

Sonja: I used to work on metazoan fish parasites, but then my postdoc supervisor, Professor Brian Leander at the University of British Columbia, Canada, introduced me to protists. Roughly since 2007, I was hooked, with a focus on a specific protist group, the gregarine apicomplexans. There are a lot of species described, some of which I actually described, but there is still so much to learn about these fascinating organisms.

Anastasios: During my PhD studies I was introduced to the evolutionary cell biology field, where I was studying the adaptations of various single-celled parasites. A few years later, after attending my first protists' meeting, I was really fascinated about the diversity, biology and adaptations of these organisms, which subsequently triggered my interest to work with them.

Why is it important to be part of a membership society like Protistology-UK and the Microbiology Society?

Fiona: Both societies are very welcoming and provide a great source for networking, news and skills development.

Sonja: Membership societies provide you with the opportunities to interact with your research community. While it is clear that there is a lot of knowledge exchange going on, e.g. at conferences, it is often the small conversations that you have or new people you meet that spark new research projects. There is also a lot of support offered, especially for young researchers to help them with their career paths, networking, skills development, and monetary help to attend scientific meetings, which are all extremely valuable.

Anastasios: Both societies provide great opportunities for networking and diversification of knowledge.

News



Microbiology Society is now a member of EDIS

We are pleased to announce that earlier this year the Microbiology Society joined the Equality, Diversity and Inclusion in Science and Health (EDIS) group as a member organisation. In line with one of our core values, welcoming anyone interested in microbes, their effects and their uses, we are delighted to be a part of this coalition of organisations working together to improve the science and health landscape.

Join us in celebrating the Society's diversity for LGBTQ+ STEM Day

LGBTQ+ STEM Day is an annual awareness day that celebrates diversity in sexuality and gender identity whilst also highlighting obstacles and challenges faced by LGBTQ+ scientists.

To mark this year's event, we are hosting an online discussion that will include the participation of openly LGBTQ+ scientists representing different career stages, both in academia and the biotech industry. We will talk about the challenges that LGBTQ+ researchers face in their careers and how they overcome these obstacles through community-building and learning from leaders in the field.

We have a fantastic line-up of panellists and speakers: Professor Bryan Bryson (Massachusetts Institute of Technology, USA), Dr Anna Fagre (Bat Health Foundation, USA), Dr Kevin Maringer (The Pirbright Institute, UK), Dr Jason Mellad (Start Codon, UK), Charlotte Roughton (Newcastle University, UK) and Professor Michael Sauer (Institute of Microbiology and Microbial Biotechnology, Austria).

The event is open to everyone and will take place virtually on **18 November 2022 from 15:00 to 16:30 GMT**. Register on our website at microbiologysociety.org/QueerInMicro.

...we believe fostering and promoting greater diversity and inclusion amongst our membership will ensure we reach the full potential of microbiology research and the impact it has on our current societal issues.

*Professor Gurdyal Besra FMedSci FRS,
President of the Microbiology Society*

By joining the EDIS group the Society has committed to contributing towards their objectives whilst contributing resources. Learn more about the EDIS group and their aims at EDISgroup.org.



Protistology-UK Autumn meeting 2022

Protistology-UK will be hosting their Autumn meeting on **1–2 December 2022** at the Natural History Museum in London, UK. The hybrid meeting will focus on the theme of recognising the value of core methods, and how these methods should be retained and married with new methods.

Find full details about the Autumn meeting and register to attend on the Protistology-UK website at protistology.org.uk/autumn-meeting-2022.

News

Microbiology 75

This year marks 75 years of our founding journal, *Microbiology* (mic.microbiologyresearch.org), and 75 years of publishing for the community. Throughout the year, there have been a series of activities celebrating this milestone, and we are pleased to highlight the second of three historical articles that are being published this year. 'How *Microbiology* was run' (doi.org/10.1099/mic.0.001234) explores what was involved in running the journal, the challenges it faced at different times, and how a general microbiology journal fit in an evolving discipline.

In line with the biennial bacterial cell–cell communication meeting which took place in June last year, *Microbiology* launched the Environmental Sensing and Cell–Cell Communication collection. Guest edited by Martin Welch (University of Cambridge) and Anugraha Mathew (University of Zurich), submissions are welcomed on microbial sensing and signalling pathways, quorum sensing, chemoreception, secondary metabolism, and the complex interplay between different sensory pathways.

The final collection of the year will focus on the journal's newer section category, Microbial Evolution, and aligns with the Understanding and Predicting Microbial Evolutionary Dynamics meeting. This collection and meeting are organised by *Microbiology* Senior Editor and Editors: Michael Brockhurst (University of Manchester, UK); Jenna Gallie (Max Planck Institute for Evolutionary Biology, Germany); James Hall (University of Liverpool, UK); Stineke Van Houte (University of Exeter, UK). More information on how to submit will be released soon, so keep an eye out!

We would like to thank everyone who has supported *Microbiology* so far. We look forward to our Open Access future, which you can learn more about in Gavin Thomas' article on page 75, and hope that you will join us on our journey and influence the future of *Microbiology*.

From January 2023, all articles published in *Microbiology* will be Open Access. The Microbiology Society is a not-for-profit publisher, publishing for the community, and all journals income is invested back into the Society.

Claudio Ventrella/Stock



Supporting Open Access: the growth of Publish and Read

The Society continues to expand its successful Publish and Read model, now facilitating Open Access (OA) at 270 institutions across five continents. The Society's business model, created in collaboration with other membership organisations in the Society Publishers' Coalition, enables libraries to repurpose subscription spend and simplify administration for OA publishing. Affiliated researchers are entitled to uncapped, fee-free OA publishing, including in our fully OA titles, and access to all content on the platform.

The model continues to go from strength to strength, onboarding individual institutions as well as national consortia in the UK (JISC), Australia (CAUL) and Canada (COPPUL, BCI, CAUL-CBUA, OCUL). The Society is actively working to grow the reach of this transformative agreement as a key tool in its journey to a sustainable OA future.

What's more, by publishing with a Society journal, you will also support funding for our grants, events and activities for the community. Find out more at microbiologyresearch.org/publish-and-read.



Wladimir BulgarThinkstock

Microbiology Society launches open research platform

Our sound science journal, *Access Microbiology*, has re-launched as an innovative open research platform, embracing smart manuscript review tools, transparent peer review and Open Data. The Open Access platform offers a new service for members of our community to disseminate their work rapidly, transparently and rigorously, and is a home for all research outlets, not just traditional research. *Access Microbiology* welcomes work from all branches of microbiology and virology, including replication studies, negative or null results, interdisciplinary work and more. It is a symbol of the wider transformation that is to come at the Society towards a world of Open Science.

The platform is now open for submissions – free to publish until June 2023 (acmi.microbiologyresearch.org).

News



Giuseppe Miglino/Stock

Annual Conference 2023

The Microbiology Society Annual Conference 2023 will take place **Monday 17 April–Thursday 20 April 2023** at Birmingham International Convention Centre. We plan to curate a diverse scientific programme featuring

scientific symposia, workshops, professional development sessions, Prize Lectures and Hot Topics, and much more. Registration and abstract submissions will open in October 2022, and updates can be found on the event webpage (microbiologysociety.org/microbio23).



Federation of Infectious Societies (FIS) Conference 2023

Following the success of FIS/HIS 2022 in September, the Society is pleased to announce we'll be hosting the Federation of Infectious Societies (FIS) Conference 2023 on Tuesday 14–Wednesday 15 November in Edinburgh and one day for an online meeting (date to be confirmed). Find out more and register your interest on the event webpage at microbiologysociety.org/FIS23.

Connect with the Microbiology Society on social media:



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Upcoming grant deadlines

Date	Grant
1 December 2022	Travel Grant for eligible members wishing to present at conferences or attend training events taking place between 1 January and 31 March 2023. Events can take place in-person or virtually.
20 November 2022	Society Supported Conference Grant to support members who wish to organise a conference (in-person or virtual) in any field of microbiology, either independently or in partnership with another Society.
20 February 2023	Harry Smith Vacation Studentships to support undergraduate research projects during summer 2023.
1 March 2023	Travel grant for eligible members wishing to present at conferences or attend training events taking place from 1 April to 30 June 2023. Events can take place in-person or virtually.

For more information please visit the website (microbiologysociety.org/grants).



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Microbiology goes Open Access

The opening of 2023 marks a significant event in the history of the Microbiology Society, with the transitioning of its flagship and oldest scientific journal, *Microbiology*, to full Open Access (OA). While our sister journal *Microbial Genomics* has been OA since it started, this is the first of the Society's long-established journals that is 'flipping' to OA.

There is nothing worse than putting your heart into a piece of written work, for it to be published, but then for hardly anyone to be able to read it due to a paywall and for its impact to not be truly realised. With the switch to OA and our Publish & Read (P&R) deals available from the Microbiology Society it is now easier than ever to publish in our journals so that your research and ideas can be heard.

The advantages of your paper being published in an OA journal are clear. Its visibility is assured, meaning more people can read and download your paper, from a much wider audience, leading to more opportunity for citation as shown in the figure below. This wider inclusivity for readers outside traditional 'subscription' institutions is a massive benefit. The Society also removes the cost barrier for authors from countries covered by Research4Life to publish OA for free to promote their fields across the globe. For authors in neither P&R nor Research4Life institutions, you can pay the article processing charge (APC).

While this is clearly the right thing to do, it is not without its risks for the Society. You may not be aware how dependent the Society is on income from journal subscriptions, which are now being replaced by our pioneering P&R model. It is critical that P&R is successful for the Society to continue to function as a charity supporting the science of microbiology in the UK and beyond. Annual Conference, grants, policy activities and much more are all supported primarily through the publishing

Visibility of OA articles

Usage and citations are key indicators of the impact of research articles: on average these metrics increased when published OA by the following factors.



Based on averages in all journals with citation data from Web of Science

I'm delighted that my institution has signed up to P&R. It's a requirement of my funder, but also a point of principle, that we publish our work open access. I know I can submit our manuscript to any of the Society's journals without needing to have discussions with my line manager or librarian either before or, more awkwardly, after submission about how we might cover an article processing charge.

Frank Sargent (Newcastle University, UK)

arm of the Society: your membership fees only constitute a tiny proportion of the Society's income.

We in the journal leadership team have known this for many years and have been working hard to increase the visibility and reputation of *Microbiology*. Now we need you as members to help us, and there are two clear ways to do this. The first is that if you are working in an institution or organisation that is not signed up to P&R to lobby them to consider signing up. Pricing is tiered so that the conversion to P&R is as cost neutral as possible; for instance, at Tier 1, the lowest tier, the P&R deal is effectively paid back from the first OA article authors publish in Society journals that year. That is in any of our journals, right across the portfolio of microbiology, including our new journal *Microbiology Access*, which has open peer review and a focus on publishing all robust research data.

The second, and single most important thing you can do as a member, is then to publish in our journals and encourage others to do the same.

We will always need to publish, but let's think a little more about where we publish and where the profits from those activities end up. Publish OA with us. Increase your impact. Expand your reach. Support your community.

Gavin Thomas

Editor-in-Chief, *Microbiology*

The trojan horse relationship between amoebae and bacteria

Ronnie Mooney, Elisa Giammarini, Jackie Parry and
Fiona L. Henriquez

Predator–prey interactions are amongst the most significant driving forces of evolution throughout all kingdoms of life. Evermore complex strategies for predation or evasion continue to be uncovered, and perhaps the interactions with the biggest impact on life occur at the microbial level. The free-living amoebae (FLA) present an interesting group of protists that obtain much of their nutrients through the predation of other microbial species, in particular bacteria. The FLA are essential in the regulation of bacterial communities within soil and aquatic ecosystems, engulfing and feeding on captured bacteria in a process known as phagocytosis (Figure 1). Generally, the predation of bacteria by protists is considered beneficial, and as much as 60% of bacterial species are regulated by amoebic phagocytosis, promoting ecosystem health and diversity. The efficiency whereby the FLA and other predatory protists can reduce bacterial populations has been exploited in water treatment processes to improve water quality and reduce the presence of bacterial pathogens. What we often fail to consider, however, is the impact of these interactions on human health. As protists have evolved strategies to predate bacteria, bacteria have evolved strategies to evade protists. While bacterial predation is largely beneficial, generations of predation by FLA on bacteria have given rise to sophisticated strategies that allow bacteria to evade the phagocytic mechanisms employed by the FLA. The evasion strategies are complex and many; while some allow the avoidance of detection by the amoebae, others permit intracellular survival. Herein, we focus on those bacteria capable of surviving intracellularly within FLA (amoeba-resistant bacteria) and discuss how this ongoing evolutionary arms race may have far-reaching implications on human health, driving antimicrobial resistance, complicating detection of pathogens and influencing disease outcomes.

The genetic melting pot – amoebae, bacteria and antimicrobial resistance

Antimicrobial resistance (AMR) is undoubtedly one of the most significant emerging threats facing human health.

Our reliance on effective antimicrobials might prove to have severe long-term consequences unless we can formulate effective mitigation strategies to slow the spread of AMR in the environment. To do this, we need to understand the factors that drive the evolution of AMR. Industrial pollution, pharmaceutical manufacturing, aquaculture and agriculture are commonly cited factors influencing the presence of AMR within the environment, and rightly so, yet the wider interactions between different micro-organism groups are less considered. Horizontal gene transfer (HGT) is the transfer of genetic material between two micro-organisms. In bacteria, this transfer of genes promotes genetic diversity and is a major contributor to the spread of AMR genes throughout bacterial populations. Briefly, genes that confer AMR can be passed between bacteria, occurring more frequently when the organisms are in close contact. Organisms that possess these genes gain a selection advantage when exposed to specific antimicrobials within the environment, which may prompt further spread of the gene. Interestingly, the conditions that promote gene transfer can be amplified during intracellular survival within amoebae. The intracellular environment of the amoebae has been described as a ‘genetic melting pot’, an environment that serves to fast track the transfer of genetic material between engulfed organisms. The ingestion of multiple phagocyte-resistant bacteria results in a highly dense population of cells within the amoebae, increasing the likelihood that gene transfer events might take place. Additionally, intracellular survival within the amoebae might also serve to reduce exposure to environmental antimicrobials to sub-inhibitory levels, ultimately selecting for increasingly resistant bacteria. Recently, genomic analysis of intracellular bacteria within amoebae revealed that HGT events were ongoing within the amoebae and identified transferred genes important in antibiotic resistance, stress tolerance, amoeba–bacteria interactions and virulence. Interestingly, the gene transfer events are not uniquely between bacteria, with studies demonstrating the acquisition by amoebae of genes from bacterial symbionts that might aid in reducing oxidative stress.

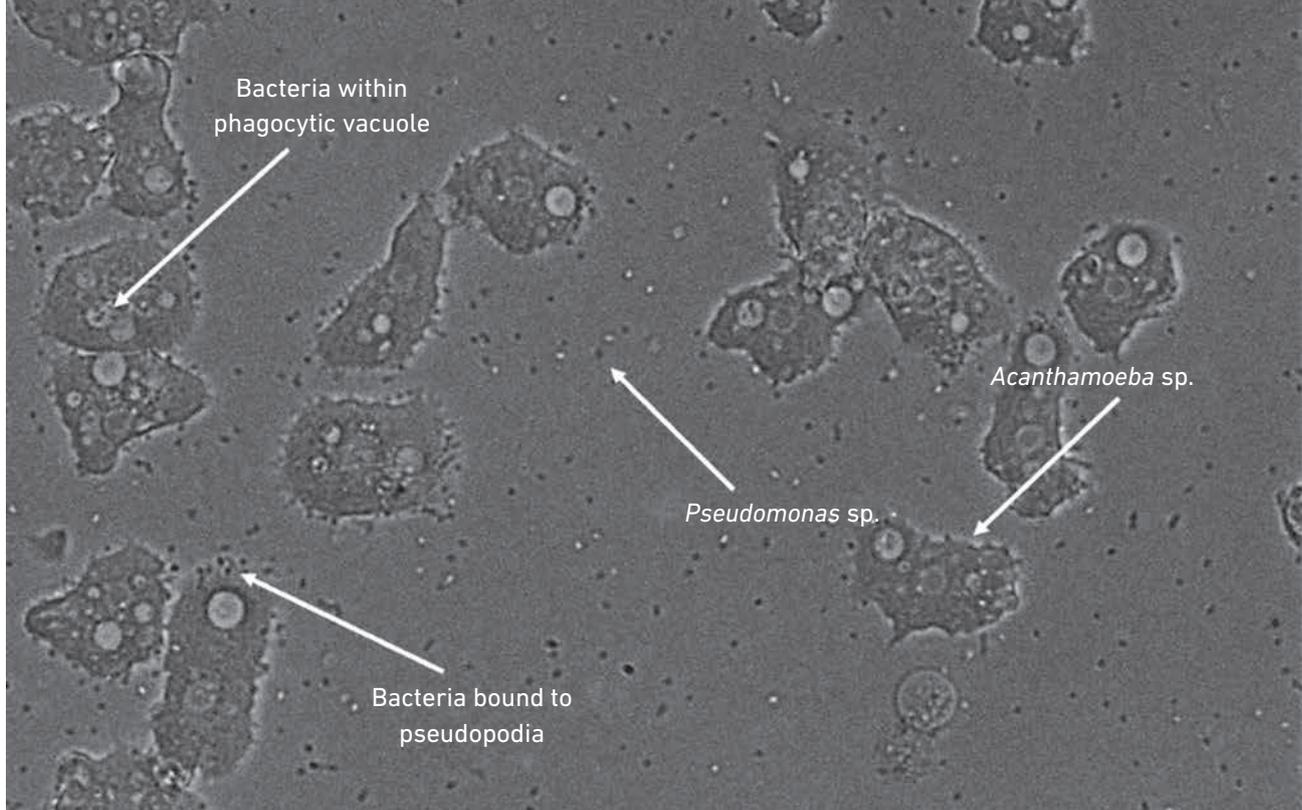


Figure 1. Predation of *Pseudomonas aeruginosa* by *Acanthamoeba castellanii* trophozoites. Bacteria are taken into the intracellular region of the amoeba via phagocytosis. Ordinarily, these bacteria are degraded and used as a food source; however, many species have evolved survival strategies that permit intracellular survival. Ronnie Mooney

Understanding these interactions will improve the efficacy of mitigation strategies and will be an essential aspect of combatting AMR globally.

The microbial Trojan Horse

Resistance to antimicrobials is not only facilitated by the increased likelihood of gene transfer events; the ability to resist phagocytosis and remain viable within the amoebae also directly limits exposure of the bacteria to the external environment and, as a result, exposure to antimicrobial therapies. Clinically, the implications of increased tolerability to antimicrobials within FLA is significant, particularly within high-risk areas such as artificial water systems or during food processing treatments. Amoeba can function as a microbial Trojan Horse, shielding pathogenic bacteria from the external environment and delivering them to a vulnerable human host. Indeed, *Legionella pneumophila*, *Pseudomonas* spp., *Helicobacter* spp., *Mycobacterium* spp., *Aeromonas* spp., *Salmonella* spp. and *Escherichia coli* have all been shown to survive within FLA after exposure to antimicrobial treatments. Many amoebae have an increased tolerance to commonly used disinfection strategies such as chlorine or heat treatment and as such can shield intracellular bacteria from the effects. Sodium hypochlorite, for example, is a commonly used disinfectant within hospitals and is often used in the treatment of potable water; research has shown, however, that killing intra-amoebic bacteria requires concentrations four times higher than is required for extracellular bacteria. Similarly, broad-spectrum biocides such as quaternary ammonium compounds used

in cooling tower disinfection are significantly less effective in killing bacteria when cells are co-cultured with amoebae. Heat treatment is also less effective against intra-amoebic bacteria; *L. pneumophila* can survive in temperatures as high as 90°C when internalised, posing a significant risk to facilities using heat treatment as a disinfection strategy. Commonly used contact lens biocides are woefully ineffective against certain amoebic species and as such can often fail to prevent corneal infections resulting from contact lens wear. The increased tolerance of bacteria within amoebae is something that requires consideration when implementing effective disinfection strategies and, while unexplored at present, it could be speculated that antimicrobial exposure at sub-inhibitory concentrations within amoebae could select for increasingly resistant bacteria, which in turn might be a contributing factor to rising levels of AMR.

The amoebae 'switch' for VBNC bacteria

Amoebae can also trigger physiological changes within bacteria that can increase resistance and limit detection. In times of environmental stress, bacteria can transition to a quiescent life stage better suited to the extracellular pressures they are exposed to. These bacteria are termed viable but non-culturable (VBNC) and have demonstrated an increased tolerance to many disinfectants as well as being able to evade culture-based detection. For reasons yet unknown, the conversion between the vegetative and VBNC stage can be triggered in both directions upon ingestion by FLA. In many instances, this intra-amoebic switch causes bacteria



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to convert much quicker than is observed in the extracellular environment. For example, *Aeromonas hydrophila* has been shown to enter the VBNC form twenty days quicker within amoebae than it does alone; whilst in *P. aeruginosa*, the shift from the VBNC stage to the active state can occur in as little as two hours upon amoebic ingestion. Amoeba-driven VBNC conversion of bacteria is a fascinating by-product of their co-evolution and one that might prove to have significant clinical implications.

Bacterial gymnasia: how amoebae alter the pathogenicity of bacteria

Not only does the intimate relationship with amoebae protect bacteria from detection, disinfection and treatment, but it can also alter bacterial pathogenicity, allowing bacteria to become resistant to immune responses in their hosts. Amoebae and macrophages have similarities in phagocytosis. It has

been proposed that the same strategies which evolved over generations to evade phagocytic predation in amoebae have equipped bacteria for macrophage survival in the human body. For example, *Legionella* spp. can infect and kill both amoebae and macrophages, causing severe disease in human hosts. Moreover, *Mycobacterium abscessus* upregulates the secretion of the proteins that allow this bacterium to survive in a hostile environment and adapt to live intracellularly in FLA and consequently macrophages. Understanding how bacteria can survive within FLA can help dissect the pathogenesis of these bacterial infections.

Conclusion

The interactions between FLA and phagocyte-resistant bacteria present just one specific area in an almost endless supply of microbial interactions. Indeed, the interactions between amoebae and fungal or viral pathogens has not

been discussed here, yet it is another aspect of an already complex web. The spread of antimicrobial resistance, disinfection efficacy, accurate detection and diagnosis and disease outcome are all influenced by cross-kingdom interactions; thus, it is imperative that as our understanding of these microbial relationships grows, so too does our approach to combatting the effects.

About the authors



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Ronnie is a postdoctoral research fellow. His research bridges biomedical and environmental sciences, investigating the interactions between amphizoic amoebae and their bacterial endosymbionts. He is interested in the role of these interactions in facilitating the spread of antimicrobial resistance and how this relationship can influence pathogenicity and detectability.



Elisa Giammarini

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Before becoming a PhD student, Elisa was awarded a Bachelor's in Biotechnology and three Masters' degrees in Biological Sciences, Management of Marine Resources and Advanced Biomedical Sciences. Elisa worked as a high school science teacher for four years then moved to Scotland from Italy four years ago, with the ambition to realise her dream of becoming a scientist.



Jackie Parry

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Jackie has been studying phagocytic processes in free-living protists (flagellates, ciliates and amoebae) since 1990. She specialises in receptor-mediated uptake of prey and its subsequent digestibility (or lack of it) and how this might influence the evolution of pathogenicity within bacteria in the environment.



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Fiona has been researching free-living amoebae for approximately 20 years, with over 80 research outputs in the field focused on the development of new treatments and prevention measures for human and animal health, understanding how amoebae can be vectors for bacteria, and their distribution and impact in the environment.

What inspired you to work in protistology?

Ronnie: My inspiration for choosing a career in protistology began during my undergraduate degree. Despite originally studying zoology, I found myself more interested in the parasitic protists that infected animals than in the animals themselves. After hearing stories of brain-eating amoebae, mind controlling apicomplexans and immune evading kinetoplastids it was impossible to choose any other career path.

Jackie: They were more interesting to look at down the microscope and they have obvious personalities!

Fiona: Their capability to cause infection and the challenge to find effective treatments has inspired me to continue to work in this field.

Elise: I discovered the passion for protistology as I found out that it was a field still quite unexplored and, having a curious nature, it brought up the challenge of the discovery.

What is the most challenging part of your job?

Ronnie: Finding the motivation to leave the lab and open my emails!

Jackie: Balancing research with teaching and engagement commitments.

Fiona: There are many aspects of protistology that are still unknown. We cannot culture them easily and this is challenging.

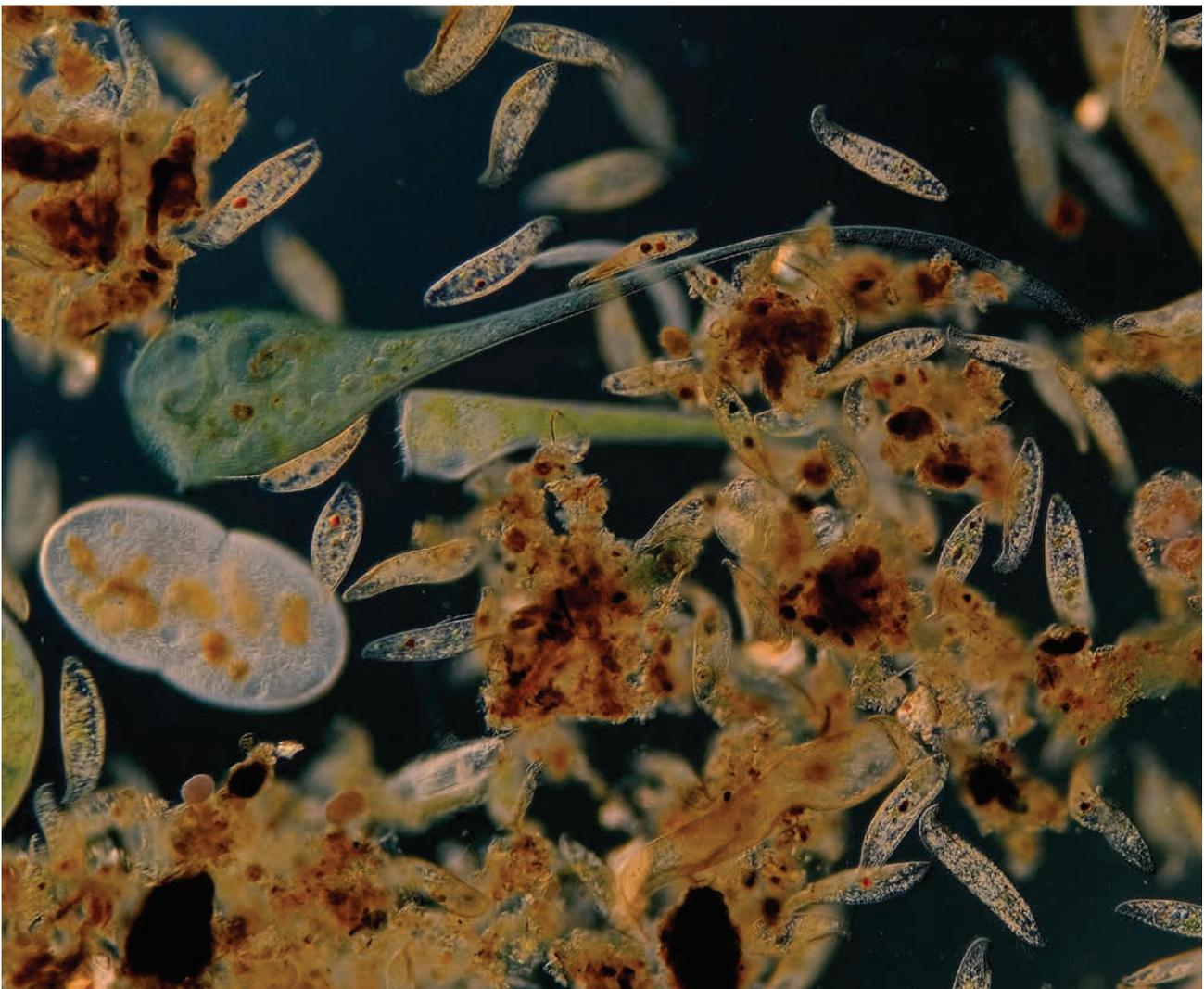
Elise: To remember that there's a world outside the lab and beyond the microscope. It's not always easy to find a balance when you work on a such interesting field.

Protists galore for engaging the public

James Weiss and Genoveva F. Esteban

Your first time gazing through a microscope is a whole new experience for the eyes. The first stroll into a new plane of existence; everything is different from what you've seen in your life. It's like walking on a new planet teeming with aliens, and knowing that this 'exoplanet' was under your nose the whole time even makes it stranger. You see life in its purest form; they lack a brain or even a

nervous system; nonetheless, they appear intelligent. They swim around, roll, twirl, stretch, contract... and colours, so many colours. Baby blue tiny giants *Stentor coeruleus*, thumbling golden colonies of *Synura*, evergreen of squishy *Euglena*. Everything seems so busy and so alive, yet unreal. Your first time with a microscope is a memory you will never forget.



James Weiss



James Weiss

We run microscope hands-on events for the local community, revealing the hidden microbial world to them. We give them the opportunity to experience the first glance into this unusual world by setting up some microscopes and preparing some slides with our protist cultures. Protist is a taxonomic term to cover a bunch of different, and quite unrelated, groups of single-celled eukaryotes, and

since protists are quite common and diverse, it just makes microscopy more enjoyable, which one can describe as going on a Safari in a drop of water. We do so by showing living protists of diverse types, shapes and colours, and always in big numbers, which is bound to impress the observant mind. Watching thousands of 'green slugs' (i.e. *Euglena*) in a tiny drop of water, or pink 'sausages' (i.e. the ciliate *Blepharisma*)



Genoveva Esteban



darting across the field of view, prompts a response that is fun to experience. "Wow!" or "gross!" is the verbal reaction from toddlers to nonagenarians and beyond when looking for the first time down a microscope. Invariably, we hear "wow!" far more than "gross!" and other enthralled noises from the person glued to the eyepiece, inciting the waiting queue to become even more fidgety in expectation.

To help them successfully complete the challenge, our activities are all interactive; children and their families handle the harmless protists, the microscope and the slides, and the identification diagrams depicting protists by shape (*Asterionella*, *Toxarium*, *Closterium*), colour (*Euglena*,

Blepharisma, *Haematococcus*) and numbers (diatoms, flagellates, *Euglena* or any other rich protist culture). We hear people's excited murmurs and answer their big-eyed questions. The questions keep coming non-stop throughout the activity; they mostly relate to microbes, global warming, climate change, origin of life on Earth, food chain, pollution, other life in the universe, and the relevance of microbes in their daily lives and even our own research. Whilst some have rather fewer complex answers...

"What is that?"

"It's an air bubble!"

People's fascination with the microbial world is not new. The infamous draper and the father of microbiology, Leeuwenhoek, was the first to open that gate to the public. With his handheld, single-lens microscopes, he bewildered his audience whether they were scholars from the Royal Society of London or just working-class relatives. It seems like microscopy was always there to inspire people after Leeuwenhoek; for centuries many explained the scenery through a microscope with words and illustrations. German naturalist Ehrenberg left behind thousands of colourful paintings of microbes in collections that inspired and mesmerised anyone who were lucky enough to see them. But, throughout the ages, information always had its limitations; in 1969 during the Apollo 11 Mission, only five photos of the first person who ever walked on the Moon were taken. Today, with the arrival of social media, information is so easy to generate and share with the public, one can create a video or a photo of their microscopy observations and post it online to be seen by millions, making microscopy more influential than ever before. Facebook, TikTok, Instagram, YouTube, Twitter and many other online platforms. Numbers of followers topping millions, and reaching-out stats crowning tens of millions. The scientific value of these microscopy social media accounts varies; while some just share pictures and occasional videos with no or very few facts, others give quite accurate information on the topic. Another challenge is that reaching millions is often not the case to inspire people into microscopy; however, some accounts on social media achieve that quite beautifully. They share their microscopy content with such passion and aesthetics; they capture the attention of their audience. They reveal the microworld in a colloquial and easy-to-understand way, so regardless of their audiences' background they make the topic graspable for everyone, reaching huge crowds that would rarely be matched by citations of scientific publications.

About the authors



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James Weiss is a professional microscopist with passion for the microbial world. He runs a private laboratory and spends many hours

examining pond samples, capturing protists on video, and discovering new and rare species. James is part of the very successful YouTube Channel, Journey to the Microcosmos ([youtube.com/microcosmos](https://www.youtube.com/microcosmos)). You can find some of his outstanding videos [@jam_and_germs](https://www.instagram.com/jam_and_germs) on Instagram.



Genoveva F. Esteban

Professor of Microbial Ecology at Bournemouth University, UK

staffprofiles.bournemouth.ac.uk/display/gesteban

Genoveva's research is currently focusing on the morphological and molecular characterisation of the very rare protists and microbial consortia that thrive in fresh waters. Genoveva is an award-winning and dynamic STEM Ambassador. She is a Microbiology Society Champion and has been a member of both the Microbiology Society and Protistology-UK for many years.

Why does microbiology matter?

James: Even though life around us looks quite different from each other, at the cellular level we are quite alike. Investigating microbes is like looking at that life at its purest form, which is personally fascinating to me! And not just that, but also the behavioural and morphological patterns larger life exhibit can be traced back to the topic of microbiology, hence one can tell a lot about our human existence on Earth by just studying microbes. After all, our consciousness is just a result of a trillion cells working together.

Genoveva: Most life on Earth is, and has always been, microbial. Microbes are responsible for the functioning of ecosystems and for their recovery after disturbance or pollution. More than this, microbes are also responsible for human diseases and food production. Microbiology is a discipline that helps us understand microbes and the processes in which they are involved – that's why microbiology matters.

What advice would you give to researchers trying to engage with the public?

James: Telling a unique story with a simple language everyone can understand is the way to engage with the public. People love original and personal anecdotes; if you can find a way to make people relate to your passion and curiosity, then you can get the attention of the public.

Genoveva: Keep it simple so that anyone of any age can understand; try to impress the audience with a visual demonstration; show enthusiasm and, above all, enjoy it!

Love knows no oxic–anoxic boundaries: anaerobiosis in ciliates provides rich opportunities for microbial symbiosis

William H. Lewis and Ross F. Waller

The diversity of anaerobic life and the environments where it is found

We often think of our planet as an oxygenated habitat, but anoxic environments are relatively widespread on Earth. They most often occur where there is an accumulation of dead organic material and the diffusion of oxygen is limited. Such environments include the deeper aquatic layers and sediments of ponds, lakes and oceans, as well as the digestive tracts of many animals. These environments provide habitats for highly diverse anaerobic microbial communities that thrive in low- or no-oxygen conditions and, therefore, produce energy using metabolic pathways independent of oxygen. Highly diverse metabolisms have evolved over billions of years in prokaryotes to generate energy from a range of different substrates in these anoxic environments. These include different types of fermentation, as well as different forms of anaerobic respiration using electron transport chains with alternative terminal electron acceptors to oxygen.

Living alongside the prokaryotes in anoxic environments there are also anaerobic microbial eukaryotes (protists) that evolved more recently from aerobic eukaryote ancestors. This transition from aerobe to anaerobe has occurred in several protist groups in parallel, for example in metamonads, amoebozoans, stramenopiles, rhizarians and ciliates. The transition to anaerobe is typically achieved by transforming aerobic mitochondria into hydrogen-producing anaerobic versions called hydrogenosomes. Hydrogenosomes lack key mitochondrial metabolic pathways, most notably the electron transport chain for oxidative phosphorylation. Instead, they make ATP by oxygen-independent fermentation reactions and substrate phosphorylation, with molecular hydrogen as a by-product. In actuality, aerobic mitochondria and hydrogenosomes can be considered as two extreme states on a spectrum of mitochondrial adaptation to anoxia, with examples across this spectrum found widely in different protist lineages.

Ciliates are anoxia specialists with a proclivity for hosting symbionts

Ciliates are one group of eukaryotes that have been particularly successful at adapting to anoxic environments. At least 15 ciliate lineages have independently undergone the transition from aerobe, with canonical mitochondria, to anaerobe with hydrogenosomes (or hydrogen-producing mitochondria) – more times than any other eukaryotic group. A key to the success of ciliates in making this transition is their FeFe-hydrogenase, which is responsible for hydrogen production during energy metabolism. The ciliate version of this enzyme has an unusual and characteristic domain structure including an additional two bacterial-like NADH-dehydrogenase domains at the C-terminus. But more surprising is phylogenetic evidence for the different anaerobic ciliate lineages having inherited this enzyme vertically from their aerobic forebears. This is surprising as FeFe-hydrogenases require anoxic conditions to function and are inhibited by oxygen, so their purpose in aerobic ciliates is unclear. Nevertheless, this ancestry does provide a rationale for why multiple independent developments of anaerobic lifestyles have occurred in ciliates – they already had some key kit for the transition.

A second reason for the metabolic flexibility of ciliates is that many host microbial endosymbionts. There are probably two main features of ciliate cells that promote this proclivity for symbiosis. The first is their cell size; ciliates can be huge, ranging from 10 μm to 4 mm in length. Many ciliates, therefore, have large cell volumes that provide ample space to host numerous smaller endosymbiont cells. The second feature is that ciliates are predators that feed by phagotrophy, engulfing large numbers of microbial cells that are digested in food vacuoles. This regular internalisation of diverse microbial cells likely increases the chance of a microbe finding its way into the ciliate cytoplasm, with escape from a food vacuole being more probable than invading across the outer layers of a eukaryotic cell. Thus, the frequency of ciliates encountering novel potential

partners would be great. Anaerobic ciliates, in particular, have acquired diverse endosymbionts that likely provide a variety of metabolic traits and utilities to the host ciliate. Our understanding of many of these relationships, however, remains quite poor. The availability and affordability of molecular sequencing technology over recent years has provided new opportunities to investigate the metabolic basis of these new relationships. Examples of these are giving new insights into how endosymbiosis has been a key player in enabling the oxic–anoxic boundary to be crossed, both over longer evolutionary timescales, as well as multiple transitions per day.

Anaerobic ciliates with methanogenic endosymbionts

Most anaerobic ciliates have endosymbionts, and most of those endosymbionts are methanogenic Archaea (methanogens). Methanogens possess a cofactor called Cofactor F_{420} , which

functions in their methane-producing metabolism. This cofactor is named according to the characteristic fluorescence that it emits when illuminated with 420 nm λ light. Thus, methanogen endosymbionts can be readily detected by simple fluorescence microscopy (Figure 1). The reason that anaerobic ciliates provide such a hospitable habitat for methanogens is that these symbionts require molecular hydrogen as an electron donor for their methane-producing energy metabolism. Hydrogen production from the ciliate hydrogenosome is, therefore, an excellent source for the symbiont. Indeed, many methanogen endosymbionts maximise their surface area that is in contact with ciliate hydrogenosomes to facilitate this acquisition of hydrogen. This exchange also benefits the ciliates as continuous hydrogen removal decreases intracellular partial pressure in the ciliate cell, which improves the efficiency and function of their hydrogenosomes. Furthermore, ciliate feeding experiments using ^{13}C -labelled bacteria demonstrated that

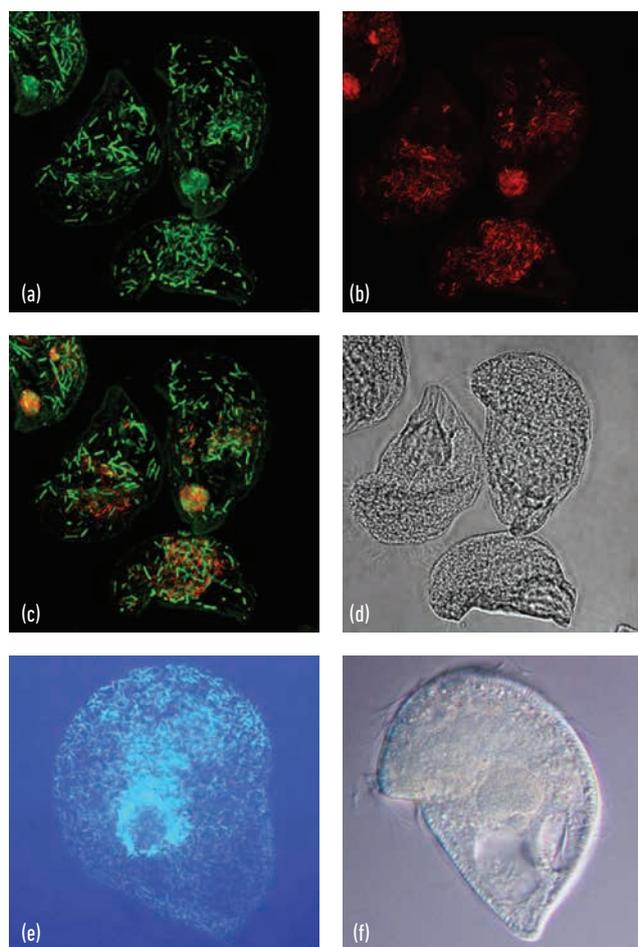


Figure 1. Endosymbionts can be identified and distinguished by taxa-specific fluorescent molecular probes targeting taxa-specific regions of rRNA. Here, endosymbiont cells in the anaerobic ciliate *Metopus striatus* (d, f) are labelled using this method; archaea methanogens in red (b & c) and bacteria in green (a & c). The methanogen endosymbionts also naturally autofluorescence without any labelling when illuminated with 420 nm λ light (e). William Lewis

methanogen endosymbionts also utilise CO₂ derived from the ciliate's digestion of prey.

Methanogens were some of the first endosymbionts of anaerobic ciliates to have their genomes sequenced and analysed. These studies revealed that their genomes are similar in size to their free-living methanogen relatives, in contrast to many bacterial endosymbionts in other eukaryote hosts that often have undergone substantial genome reduction. Nevertheless, at least some methanogen endosymbionts have lost genes for the biosynthesis of several amino acids, suggesting that they have become obligate symbionts that are dependent on their ciliate hosts for providing some of their essential organic molecules. Several methanogen-containing anaerobic ciliates, including *Trimyema compressum*, *Metopus striatus* and *Cyclidium* spp., also have endosymbiotic bacteria. These represent some of the few known cases of both archaea and bacteria living stably within eukaryote cells. These complex consortia indicate further development of metabolic partnerships; however, as yet we know little about the bacterial partners in these consortia including interactions between the prokaryote symbionts or either with their hosts.

Ciliates with green algae and purple bacteria endosymbionts

A further complex symbiotic consortium is found in the ciliate *Pseudoblepharisma tenue* that has two endosymbionts; one a purple Gammaproteobacteria capable of anoxygenic photosynthesis and the other a green algae eukaryote capable of oxygenic photosynthesis (Figure 2). The combined metabolisms of these separate symbiotic partners create a complex mixotrophic physiological niche for the ciliate, yet also make it somewhat flexible in oxic/anoxic habitat choice.

Comparative genomic analysis of these three symbiotic partners suggests that each can switch between anaerobic and aerobic metabolic pathways depending on the availability of oxygen. *P. tenue* is not an anaerobic ciliate in the strictest sense since it appears to have aerobic mitochondria, rather than hydrogenosomes, that likely require oxygen to perform oxidative phosphorylation. The two endosymbionts adapt their metabolisms between photosynthetic and non-photosynthetic fermentative or respiratory metabolic pathways, depending on the availability of light. In the dark, it is likely that the ciliate prefers to occupy an aerobic environment so that all three symbiotic partners can utilise their more efficient aerobic respiratory pathways, rather than their fermentative anaerobic pathways. However, when light is present, it is likely that the

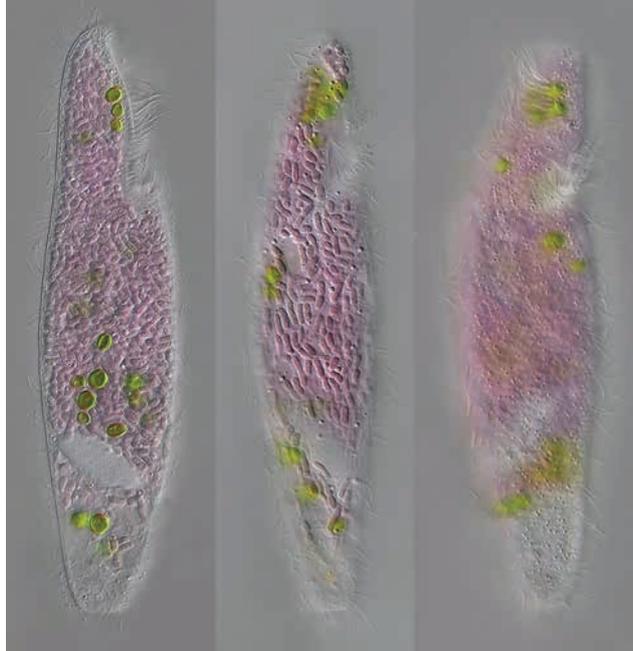


Figure 2. Purple Gammaproteobacteria and *Chlorella* green algae endosymbionts in the freshwater ciliate *Pseudoblepharisma tenue*. Martin Kreutz

ciliate moves between both oxic and anoxic environments, to provide both its endosymbionts with opportunities to photosynthesise. Thus, *P. tenue* occupies the oxic–anoxic boundary regions of the freshwater ponds in which it is found. Moreover, its anoxygenic photosynthesising bacterial endosymbionts likely enable it to ‘SCUBA-dive’ into deeper anoxic environments, providing opportunities to access alternative sources of microbial prey.

Genomics-based metabolic reconstruction enabled further inferences of the biochemical basis for the interaction between these separate partners. It seems possible that the ciliate provides the bacterial endosymbionts with organic compounds, in the form of acetate and propionate, and nitrogen in the form of ammonium. In exchange, the photosynthesis of the bacteria fixes CO₂, making small inorganic molecules that it might export as an alternative source of organic carbon for the ciliate. There are other described anaerobic ciliates with purple photosynthetic bacterial endosymbionts, and these might provide insights into the intermediate stages of development of the three-way partnership seen in *P. tenue*. However, as for *P. tenue*, none have been successfully brought into culture, creating a barrier to experimental investigation of these complex symbiotic systems.

Ciliates with endosymbiotic nitrate-respiring bacteria with similarities to mitochondria

An anaerobic plagiopylean ciliate recently discovered from the deep anoxic water layers of Lake Zug in Switzerland has the only known example of an endosymbiont capable of anaerobic respiration using nitrate as a terminal electron acceptor. Molecular analysis suggests that ATP is produced by nitrate respiration in the endosymbiont. This could be exported to the ciliate and, if so, would be equivalent to mitochondrial export of ATP as the product of aerobic (oxygen) respiration.

The ancestors of modern-day mitochondria were also endosymbiotic bacteria, a partnership that was seminal to the origin of all eukaryotes. The endosymbionts in the ciliate from Lake Zug have, therefore, been proposed as a possible modern-day anaerobic analogy for mitochondria. Understanding this new ciliate symbiosis could elucidate common biological processes relevant to the initial establishment of mitochondria, an event so ancient that it is almost impossible to otherwise investigate.

The Lake Zug ciliate is a remarkable case of the reintroduction of respiration into a eukaryote that had lost it. The ciliate retains fermentative ATP-producing hydrogenosomes, so presumably ATP produced from the nitrate respiration of the symbiont is not sufficient for outright loss of this anaerobic mitochondrial relict. But in the endosymbiont, multiple biosynthesis pathways for essential molecules such as nucleotides, phospholipids and lipopolysaccharides have been lost. So, the symbiont is dependent on its ciliate host and these are the hallmarks of an already well-integrated partnership.

As with each of the ciliates discussed, much more could be learned about the ciliate from Lake Zug if it could be cultivated. Whilst there has been much success culturing numerous anaerobic ciliates that have methanogen endosymbionts, those with more novel endosymbionts have proved more difficult. This could reflect their more complex, or less well understood metabolic requirements, which are more difficult to identify and replicate in a laboratory culture setting. However, the prize for overcoming this hurdle is potentially great, as cultivation opens the door to a range of experimental techniques that can provide far deeper insights into the interactions between these fascinating and intricately associated microbes. In any case, ciliates already demonstrate the possibilities that microbial symbioses offer, and where the challenges of oxic–anoxic boundaries can in fact become opportunities for new niches to exploit.

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Acknowledgements

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Why does microbiology matter?

Will: Microbes form the vast majority of life on Earth and have evolved diverse forms, colonising essentially every environment that exists on our planet. Without microbiology, how can we even begin to understand and appreciate the living world around us?

Could you describe one of your typical workdays?

Will: Currently, my typical workday is comprised of growing algal cultures and performing experiments on these in the lab, as well as analysing transcript or protein data from these organisms computationally, normally using mostly Linux-based tools. My current work aims to understand the evolution and integration of plastids and photosynthetic endosymbionts that have evolved independently in several different species of dinoflagellates.

Gregarine apicomplexans – model organisms to uncover the evolutionary path to obligate intracellular parasitism?

Kevin McKinley, Emma Betts,
Anastasios D. Tsaousis and
Sonja Rueckert

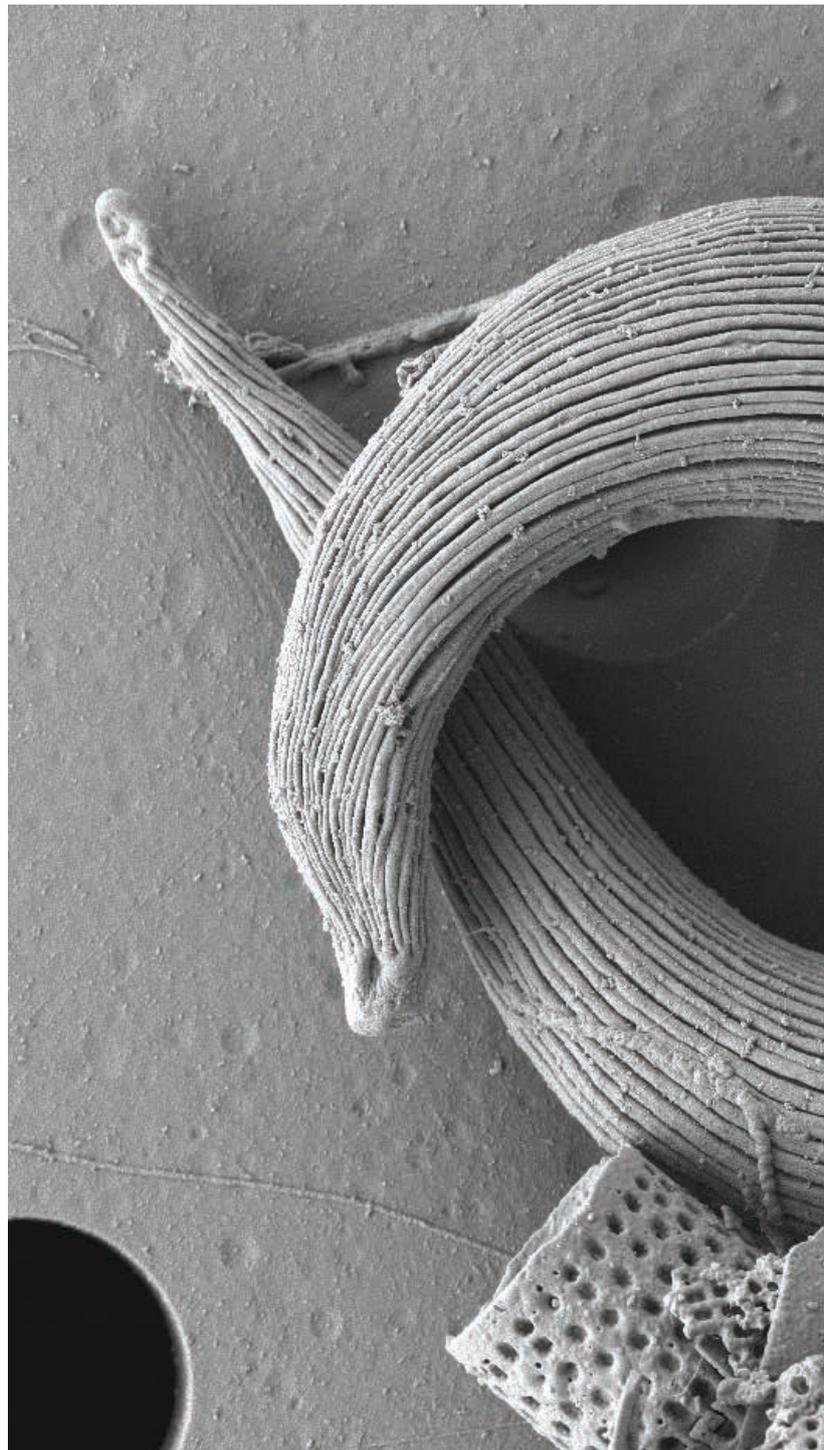
Every organism is supposed to be infected by at least one parasite in its lifetime. While we normally treat parasites as foes, could they actually be our friends? For most people in our society, it might sound odd that it could be beneficial to have a parasitic infection. Especially if we look at organisms that belong to the phylum Apicomplexa, a group described as obligate parasites. Included in this group are the causative agents of potentially fatal infectious diseases in humans such as malaria and toxoplasmosis. Nonetheless, scientists have shown that the presence of some apicomplexan species can have either no or beneficial effects on their hosts. This is especially true for the gregarine apicomplexans, which can be found on the whole spectrum of symbiosis from mutualism to parasitism.

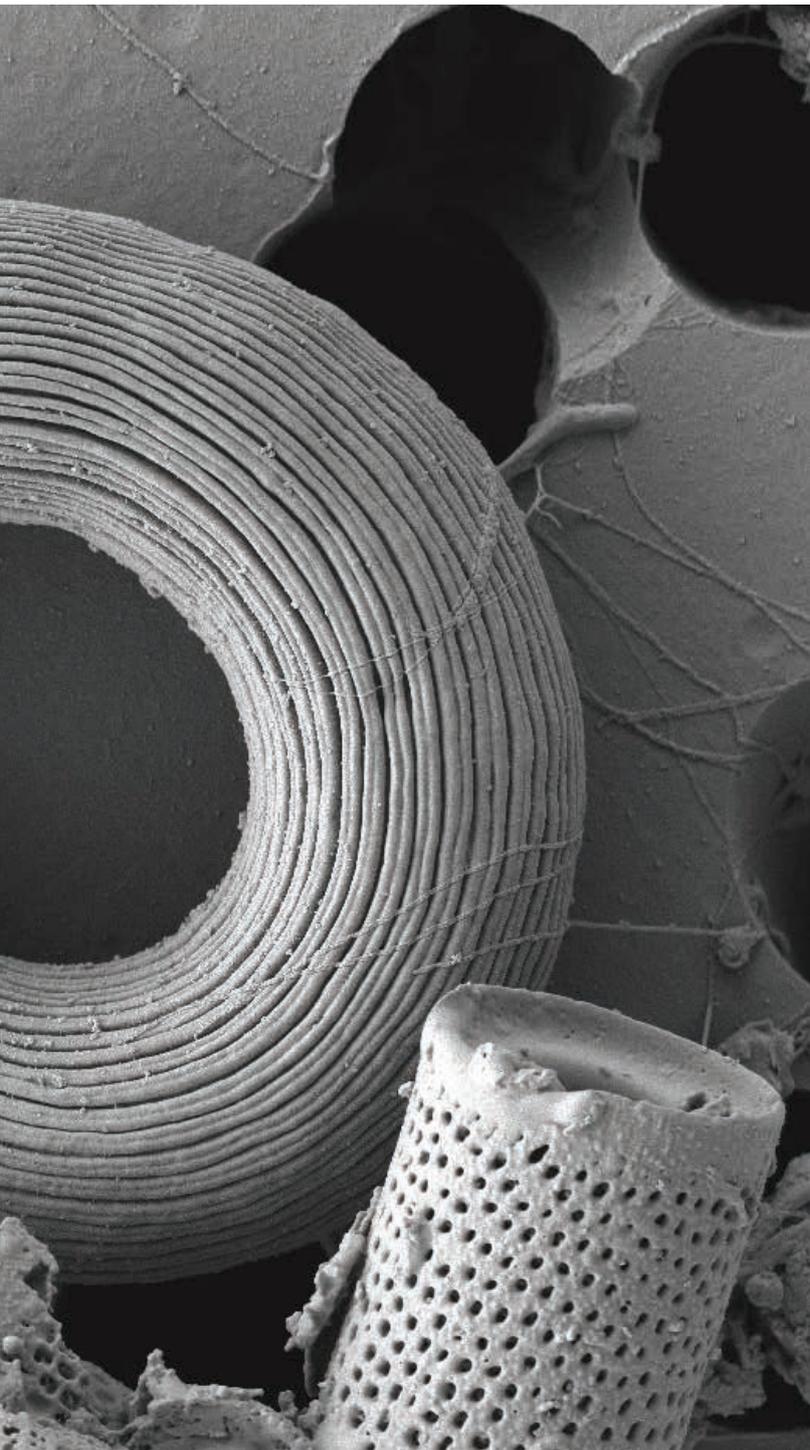
In this article, we are going to introduce gregarine apicomplexans and discuss how they can help us to understand the evolution of parasitism in this phylum.

Gregarine apicomplexans

Gregarines infect a broad range of freshwater, marine and terrestrial invertebrates, and some species have a wide geographic distribution. Most gregarines are host specific, but some species are capable of infecting multiple host organisms. What differentiates gregarines from other apicomplexans are stages within the gregarine life cycle that are only found within this group. There are around 1,800 gregarine species described from various hosts. Gregarines have been described from a fraction of existing invertebrates, leaving many to still be discovered.

Gregarines belong to the class Conoidasida and are still often lumped into three major groups, the archigregarines, eugregarines and neogregarines, as the taxonomy is in steady flux. Neogregarines infect only terrestrial, primarily insect hosts and the majority of these hosts belong to the Diptera. Neogregarines can be found in their host's fat bodies, haemocoel, Malpighian ducts and intestines. Archigregarines





exclusively infect marine invertebrates and mostly their intestines. Eugregarines contain most of the known species and are found in marine, freshwater and terrestrial habitats. Eugregarines inhabit the intestines, coeloms and reproductive vesicles of their invertebrate hosts.

Friends or foes?

Symbiotic relationships can be either mutualistic (beneficial), commensalistic (no effect) or parasitic (harmful). They can lead to behavioural changes in the host, which could affect the host's ability to escape predation or compete for space and resources. A recent review by Rueckert *et al.* (2019) has proposed that gregarine apicomplexans can be found across the entire symbiotic spectrum. A few examples will be presented below.

In earwigs, it was observed that food-deprived insects survived longer when they had a gregarine species colonising their gut compared to those without, showing a beneficial relationship between the gregarine and its earwig host. In pseudoscorpions, high prevalence and infection levels of gregarines were reported to be neither beneficial nor harmful. Dragonflies, however, show a decrease in fat content when infected with gregarines. This results in lower muscle power output which negatively affects motility leading to lower mating success.

Our understanding of the biological processes that are associated with mutualism, commensalism, and parasitism in the various gregarine species is currently limited. However, the utilisation of a combination of traditional methods and state-of-the-art -omics technologies can help to pinpoint major steps along the symbiotic spectrum that led to the evolution of parasitism.

The evolutionary path to obligate intracellular parasitism

Despite being of medical and ecological importance, a lot is still to be discovered in the evolution of parasitism in the apicomplexans. It is known that apicomplexans evolved from algal ancestors, but the processes that drove the evolution from a free-living photosynthetic organism to an intracellular

Scanning electron micrograph (SEM) showing the general morphology and surface ultrastructure of the archigregarine *Selenidium fallax*. Sonja Rueckert

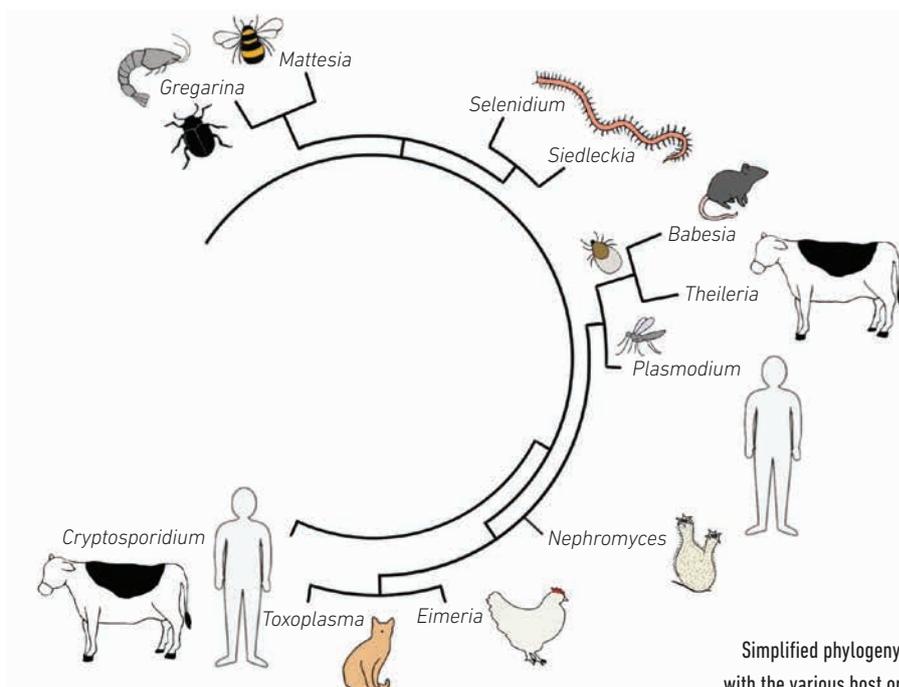
parasitic lifestyle need further exploration. Gregarines are early branching Apicomplexa potentially having undergone extraordinary radiation along with their marine and terrestrial hosts.

So far, molecular information in gregarines has mainly been used to differentiate species and describe their phylogenetic relationships. Studies over the past decades have provided evidence of a remnant plastid (small organelles usually found in photosynthetic organisms), the so-called 'apicoplast', in many apicomplexan species. The presence of this organelle in gregarines has been proven with molecular techniques only recently, adding to the evidence of a common photosynthetic origin. These findings support the loss of photosynthesis in the evolutionary path of gregarines in the transition to a symbiotic lifestyle. This evolutionary process has happened multiple times resulting in multiple lineages of similar symbionts. Some gregarines, likewise with *Cryptosporidium*, seem to have lost the apicoplast, which is essential to many other Apicomplexa. It is important to understand how gregarines and other closely related organisms have coped with the complete loss of the apicoplast, and how their metabolic and cellular machinery has adapted over evolutionary time. While recent transcriptomic and genomic studies have provided the first ideas about these transitions, the use of genetic and cell biological techniques in organisms across the symbiotic spectrum will provide the answer to our questions.

Gregarine apicomplexans – a useful experimental model?

Our limited knowledge regarding gregarines is in a large part due to the lack of available culturing techniques. Currently, there are no *in vitro* culture methods to culture gregarines in a laboratory environment. The current culture methods are limited to the culturing of the host organisms, which can be restricted due to seasonality (for collection of hosts), costs (to maintain complex host life cycles) and labour-intensiveness (for regular feeding, cleaning and maintenance of host culture systems).

In a Gordon & Betty Moore Foundation funded project co-ordinated by Edinburgh Napier University, UK, with partners at the University of Kent, UK, the University of Rhode Island, USA, and the Institute of Parasitology at the Biology Centre CAS, Czech Republic, we are working on the development of an *in vitro* culture platform for gregarines. The ability to culture gregarines in a laboratory environment would allow a consistent and host-free supply of gregarine material. This in turn would enable the scientific community to not only generate transcriptomic and genomic data more easily but utilise the gregarines *in situ* environments to explore their biological functions (using -omics) and symbiotic roles. The latter could be achieved by integrating novel microfluidic devices along with specialised polymers; these technologies have been used in the past to investigate microbiome–host interactions in humans and other animals.



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Kevin McKinley is a PhD candidate at Edinburgh Napier University in Scotland. His main interest is in parasitic protists, with his current research focusing on establishing the foundations of an *in vitro* axenic culture system for gregarines that is animal and tissue free.



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Emma Betts is a postdoctoral researcher in the laboratory of Professor Patricia Johnson at UCLA. Emma received her PhD in Microbiology from the University of Kent (Dr Tsaousis' group), and her research has primarily focused on investigating symbiotic relationships between protozoa, the microbiome and the host.



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Anastasios Tsaousis' research is focused on investigating the adaptations of microbial eukaryotic (protists) organisms. His laboratory is combining detailed bioinformatics analyses of newly generated genomic/transcriptomic/metabolomic results with field, cell biological and biochemical methods to investigate the parasitic and free-living microbial eukaryotes living in diverse and extreme environments.



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Sonja Rueckert is Associate Professor in Marine Biology/Parasitology at Edinburgh Napier University in Scotland. Her research is focused on the morphology, diversity, phylogeny, biology, ecology and evolution of eukaryotic microbes, with a focus on the gregarine apicomplexans. Understanding the symbiotic relationships with their hosts is one of her main goals.

What advice would you give to anyone starting their academic career?

Kevin: Don't hide from the rest of the academic community. Discuss potential ideas with your supervisors and your colleagues. Go to academic conferences and seminars, and reach out to those who you think may aid in your research. We can learn a lot from colleagues in parallel fields.

Could you describe one of your typical workdays?

Kevin: My workload contains a mixture of field-based and lab-based work. One day I could be in the field, kick-sampling in a river to collect amphipods that I'd later examine for gregarine infection. Another day could be spent in the lab growing and maintaining cell lines that I aim to infect with gregarines.

Coevolution in the termite–protist symbiosis

Gillian H. Gile

Termites are best known as pests thanks to the damage they inflict on wooden structures, though many species have important ecological roles, especially in the tropics. Most wood-feeding termites, including the destructive pest species, rely on an assemblage of eukaryotic microbes (protists or flagellates) in their hindguts to help digest wood. The termites grind wood into tiny particles using their specialised hardened mandibles. These particles are then engulfed by the protist symbionts and digested, releasing carbohydrates for energy. Termite-symbiotic protists are the only microbes known to engulf and digest wood particles in this way; it is far more common for microbes to digest wood by secreting enzymes out of their cells and then importing the digestion products (as bacteria and fungi do). This nutritional partnership between termites and their protist symbionts is mutually obligate: the protists cannot survive outside their hosts, and the termites will starve to death despite continued feeding if cleared of their protists.

The obligate symbiosis between termites and protists has been remarkably stable over time: it was already well established in the common ancestor of termites and their closest insect relative, the wood-feeding cockroach *Cryptocercus*, more than 150 million years ago. Since that time, the protists have been faithfully passed on from generation to generation of hosts by a process called proctodeal trophallaxis (anal feeding), allowing them to evolve and diversify in parallel with their hosts. Today there are roughly 800 wood-feeding termite species, each of which harbours its own unique community of symbiotic protists. These protists tend to be much larger and more complex in cellular structure than related protists that live in anaerobic sediments or vertebrate guts, making them the charismatic megafauna of the microbial world (see Figure 1).

The fact that termite guts are packed with dense masses of writhing protists, most of them very large, filled with wood particles and covered with flagella, was first noticed and

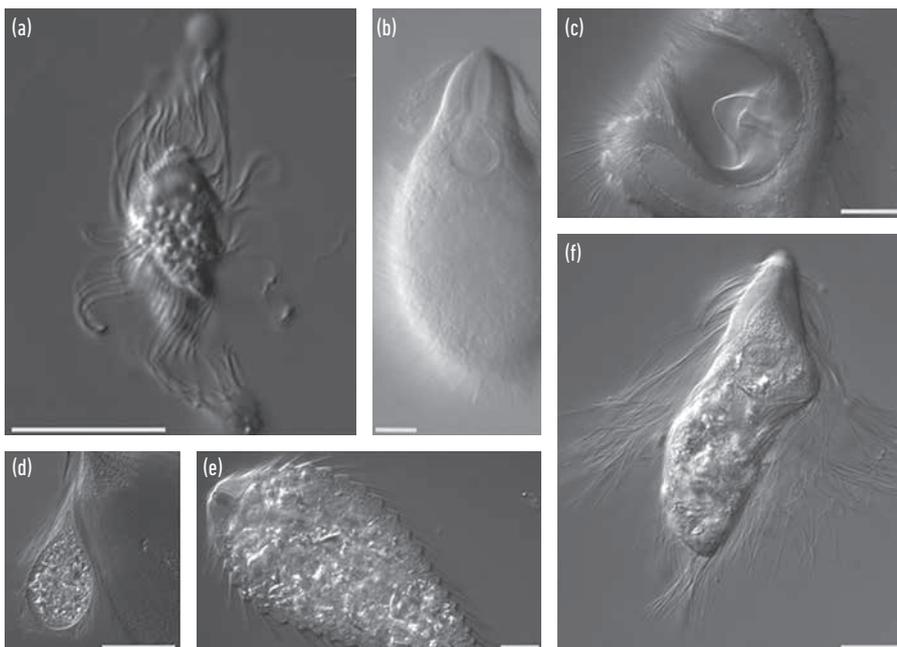


Figure 1. Termite hindgut protists: the charismatic megafauna of the microbial world. Note the angular birefringent (shiny) particles of ingested wood in (d)–(f). (a) *Holomastigotes* sp. (b) *Eucomonympha* sp. (c) *Pseudotrichonympha leei*. (d) *Holomastigotoides* sp. (e) *Teranympa mirabilis*. (f) *Trichonympha* sp. All scale bars indicate 20 μm . Gillian Gile

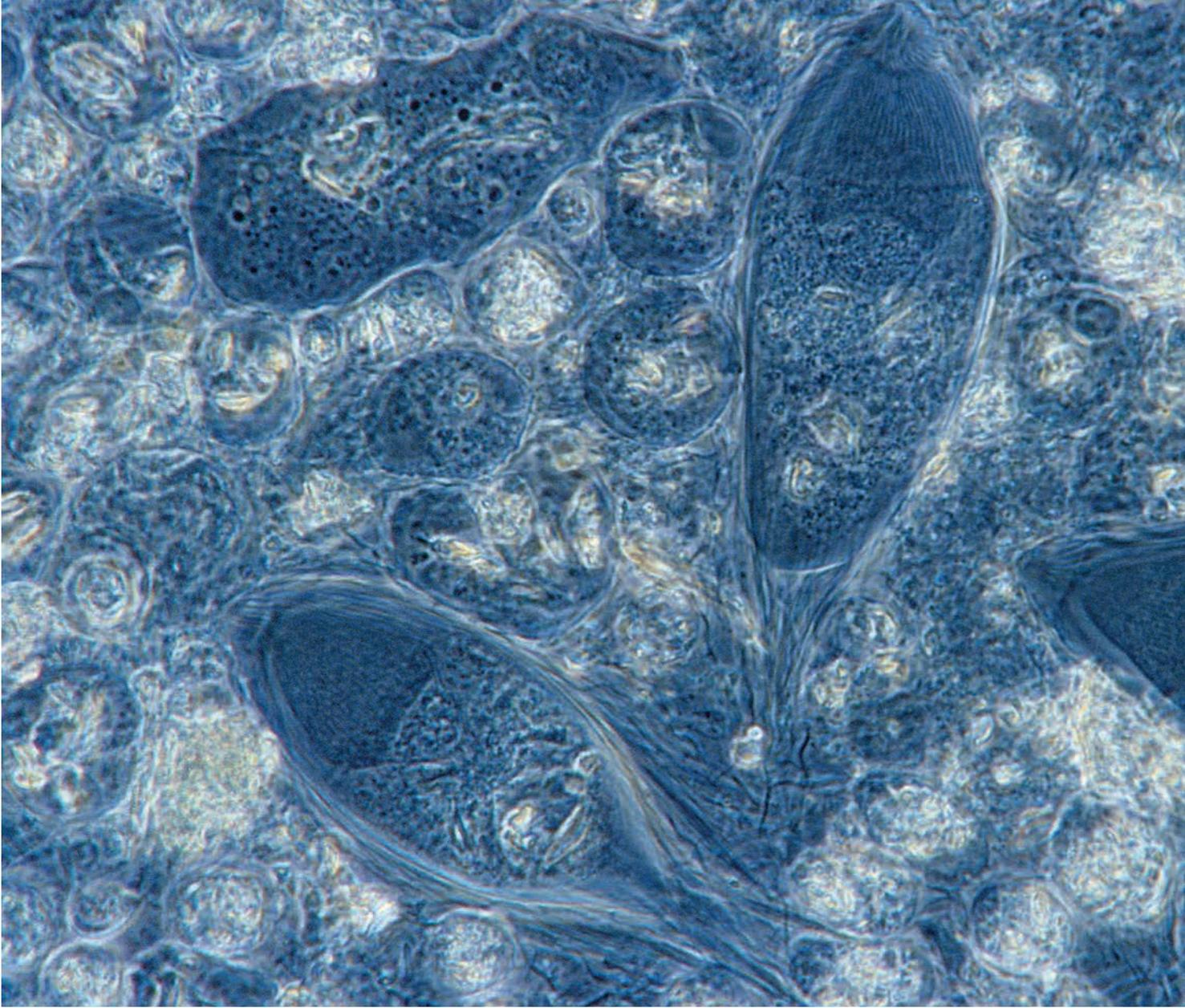
reported in the late 19th century. This captured the attention of protozoologists who began to study termite microbiota in more detail and build a classification system for the protists. These early researchers relied solely on light microscopy of live or fixed, stained specimens to study the protists. As more termite species were investigated and the number of described protist species increased, the distribution of protist species across termite species emerged as an intriguing puzzle. One question articulated in 1937 by Harold Kirby of the University of California at Berkeley, a major figure in termite protist research, still endures today: what is the degree of host-symbiont specificity?

In Kirby's day, as today, the short answer was "it varies". It is clear that some protist lineages are restricted to certain termite lineages while others have broader distributions across multiple termite lineages. For example, it was known by 1937, and still holds today, that the protist genus *Pseudotriconympha* can only be found in members of the termite family Rhinotermitidae, while the protist genus *Triconympha* is present (albeit patchily) in most termite families and *Cryptocercus*. But our understanding of other key distributions has changed dramatically with the application of molecular approaches. For example, the protist genus *Spirotriconympha* has been reported to inhabit several distinct lineages of termites, on the basis of morphology. But after gene sequences were determined, it emerged that *Spirotriconympha* actually comprises multiple distinct protist lineages that happen to share a similar morphotype. Moreover, these '*Spirotriconympha*' lineages were each confined to a distinct host lineage. *Spirotriconympha* from *Reticulitermes* hosts will keep the name because they have taxonomic priority, but '*Spirotriconympha*' species from *Coptotermes* and *Heterotermes* are now *Cononympha*, and the '*Spirotriconympha*' from *Paraneotermes* is now *Cuppa*. This case highlights the difficulty of determining relatedness among termite-associated protists by morphology alone, but more importantly, it increases the degree of host specificity that we can observe in this symbiosis.

Another discovery that impacted our view of host specificity was the protist fauna of *Hodotermopsis sjostedti*, a

damp wood termite from an early diverging lineage, whose symbionts were first investigated in the 1990s. In 1937, the protist genera *Pyrronympha* and *Dinenympha* were only known to inhabit *Reticulitermes*. But this was a mystery because the closest relatives of *Reticulitermes* do not harbour any protists related to *Pyrronympha* or *Dinenympha*. Their discovery in *Hodotermopsis*, along with several other protists that are otherwise unique to *Reticulitermes*, solved this mystery. It seems that the ancestor of *Reticulitermes* underwent a complete faunal replacement, losing the characteristic protists of its rhinotermitid relatives and replacing them with a fauna very similar to that of *Hodotermopsis*. How exactly this happened is a matter of speculation, but termites occasionally lose their protists as a result of a cold shock or other acute stressors (note that *Reticulitermes* inhabit colder areas than other termite lineages). If the ancestors of *Reticulitermes* experienced this and then had a skirmish with a *Hodotermopsis* colony, the protists could have been transferred during the necrophagy that typically accompanies termite warfare. Regardless of the specific mechanism, the distribution of protists is very difficult to explain except by symbiont transfer. This case adds nuance to the idea of host specificity by demonstrating that while symbionts are largely maintained within a host lineage (e.g. for ~60 million years of *Reticulitermes* evolution), they can also be transferred from one termite lineage to another.

But the question of host specificity is perhaps more appropriately addressed on a finer taxonomic scale, i.e. can a single protist species be found in multiple host species? Here the paradigm seems to have shifted the most as a result of our molecular perspective. Whereas many, if not most, protist morphospecies were previously reported to inhabit multiple host species, gene sequences have revealed significant evolutionary distances between protist species from distinct hosts. *Triconympha agilis*, *Cononympha octonaria*, and *Staurojoenina assimilis* are perfect examples of this: they were each reported to inhabit multiple host species, but molecular data have demonstrated distinct phylotypes for these species in each of their hosts. Consistent with this view,



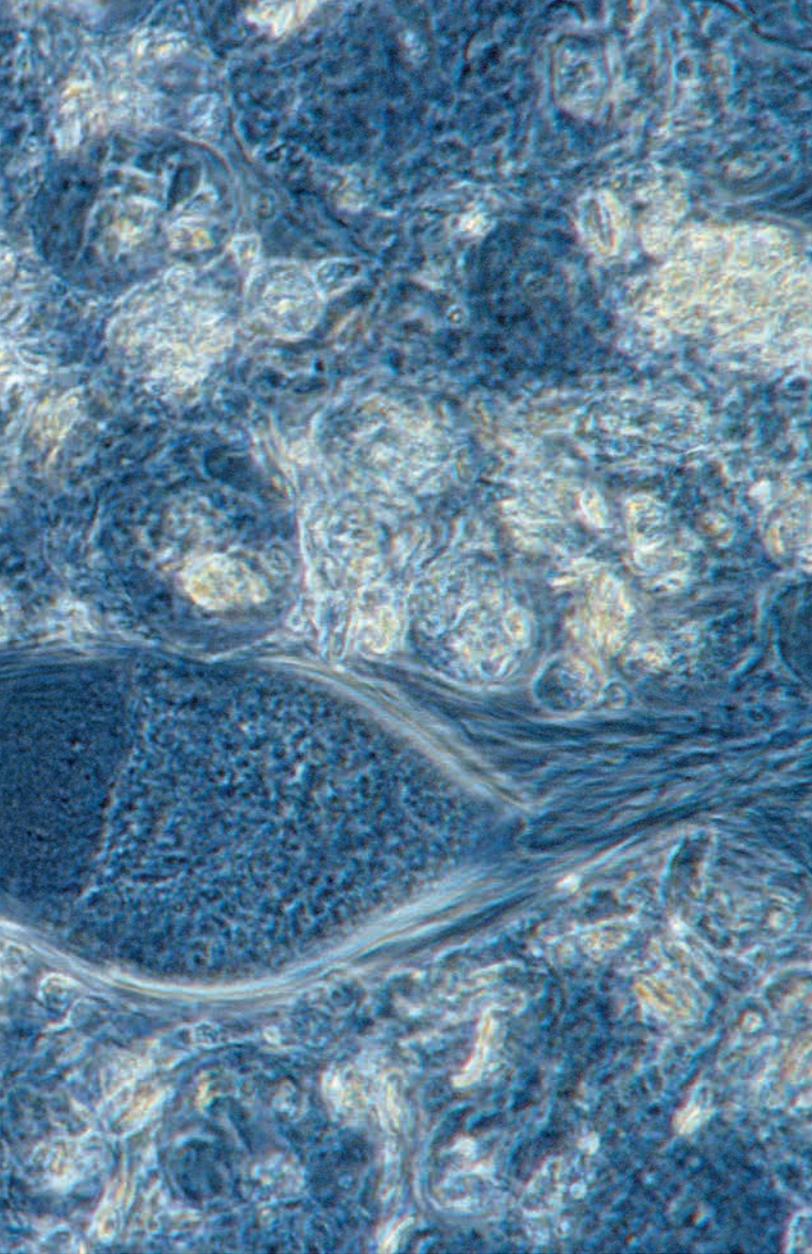
every newly investigated termite species seems to yield new sequence types for its protists (the many examples range across multiple termite-associated protist lineages). However, 'one protist, one termite' may not be the final word. Two species of *Zootermopsis* each harbour the same nine protist species, as suggested by morphological observations and confirmed by molecular data. Nevertheless, the level of host specificity in termite-associated protists is higher than early researchers imagined. This further suggests that the number of termite-associated protist species has been drastically underestimated.

Today, the longer answer to Kirby's question is that the degree of host specificity is very high, owing to vertical inheritance and co-diversification, but this fact is obscured by other evolutionary processes. One of these, as we have seen between *Hodotermopsis* and *Reticulitermes*, is symbiont transfer. This is probably rare, given the distribution of protists across hosts, but it may be more common than is currently

appreciated. Another is lineage-specific loss of symbionts, which is certainly common and has a clear mechanism related to the establishment of new termite colonies. This is the cause of *Trichonympha*'s patchy distribution across host lineages. Yet another is speciation of protists within a host lineage, which has been detected in *Holomastigotoides* symbionts of Rhinotermitidae and may also be more common than currently appreciated. In this way, coevolution in the termite-protist symbiosis resembles the coevolution of genes and organisms: their fundamentally parallel phylogenies are made incongruent by the same processes of gene transfer, lineage-specific loss, and independent diversification (gene duplication).

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Gillian H. Gile is an Associate Professor in the School of Life Sciences at Arizona State University, USA. Her research passions are microbial

eukaryote diversity, systematics and symbiosis, especially termite symbiotic protists and their long history of co-diversification with their hosts. She integrates these research passions into the classroom by carrying out research projects with her undergraduate students.

Why does microbiology matter?

Eukaryotic microbiology matters because it tells us about the function and evolution of our own cells. It teaches us the importance of symbiosis in evolution, as endosymbiosis has given rise to mitochondria and many types of photosynthetic organelles.

What do you love most about your job?

I love spending time on the microscope discovering new protist species and observing their complex morphologies. I also love working collaboratively with my students and colleagues.

The genetics of prominent plant symbionts: the arbuscular mycorrhizal fungi

Nicolas Corradi

The arbuscular mycorrhizal symbiosis: a keystone terrestrial mutualism

The roots of most known land plants associate with underground fungi called arbuscular mycorrhizal fungi (AMF). In this mycorrhizal (meaning fungi within roots) association, the fungal hyphae emerge from AMF spores and penetrate the plant root cortex, thereby producing tree-like structures called arbuscules that give these fungi their name. These unique structures represent the site of nutrient exchange between the symbiotic partners, and through these the fungus helps plants improve uptake of soil nutrients in exchange for carbon sources fixed photosynthetically by the plant; primarily lipids and sugars.

Generally, though not always, AMF are beneficial for plant hosts and crops. In particular, the arbuscular mycorrhizal (AM) symbiosis has been shown to improve plant fitness and crop yield and can result in increased protection against fungal plant pathogens (such as the head blight agent *Fusarium* spp.). Moreover, AMF taxonomic diversity increases plant biodiversity and ecosystem productivity. Consequently, AMF are keystone mutualists in terrestrial ecosystems, and it is thus unsurprising to see a growing number of industries specialising in their production to use them as bio-stimulants in agriculture, forestry or plant nursery practices.

The genetics and genomics of multinucleate arbuscular mycorrhizal fungi

Besides their obvious benefits to plants in terrestrial ecosystems, AMF are known for their unusual cellular

biology. Specifically, these fungi form large and unsegmented underground hyphal networks whereby several thousands (potentially millions) of nuclei co-exist within one large syncytium (Figure 1). In contrast to other multinucleate fungi, there is also no known stage in the AMF life cycle where only one (or two) nuclei are found in one cell or in individual spores. Furthermore, there is no formal observation of sexual reproduction in these organisms. The continuing co-existence of nuclei within AMF spores and mycelium, together with their apparent lack of sexual reproduction, has led to the emergence of a long-held belief that AMF carry unique 'non-Mendelian' genetics and that these fungi never underwent sexual reproduction.

The advent of genomics, and in particular single-nucleus sequencing, has ultimately challenged those hypotheses. The community now overwhelmingly agrees that AMF genetics follow patterns seen in other fungi. Furthermore, data have shown that these fungi have found ways to generate genetic diversity either via sexual (meiotic) or parasexual (somatic) recombination (or both). Genome data and single-nucleus sequencing revealed that AMF strains separate into two 'genetic categories'. Specifically, some strains of the model species *Rhizophagus irregularis* carry a nuclear organisation in which all co-existing nuclei are genetically homogeneous (AMF homokaryons), while few others carry thousands of co-existing nuclei deriving from two parental strains (AMF heterokaryons). The existence of homo-heterokaryotic stages resembles transitions seen between clonal and sexual strains in sexual fungi (particularly basidiomycetes). Indeed, a genetic locus

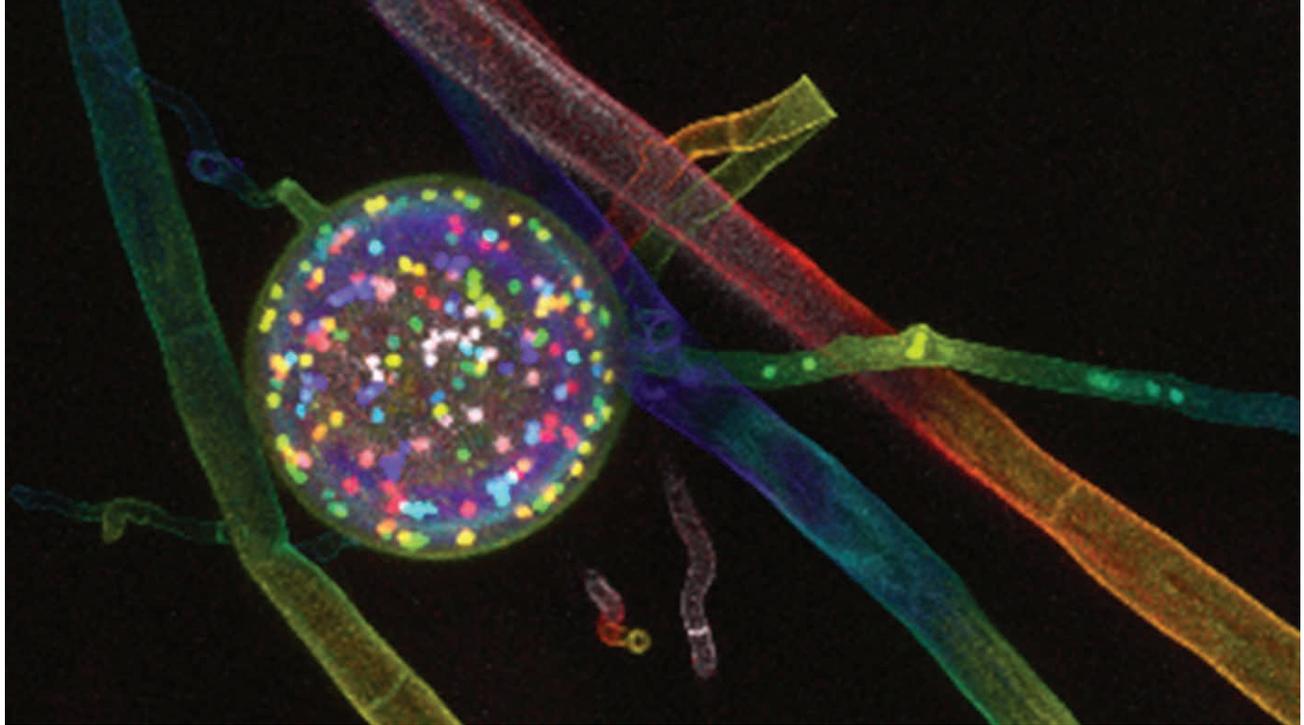


Figure 1. Nuclear content of an individual spore isolated from an arbuscular mycorrhizal fungus. The spores and cells of arbuscular mycorrhizal fungi are, to the best of our knowledge, constantly multinucleate. At the extreme, individual spores of species such as *Gigaspora gigantea* can carry over 20 thousand nuclei within large spores. When the entire belowground mycelium is considered, a single individual may carry hundreds of thousands of nuclei within one large cell (a coenocyte). The image was obtained using confocal microscopy. The final images are colour coded along z axis for depth recognition. White and red colours are closer to the observer while blue colours are the furthest. Nuclei are visible due to staining with SYTO 13 green fluorescent nucleic acid dye. Each image is the result of approximately 300 z stacks (0.35 μm intervals). Vasilis Kokkoris

potentially involved in mating, that is, a mating type (MAT) locus, was reportedly found in AMF, adding support to the notion that these prominent symbionts are not purely asexual organisms.

Genome analyses have also revealed important aspects of their lifestyle. In particular, genome sequences from all known families showed that AMF lack genes involved in the production of fatty acids and sugars, meaning that they are completely dependent on their plant hosts for basic nutrition (and survival). Investigations also revealed that AMF genomes are relatively large compared with those of relatives in the fungal kingdom, ranging from 50 Megabases to well over one Gigabase. This large size strongly correlates with their repetitive nature, with large AMF genomes containing many transposable elements and redundant gene families (some gene families carry well over 2,000 members), while smaller ones like the early branching lineage *Paraglomus* are significantly more streamlined. Another notable aspect of AMF is that their genomes can vary dramatically in content among closely related strains. For example, multiple strains claimed to belong to the model species *R. irregularis* can at the extreme vary by up to 50% in gene and repeat content. While this suggests that these strains may actually represent distinct species (or a species complex), the high among-strains genome variability identified in AMF also underpins its role in allowing these organisms to rapidly tackle environmental changes and colonise different plant hosts. It may also explain why they are so ubiquitous across diverse ecosystems globally.

Genetic and genomic interactions between the symbiotic partners

The identification of AMF strains carrying multiple nuclei deriving from two parental (and presumably homokaryotic) strains provides strong evidence that the genetics of these symbionts follows patterns seen in other fungi. Specifically, in many fungi compatible 'monokaryotic' strains can exchange nuclei to produce a dikaryotic progeny carrying two nuclei per cell; that is a 'dikaryotic cell'. Eventually, though not always, these genetically different nuclei fuse and undergo meiosis (sex) to produce a recombined progeny, and there is evidence that analogous mechanisms also occur in AMF.

In non-AMF fungal dikaryons (two nuclei per cell), the co-existence of two parental genomes was shown to benefit fungal strains in many ways. Dikaryotic strains can have an advantage over monokaryotic relatives, including a superiority in terms of fitness and function by producing unique proteins or increased enzymatic activity. Similar distinctions may also affect AMF, with recent work showing that AMF heterokaryons are significantly different from AMF homokaryons in terms of ecological traits and function. For example, AMF heterokaryons tend to produce a different number of spores and generate hyphal networks of larger size, highlighting the different roles that each nuclear organisation may play in terrestrial ecosystems.

In AMF heterokaryons, the relative abundance of two parental nuclei varies depending on the strain. In some strains parental nuclei are found, on average, at approximately the same rate across the mycelium, indicating that the fungus

evolved a unique (and yet undescribed) cellular mechanism to tightly control their relative abundance. However, in other strains one parental nucleotype always dominates within the cytoplasm. In extreme cases, one parental genotype represents up to 80% of all nuclei present within individual spores, indicating that the nuclei may compete against each other for 'dominance' within the same fungal cells.

Remarkably, the nuclear dynamics of AMF heterokaryons vary depending on the plant host. In symbiosis with carrots (*Daucus carota*) most of the nuclei from one specific parent were dominant within some AMF strains, yet changing the plant host to chicory (*Cichorium intybus*) resulted in dramatic shifts in nuclear dynamics leading to the other parental

genotype suddenly dominating in the cytoplasm. Overall, these results suggest that the plant host identity can influence the genetics of the fungal symbionts, thus revealing a previously unknown layer of genetic complexity and dynamism within the intimate interactions that occur between the partners of this prominent terrestrial symbiosis. The molecular mechanisms involved in changing AMF genetics are unknown, but it is intriguing to speculate that these are dictated by the plant host's needs. Regardless, these rapid nuclear shifts most likely affect the transcriptional content of AMF heterokaryons and, consequently, the phenotypic traits of both symbiotic partners. The notion that plant hosts can control the expression output of their AMF symbiont is also supported by recent chromatin-



Coloured scanning electron micrograph of mycorrhiza. Eye of Science/Science Photo Library

level analyses of AMF nuclei, which showed that 'repressed' regions of the AMF genome can become activated when in symbiosis with the plant host.

Genome biology of AMF: going beyond model species

While genome data from AMF are regularly published, the overall genome quality of those assemblies has until recently been rather poor. Most genome sequences obtained to date are highly fragmented and incomplete due to the presence of multiple and highly repeated sequences in these genomes. Recently, the use of chromatin-capture (Hi-C) sequencing has allowed for a complete view of AMF chromosomes in five model strains. This technique also uncovered the existence of two dominant chromosomal compartments (euchromatin vs heterochromatin) in AMF that carry distinct genes and repeat contents, as well as expression and methylation levels. These findings uncovered a higher order genome organisation that governs genome biology and evolution of model terrestrial symbionts and opened avenues to study the epigenetic mechanisms that modify chromosome folding during host-microbe interactions.

While a fine-scale view of the AMF genome biology is now within reach for model species in the genus *Rhizophagus*, our knowledge in this area for non-model AMF taxa is non-existent. To tackle this, it is essential to now aim sequencing, particularly high-fidelity long-read and chromatin-capture sequencing at the entire AMF phylogeny, with a particular focus on early branching taxa such as *P. occultum* and those known to carry a unique symbiotic lifestyle such as the fungus-cyanobacterial species *Geosiphon pyriformis*. Ultimately, a complete understanding of genome biology across all the AMF phylogeny will improve our understanding of this widespread terrestrial mutualism and ensure a more sustainable and widespread application of these organisms as bio-stimulants in a green economy.

Further reading

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sexual origin of heterokaryosis in arbuscular mycorrhizal fungi. *Nat Microbiol* 2016;1:16033.

Yildirim G, Sperschneider J, Malar M, Chen ECH, Iwasaki W *et al*. Long reads and Hi-C sequencing illuminate the two compartment genome of the model arbuscular mycorrhizal symbiont *Rhizophagus irregularis*. *New Phytol* 2022;233:1097–1107.

About the author



Nicolas Corradi

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Nicolas Corradi started his scientific career studying biology at the University of Geneva, Switzerland. He then went on to do a PhD, studying genome evolution in arbuscular mycorrhizal fungi at the University of Lausanne, Switzerland. Following his PhD, Nicolas received two consecutive postdoctoral fellowships from the Swiss National Foundation to work at the University of British Columbia, Canada, on the evolutionary genomics of intracellular parasites of animals called Microsporidia. It was here that Nicolas further developed his interest in genome analysis, which he applied to understand the biology of arbuscular mycorrhizal fungi and Microsporidia in his first academic PI position at the University of Ottawa, Canada. During 12 successful years as PI, Nicolas helped establish an internationally renowned research team studying microbial genomics and evolution of prominent plant symbionts and ubiquitous animal pathogens, receiving a Fellowship from the Canadian Institute for Advanced Research (CIFAR) and a University Chair in Microbial Genomics.

What inspired you to start a career in scientific research?

The ability to discover something no one else knew existed before, and shake long-held scientific beliefs.

What advice would you give to early career researchers?

Do not be afraid to question consensus/authority when contradictory evidence emerges from your work. Do not play 'politics', just always be true to yourself. Prioritise producing high-quality and reproducible work.

Annual Conference 2023

The Microbiology Society Annual Conference 2023 will take place **Monday 17 April–Thursday 20 April 2023** at Birmingham International Convention Centre.

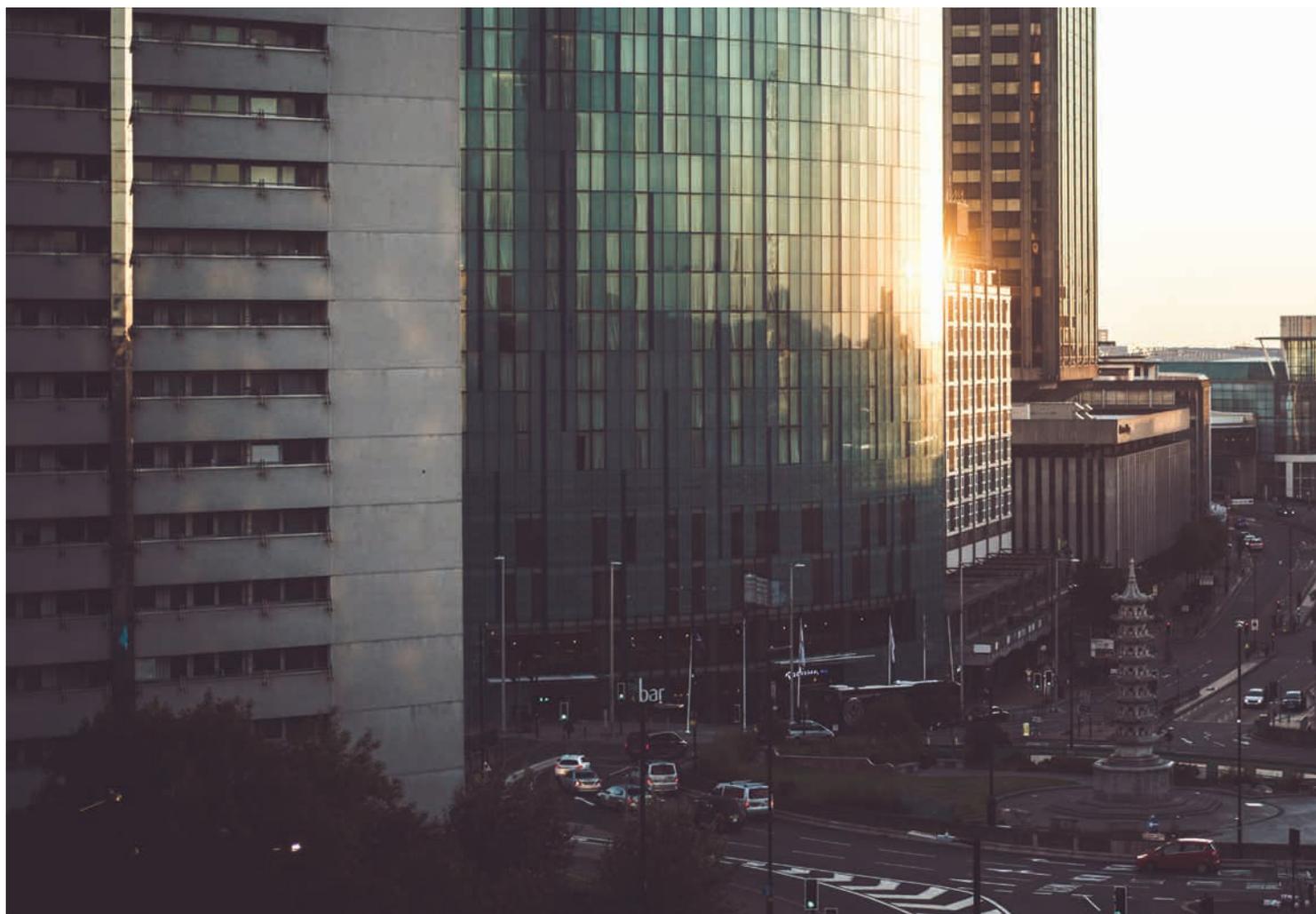
The Conference takes place over four days and features an extensive programme designed to cover the breadth of microbiology, as well as professional development sessions, social activities and lots of face-to-face networking opportunities.

Destination Birmingham

Birmingham is a city with forward-thinking architecture and expansive waterways, and is lined with history, culture and lifestyle. If you're planning on extending your stay around Conference, the city has world-class museums and galleries to explore and rewarding culture and heritage to discover.

It's a fantastic place to meet other scientists that are interested in the same things as you.

Matt Hutchings
(2019 Microbiology Outreach Prize winner)



Giuseppe Miglino/iStock

The most important thing about the Microbiology Society I think is networking. Being able to connect with other researchers across the UK, but also internationally, is something I just wouldn't have the opportunity to do otherwise.

Robert Will (former ECM Forum Impact and Influence Committee representative)

Abstracts

Annual Conference attracts around 1,500 attendees for the UK's largest gathering of microbiologists. Presenting an offered oral or poster provides an excellent platform to showcase emerging scientific research.

The key abstract deadlines for public abstract submission for Annual Conference 2023 are as follows:

Abstracts open:	24 October 2022
Abstracts close:	16 December 2022
Notification of acceptance:	w/c 23 January 2023
Registration opens:	24 October 2022
Early bird discount ends:	28 February 2023
Registration closes:	10 April 2023

Members get heavily subsidised registration fees for Annual Conference, Focused Meetings and other Society events – both online and in-person. Join now to enjoy these discounts and many other opportunities that are designed for microbiologists at all stages of their careers (microbiologysociety.org/join).

See the event's webpage for further information on specific abstract submission categories and for further booking details (microbiologysociety.org/microbio23).

Being a member of the Microbiology Society has a lot of advantages, a few of which are being able to present your work at a significant national meeting like the Microbiology Society Annual Conference, and also the networking opportunities you get.

*Arikana Massiah
(Microbiology Society Champion)*

Follow [@MicrobioSoc](https://twitter.com/MicrobioSoc) on Twitter to keep up with the latest Annual Conference 2023 updates, using the hashtag [#Microbio23](https://twitter.com/hashtag/Microbio23).



Microbiology Society Events and Focused Meetings

Early Career Microbiologists' (ECM) Summer Conference

On 12–13 July 2022, the Microbiology Society's Early Career Microbiologists' (ECM) Forum hosted its flagship Summer Conference, at the University of Sheffield, UK. The meeting kicked off with a networking icebreaker, which brought together the undergraduate, masters, PhD and early postdoctoral researchers attending, and was followed by a keynote lecture from Professor Alison Holmes (Imperial College London, UK). Attendees participated in scientific talks focused on antimicrobial resistance, and the challenges facing scientists and society today, before taking part in a collaborative peer review workshop using the new *Access Microbiology* open research platform (acmi.microbiologyresearch.org). The event was a great success thanks to all the organisers, speakers, poster presenters and delegates who got involved. Every Microbiology Society member starting out in their microbiology career is invited to join the ECM Forum, and you can find out more on our website (microb.io/2ZedLjX).



Roadshows

Our President's Roadshows are an opportunity for attendees to hear about President Professor Gurdyal S. Besra's career journey, find out more about available opportunities to get involved with Society activities and network with fellow microbiologists in their local area. May saw the launch of our 2022 Roadshows programme with the first event held in collaboration with Leicester Microbial Sciences and Infectious Diseases Centre (LeMID) and hosted by Professor Andrea Cooper (University of Leicester, UK) and member Professor Julie Morrissey (LeMID, UK) on 10 May. This was followed by a Roadshow at Northumbria University, UK, on 25 July, hosted by members Dr Amanda Jones (Northumbria University, UK) and Professor Iain Sutcliffe (Northumbria University, UK), which brought together microbiologists from across the Northeast of England.

Focused Meetings

Throughout 2022, the Society has been delivering its most varied and largest ever Focused Meeting programme, bringing together those with shared scientific and clinical interests to exchange knowledge and reconnect through much-missed face-to-face interactions.

Upcoming Focused Meetings – 2022 Microbiome and Mucosa-associated Infectious Disease: Mining for Antimicrobials and Postbiotics with Therapeutic Potential

27–28 October 2022 | Trinity College Dublin, Dublin, Ireland

With the emergence of antibiotic resistance and the decreasing effectiveness of antibiotics there is growing interest in the potential of mining the gut microbiome for



new antimicrobials. This Focused Meeting will provide an insight into the current state of research on the exploration of the interactions between the gut microbiota, pathogens and the mucosal immune system in the search for new alternatives for the treatment of infectious disease.

Protein Secretion at the Host–Pathogen Interface

3–4 November 2022 | Queen's University Belfast, Belfast, UK

Bacterial infections remain one of the top causes of human suffering and death globally and have huge economic impact

on agriculture and animal production. The ability to cause disease of nearly all important bacterial pathogens depends on secretion systems, which deliver virulence factors to the surface or directly into host cells, where they modulate host processes to the benefit of the bacteria.

There have been plenty of new scientific discoveries pushing our understanding of the molecular basis of host-pathogen interactions to new levels, and this meeting has been organised to foster exchange of information, networking and new collaborations across the research community.



Understanding and Predicting Microbial Evolutionary Dynamics

22–23 November 2022 | Hyatt Regency Manchester, Manchester, UK

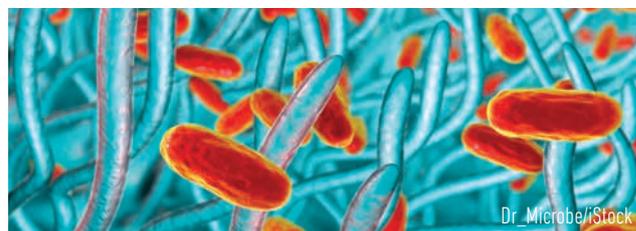
This meeting will bring together leading researchers working on microbial evolution from across varied disciplines, including infectious diseases, genomics, environmental microbiology, biotechnology and mathematical modelling. This will provide a unique opportunity to allow this multidisciplinary community to identify the common themes and shared approaches for understanding and predicting microbial evolutionary dynamics across these diverse systems and applications.



Upcoming Focused Meetings – 2023 Vaccines as Tools to Combat Antimicrobial Resistance

27–28 February 2023 | Edgbaston Park Hotel and Conference Centre, Birmingham, UK

The Society is delighted to be delivering our first Focused Meeting of 2023, Vaccines as Tools to Combat Antimicrobial



Resistance, in association with BactiVac, the Bacterial Vaccines Network. BactiVac has a global network of more than 1,200 members from 78 countries that are involved in the development of vaccines against bacterial pathogens, particularly AMR.

Currently, there are many human-specific and veterinary/zoonotic bacterial infections that either do not have a vaccine or where extant vaccines are sub-optimal. This meeting will provide a vital forum to discuss ways in which vaccines can slow the emergence of AMR by preventing infections and reducing the need for antibiotics.

Candida and Candidiasis 2023

13–17 May 2023 | Le Centre Sheraton Montreal Hotel, Québec, Canada

Candida and Candidiasis 2023 will bring together scientists studying diverse aspects of *Candida* biology, as well as interactions between these fungal species and their mammalian hosts. *Candida* species are commonly found colonising multiple niches in the human body but are also responsible for a wide variety of important diseases that range from oral and vaginal candidiasis to life-threatening systemic infections. The impact of *Candida* species on human health has recently garnered additional attention with the rapid emergence of the multi-drug-resistant species *Candida auris*. This meeting will cover a broad spectrum of subjects that relate to *Candida* epidemiology, drug resistance, infection, host response and therapeutics.



More Focused Meetings will be announced and further information about the Society's events programme can be found on our website (microbiologysociety.org/events).

Spotlight on Grants: Education and Outreach Grant

The Education and Outreach Grant is available to support relevant science teaching or promotion initiatives or to support developments likely to lead to an improvement in the teaching of any aspect of microbiology.

Earlier this year, Ruth MacLaren, Sciencedipity, UK, organised and ran her engagement project 'Invisible Worlds' in the Petroc College Campuses in the towns of Tiverton and Barnstaple, Devon, UK.

The aim of the project was for students aged 13 and upwards to learn about different aspects of microbiology with an emphasis on practical elements. The students engaged in microscopy, streak plating, aseptic technique, Gram staining and bacterial identification tests, which included a tour of a local industrial microbiology lab.

During the event, Ruth supported students to carry out their own microbiology techniques. Through this, they were able to learn about what prokaryotic cells look like, how they can play a part in addressing antibiotic resistance, why microbes are essential for the planet and the careers that are available to them in microbiology.

Ruth said that "The youngsters loved the opportunity to carry out new and relevant microbial techniques, which built on their current knowledge. I benefitted from reaching out to teens rather than my usual cohort of primary school children. I'd recommend anyone to apply for the scheme if they have a well-prepared idea or workshop for community outreach."

Now the project has ended, Ruth plans to "definitely be carrying out the same lab-based evening course that the



Ruth MacLaren

Society funded, but I also did a shorter version for home-educated teens which I would also repeat. Although this course wasn't in a lab it was still a useful, informative and practical course for them with the British Science Association's CREST Award too."



Ruth MacLaren

Applications for the Education and Outreach Grant open twice a year, in January and June, with deadlines in April and October, respectively. To find out more about the wide range of grants available to support Microbiology Society members, visit the grants area (microbiologysociety.org/grants) on our website.

Early Career Microbiologists' Forum update: reuniting ECMs

Welcome to the Early Career Microbiologists' (ECM) Forum update. I am Rebecca McHugh, a Postdoctoral Researcher from the University of Glasgow, UK, and ECM Impact and Influence Representative.

The previous quarter has been very busy for our early career members, with both Annual Conference 2022 (April) and our flagship ECM Summer Conference (July) taking place. I am sure our ECMs will agree that it has been fantastic to be reunited in our passion for all things microbial and to have a chance to finally meet the colleagues we have interacted with virtually over the past two years.

During our Annual Conference, myself and our ECM Forum Executive Committee Chair, Colman O'Cathail, hosted our pre-conference networking event in the legendary Belfast venue, Grannie Annies. The event was subscribed to full capacity, but with Colman's flight delayed, and the failure of our networking bingo cards to arrive, Society Staff were left to scramble together a new programme (and host!) at the last minute. Despite the obstacles, the event was a great success. Our Forum members were obviously very keen to network in person, which made the job of stand-in host easy for me. Colman's flight managed to arrive in time for him to take the stage to conclude what was a superb event.

Colman O'Cathail speaking at the pre-conference networking event in the legendary Belfast venue, Grannie Annies.



Annual Conference provided many opportunities for ECMs to present their work, and there were some excellent posters on display. The winner of our ECM Forum Poster Prize, Adriana Bizior, a PhD Student from the University of Strathclyde, UK, said "being at the Microbiology Society conference and receiving an ECM poster prize gave me a boost of motivation and energy in the last stages of my PhD. It is very easy to underestimate your own achievements and work – this prize helped me realise how much I have achieved and learnt in the past three years".

This year marked the return of the ECM Forum's flagship event, the ECM Forum Summer Conference. A sunny Sheffield played host to over 100 delegates from across the branches of the Society. The meeting had an 'antimicrobial resistance' theme, and the organising committee put together a varied programme which included short talks and posters from ECMs. Ainsley Beaton from the John Innes Centre, who presented her talk, said "the ECM Forum Summer Conference was a really refreshing meeting, with everyone being at a similar career stage, presenting gave lots of useful but friendly feedback. The theme of AMR gave a great focus but still included a real variety of angles on that topic so plenty of new ideas were being passed around". David Mark from the University of Glasgow presented a poster and said "this was my first time at an ECM Forum conference, and it was a great experience. It's lovely to be around other ECMs to chat about what we are working on".

Finally, on the behalf of the ECM Forum Executive Committee I would like to wish Maria Fernandes the best of luck as she leaves the Microbiology Society after eight years. Maria has been fundamental in the organisation and development of the ECM Forum and she will be sorely missed.

Rebecca McHugh



ECM Representative for Impact and Influence Committee, ECM Forum Executive Committee

Unlocking the potential of our members



We recently launched our first fundraising initiative for members who may require support, for a variety of reasons, to help them to progress and reach their full career potential.

The Unlocking Potential Grant will support the career development of promising early and mid-career microbiologists through the development of their transferrable skills. In addition to mentoring support and expansion of leadership skills, we would like to offer coaching to the recipients of the grant to support their needs, primarily focused on resilience and empowerment.

We are delighted to announce the members of the very first Unlocking Potential cohort:

Anne Wyllie Yale University, USA

Donal McGee AlgaeCytes Ltd, UK

Helen Brown Cardiff University, UK

Ioly Kotta-Loizou Imperial College London, UK

Jing Cui University College London, UK

This is wonderful news – thank you all so much. I am very excited about the opportunities this presents – both for my own personal/professional development, but the opportunities discussed during the interview and being able to be involved with the broader programming surrounding this initiative.

Anne Wyllie

I read this at the weekend, and it has brought me much Joy. I am looking forward to hearing from the career consultant and excited for doing this bit of self-work. I really think I will benefit from it.

Sariqa Wagley

Kirsty Jones Staffordshire University, UK

Sariqa Wagley University of Exeter, UK

Sophie Nixon University of Manchester, UK

Tamar Schwartz University College London, UK

Victorien Dougnon University of Abomey-Calavi, Benin

We will be sharing the journeys of some of our recipients over the coming months on our blog.

I am very excited to be offered this opportunity and I am looking forward to meeting with the careers consultant.

Ioly Kotta-Loizou

To donate to the Unlocking Potential Fund to support early and mid-career microbiologists like these, please visit microbiologysociety.org/unlockingpotentialfund.

Member Q&A: Vijay Kothari



Vijay Kothari

This is a regular column to introduce our members. In this issue, we're pleased to introduce Vijay Kothari.

Where are you currently based and what is your role?

I am currently affiliated with the Institute of Science, Nirma University, India, as a faculty member. Here, as well as guiding PhD students, I teach MSc classes in Microbiology/Biotechnology.

What area of microbiology do you specialise in?

Antimicrobial resistance (AMR).

Tell us about your career journey to date.

After earning my MSc in Microbiology from Gujarat University, India, I started my career as a Research Fellow at Ahmedabad Textile Industry's Research Association, India, where I worked on the biotransformation of chitin into chitosan. I then moved to the Center for Environmental Planning and Technology, India, which gave me my first experience of on-site sample collection and analysis. This project was about monitoring water quality and biodiversity of a wetland area called Nalsarovar. Thereafter, I have been based at Nirma University, India, since 2007.

When and why did you first become interested in microbiology?

As a child, I always found it exciting to observe objects under a magnifying lens or microscope. My school had a good biology lab with multiple microscopes, and using these triggered some curiosity about 'life at micro level'. Vacation-time reading of spiritual texts mentioning invisible life, books on the history of science, school textbooks describing the contributions of Antonie van Leeuwenhoek and Louis Pasteur, and some excellent teachers at BSc and MSc level all contributed to my interest in microbiology. It happened slowly over the years and not in any single moment.

What are some of the challenges of working in AMR?

Some of the challenges I face include loss of antibiotic resistance and virulence traits from the bacterial pathogens upon repeated subculturing in our lab over the years; finding a critical mass of people in my city/state working on similar aspects of AMR; lack of availability of authentic, well-characterised strains of antibiotic-resistant bacteria and *Caenorhabditis elegans* (the worm being used by us as a model

host); finding industrial collaborators and funding for AMR research.

Has the COVID-19 pandemic impacted your career and, if so, in what ways?

Yes, a strict lockdown resulted in the non-maintenance of worms and bacterial cultures and we, therefore, lost our worms. No new experimental data could be generated during that time. Intermittent lockdowns have negatively affected the continuity of our experiments. I particularly missed in-person conferences, which provide excellent networking opportunities with other researchers.

What has been the highlight of your career so far?

Some of the achievements I am most proud of include being awarded the Sentinel of Science (2016) by Publons; undertaking collaborative research with Atomwise, USA, under their Artificial Intelligence Molecular Screen award programme; my paper 'Effect of audible sound in form of music on microbial growth and production of certain important metabolites' being ranked among the top 5% of all research outputs tracked by Altmetric; and publishing the first-ever whole transcriptome report of a sonic-stimulated bacterial culture.

Between 2007 and 2019, I also guided 84 MSc students during their dissertation projects. Of these, 71 have gone on to publish research/review papers in various peer-reviewed, indexed journals (or citable preprints) based on their Masters' dissertations. The satisfaction of converting students into authors has been immense.

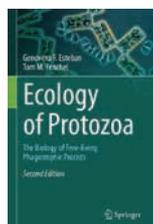
What do you hope to achieve in your career in the future?

I hope to be able to contribute meaningfully towards evidence-based validation of the anti-pathogenic potential of traditional medicine, identification of novel targets and modes of action for future antimicrobials and elucidation of the molecular mechanisms associated with microbial response to sonic-stimulation.

If you would like to be featured in this section or know someone who may, please get in touch via getinvolved@microbiologysociety.org.

Reviews

Read excerpts from the latest book reviews below. To read the full reviews, and for more reviews, please view the online edition on our website: microbiologysociety.org/MicrobiologyToday.



Ecology of Protozoa: The Biology of Free-living Phagotrophic Protists

By Genova F. Esteban and Tom M. Fenchel
Springer US (2020) £87.50
ISBN: 978-3-030-59979-9

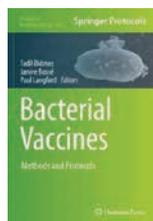
Updating the 1987 first edition text which has been cited over 1,000 times, this book is a comprehensive, extensively referenced guide detailing the important role and relevance of single-celled protists. The vast functional diversity, structure and environmental importance of protozoa are discussed in a thorough yet accessible manner.

The authors begin with chapters defining protozoa as a group, discussing their feeding mechanisms, taxis and

reproduction, before moving onto symbiotic relationships. The varied niches these fascinating organisms inhabit within freshwater and marine habitats are then detailed, alongside advancements that molecular techniques have brought to the field. Likewise, areas in which there is a lack of knowledge or that warrant further study, whether using comparative or molecular techniques, are highlighted.

This text contributes to our understanding of the relevance of protozoa to the environment. It would be of interest to ecology and protozoology specialists alike, indeed anyone with an interest in the wide-ranging functional and ecological traits shown by protozoal species.

Sarah Boyce
Sheffield Hallam University, UK



Bacterial Vaccines: Methods and Protocols

Edited by Fadil Bidmos, Janine Bossé and
Paul Langford
Springer US (2022) £159.99
ISBN: 978-1-0716-1900-1

The Editors of this book provide clear and precise information on all modern protocols applicable to developing vaccines. They highlight the importance of how applicable and significant these protocols are, especially during COVID-19 vaccine development when the Vaxign-ML tool was used to predict a SARS-CoV-2 vaccine candidate.

Many publications describing reverse vaccinology (RV) are covered in this book in detail; therefore, the research is up to date. This book also shows how important RV was to the development of the COVID-19 vaccine and how vaccines are vital to global immunity against bacterial and viral infection.

To conclude, *Bacterial Vaccines* is vital for practical application as modern methods and protocols are supplied in one location and are easy to follow, especially for replication testing.

Liam O'Connell-Perks
Baxter Healthcare, UK



Advances in Microbiology, Infectious Diseases and Public Health

By Gianfranco Donelli
Springer (2022) £109.99
ISBN: 978-3-031-01994-4

This book is a collection of the latest research done in the field of microbiology, including review papers and case studies. Most of the articles are focused on the study of micro-organisms and their increasingly resistant populations, with an emphasis on better detection

mechanisms and population surveillance. Out of the ten articles that were published, three of them stood out the most to me.

Overall, I think this is a great book to read if one wants to keep abreast of the advances in microbiology, infectious disease and public health. It covers common topics within its field, and even goes out of its way to give us a glimpse of some interesting yet uncommon issues relevant to modern microbiology.

Anindita Arpa
University of Texas at Arlington, USA

Annual Conference 2023

17–20 April, ICC Birmingham, UK

Save the date

#Microbio23





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