



Biology

News

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Department of Plant Sciences
Department of Zoology

Liam Dolan Head of Plant Sciences Department

The Department's teaching and research ranges from ecology to metabolic network modeling, and includes both pure and applied research. Moreover we are in a unique position to exploit the opportunities that arise at the interface between the life and physical sciences by virtue of being located next to some of the best bioscience departments in the world – Biochemistry, Chemistry and Zoology.

A good example is the recent development of the ChemBioPlants network, funded by the University and an Impact with Innovation award from BBSRC. ChemBioPlants is helping us to diversify the approaches that we use to address research questions in plant sciences. The network has stimulated activity in several areas including natural products research. In the short to medium term this has the potential to identify novel chemistries involved in plant defence; while in the longer term specialised metabolites will be discovered that could be the starting point for the development of new drugs.

The past year has seen exciting funding developments in the Department. Jane Langdale has launched the third phase of the C4 Rice project, a global programme that aims to increase photosynthetic efficiency in rice, with the support of the Bill and Melinda

Gates Foundation. Similarly Nick Harberd and Phil Poole have been successful in attracting funding for major collaborations with China and India respectively. Nick's work aims to increase nitrogen use efficiency in crops, while Phil's research underpins global efforts to develop nitrogen-fixing cereals.

Among colleagues establishing their careers, Steve Kelly has been awarded both an ERC consolidator grant and a Royal Society University Research Fellowship setting him up for another exciting five years in the Department. Steve has consummate bioinformatics skills and his research ranges from understanding the basic biology of economically important plant pathogens to the evolution of photosynthesis.

I am grateful to everyone who contributes to making the Department a better place to work. I am particularly proud of the way in which Louise Hill (DPhil student) and her colleagues have taken the green agenda by the horns to decrease the Department's carbon footprint. DPhil students and post-doctoral researchers have developed their own scientific and social community through the StuDoc society, highlighting the great research that they carry out and increasing the vibrancy of the Department.



Finally I am immensely grateful to the donors who have funded academic positions, DPhil Studentships and undergraduate travel in the past year. Your contributions enhance the experience our students enjoy at Oxford and fund some of the brightest minds of their generation. This is all the more important given the role that plant biology and zoology will have to play in addressing the challenges that lie ahead for humanity.

Graduate student projects

The value of species-rich grasslands

Katherine French, Trinity College



Species-rich grasslands contain a variety of rare plants and microbiota and provide a host of ecosystem services. Yet agricultural intensification

and urbanism have destroyed up to 97% of unimproved grasslands in lowland England since the 1950s. My research characterizes this fading biodiversity through vegetation surveys, soil microbial analysis, forage sampling, and ethnobotanical research at sites around Oxfordshire. Ultimately, the aim of this research is to highlight the cultural, ecological and economic value of species-rich grasslands and to show how the resources they provide – from novel soil microbiota to biomass for biogas production – can contribute to more sustainable agricultural and bioenergy production systems.

Metabolic analysis of nitrogen-fixing bacteria

Khushboo Borah, Keble College



Symbiotic nitrogen fixation by legumes provides nitrogen enrichment in agricultural systems. It is of great practical interest because it increases

sustainability by reducing the demand for nitrogen fertilizers. Nitrogen fixation involves a complex metabolic interaction between Rhizobia and their legume host plants, but the process is incompletely understood and so the aim of my research is to characterise the metabolic phenotype of the nodule-forming bacterium *Azorhizobium caulinodans*. I am using a systems-based approach, metabolic flux analysis, to quantify the metabolic adjustments that are required to permit nitrogen fixation under free-living conditions and in *planta*.

Microtubules and root growth

Clement Champion, Somerville College



Filamentous cells with rooting functions grow straight into the soil by restricting growth to their tip. Tip-growth relies on finely-tuned microtubule dynamics to

stabilise the domain of growth through an unknown mechanism. My DPhil project aims to identify microtubule-associated proteins that are required for microtubule-mediated tip-growth stability and to characterize their function with respect to cellular polarisation. To do this, I am using a combination of genetic screens in the model haploid land plant *Marchantia polymorpha*. This work will eventually broaden our understanding of the role of microtubules in the control of cell geometry in plants.

Peter Holland

Head of Zoology Department

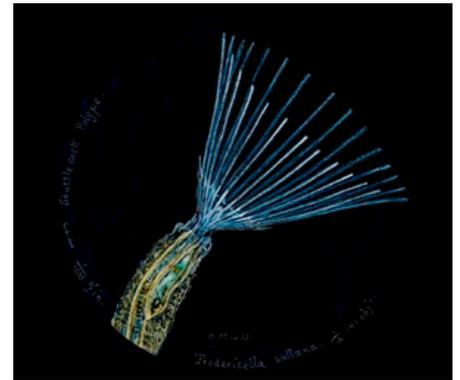
The past year has been eventful for Universities and for UK research, with a Government Green Paper on Higher Education Reform and the Nurse Review of UK Research Councils. The University has fed back comments on these topics, helping to shape policies to strengthen the world class research and higher education sectors in the UK. In the field of biology, Oxford already has a phenomenal reputation, and we were delighted to see that the recent Times Higher Education World University Rankings rank the University of Oxford 1st in the world for Life Sciences (including Zoology, Plant Sciences, Biochemistry and non-clinical biomedical science).

Within the Department, we continue to grow and diversify our research, in parallel to investing in education and teaching. Amongst our new arrivals, we welcome Professor E.J. Milner-Gulland to the Tasso Leventis Chair of Biodiversity. E.J. is particularly well-known for her work on biology and conservation of the Saiga antelope, and with her research group she has a broad range of research and policy interests in conservation. The first holder of the Tasso Leventis Chair was Kathy Willis, now Director of Science at Kew Gardens and also a Research Professor in this department. You may have heard Kathy's excellent BBC Radio 4 series 'From Roots to Riches' in

2014 and her interview on Radio 4 'The Life Scientific' in 2015. Kathy was awarded the prestigious 2015 Michael Faraday Prize from the Royal Society, recognising her outstanding work in the communication of science. Other recent awards to members of the Department include the Zoological Society of London Scientific Medal to Kevin Foster, the ZSL Charles Darwin Award to Patrick Meyer-Higgins, the Jan Bergstrom Young Geoscientist Award to Allison Daley, the Lauri "Tupu" Saxen medal to Aziz Aboobaker and the Jasper Loftus-Hills Young Investigator Award to Lucy Aplin.

There have been several important news stories from the Department over the past year. These include the far-reaching work from Martin Maiden's team on vaccination strategies for meningitis in Africa and the UK. Also in the news was Oxitec Ltd, an exciting spin-out company from Zoology set up by Luke Alphey that is using genetics to suppress mosquito populations. And we must not forget the now infamous interaction between a dentist and a lion: an outpouring of generosity from the public means that something positive for conservation will come from that unfortunate episode.

Our 2015 intake of undergraduate students were the first to use our three newly



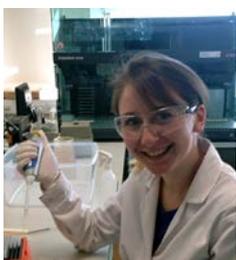
Bryozoan painted from life by H M J. Underhill (1889)

refurbished lecture theatres: gone are the hard green benches loved (?) by generations of biology students, replaced with comfortable seats and state-of-the-art dual projection and video streaming facilities. The only downside I have noticed is that the seats might be just a little too comfortable for some.... The refurbishment itself was a major task, and one that uncovered some long lost artefacts from decades of teaching. Perhaps the most exciting was a large collection of rare hand-painted lantern slides prepared by Mr. H.M.J. Underhill in the 1880s, each showing microscopic freshwater animals meticulously painted from life. One beautiful example is reproduced here.

Graduate student projects

Investigating how antibiotic resistance evolves

Isabel Frost, The Queen's College



Antibiotic resistance poses a major challenge for medicine. Bacteria are able to exchange genetic material, for example in the form of plasmids, enabling them to

rapidly acquire resistance to antibiotics. Gaining a better understanding of this process and the social lives more generally of bacteria will be important to combat pathogenic bacteria in a clinical setting. Many bacteria live in highly structured colonies, and my research looks at how this structuring affects the spread of antibiotic resistance. My background was in Chemistry and my move into biological research has been made possible through the Doctoral Training Centre in Systems Biology.

Cicadas: the loudest insects

Leonidas-Romanos Davranoglou, The Queen's College



The loudest insects are the cicadas. The organs responsible for sound production in cicadas are the tymbals, situated on each side of the first

abdominal segment. Other hemipteran insects, such as the Auchenorrhyncha (leafhoppers, etc.) and Heteroptera (stink bugs) also produce sounds or vibrations, by unknown mechanisms. My DPhil, funded by a scholarship from Queen's College and the spin-out company NaturalMotion, focusses on sound production in these insects, using state-of-the-art technology such as *in vivo* time-resolved microtomography, electron microscopy and laser Doppler vibrometry. I aim to resolve whether sound production evolved once or multiple times in Hemiptera, and to clarify the role of sound in these insects.

Collecting dung of the elephant called 'Whiskey'

Susanne Vogel, Pembroke College



Elephants raid the crops of farmers, and one idea is that this occurs when elephants switch their diet. To test this hypothesis, I collect elephant dung in the

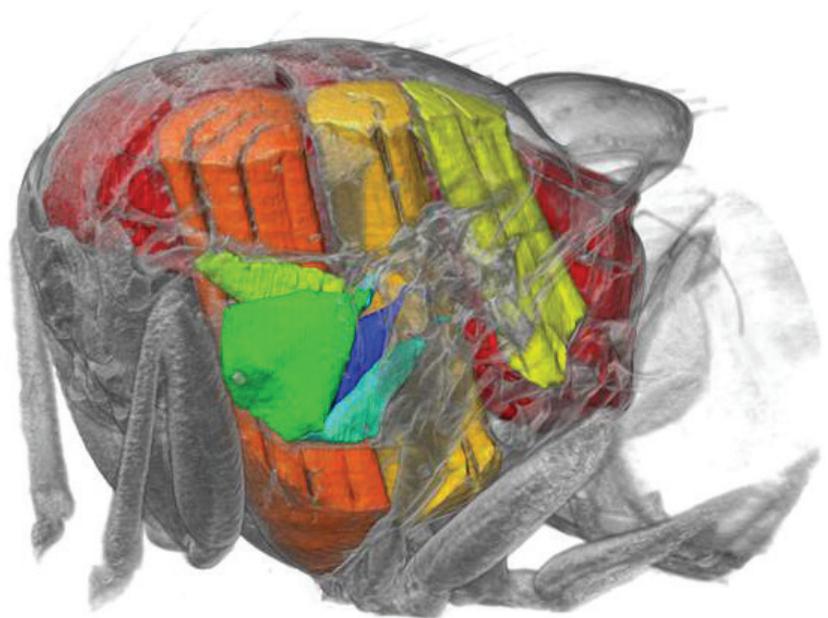
Okavango Delta in Botswana, and then apply isotope analyses to determine trends in browsing and grazing. At the same time we collect data from food plots, to quantify which plant species elephants are eating. We also analyse grass, foliage and crops to reveal nutrient value, secondary compounds and fibre content. Putting these data together should show if dietary deficiencies or other factors play a role in elephant crop raiding. My DPhil research is funded by NERC, through the new Environmental Research Doctoral Training programme.

Imaging the insect flight motor

In the time it takes us to blink, a fly flaps its wings 50 times. Attempting to understand the mechanics of the intricate flight motor that allows this rapid motion is a daunting task. Not only does it require recording of micron-scale structures moving many times per second, but many of these structures are hidden from view by the exoskeleton. Such is the difficulty in visualising the insect wing hinge that there is no consensus on how the wing even moves back and forth.

With my collaborators, Graham Taylor (Oxford), Holger Krapp (Imperial) and Rajmund Mokso (Lund), I am exploring the insect flight motor using cutting-edge techniques such as time-resolved microtomography. This method uses high-powered X-rays, which can only be found at a synchrotron such as the Swiss Light Source at the Paul Scherrer Institute in Switzerland where we perform our experiments. The resulting visualisations provide unprecedented views inside the insect thorax during actual flight, allowing us to study a range of previously hidden aspects of the flight motor.

Our data show that the exoskeleton functions as a complex, flexible mechanism, whose deformations form an integral part



Cutaway three-dimensional visualization of a blowfly thorax created using in-vivo time-resolved microtomography, highlighting several of the flight muscles

of the insect flight motor. My research aims to understand how the thorax is used to amplify and transform the small linear, strains produced by the flight muscles, into the large, nonlinear flapping motion of the wings. This work will help me

understand how natural selection has shaped the insect flight motor, but also has wider applications towards the development of micromechanical devices.

Simon Walker

Undergraduate student projects

Diet of invasive lionfish in Honduras

Christina Hunt, Somerville College



Two species of lionfish (*Pterois volitans* and *Pterois miles*) from the Indo-Pacific have become invasive in the western Atlantic. Lionfish reduce the abundance and richness of shallow

coral reef fish through predation, however their effects in deeper water are less well studied. I compared the diet of lionfish from shallow (0–25m) and deep (>25m) coral reefs in Honduras by conducting stomach content analysis. I found that lionfish from deep reefs consumed significantly more fish than lionfish from shallow reefs. This means that the detrimental effects exerted on fish communities may be more severe at depth.

Red-tailed bumblebee (*Bombus lapidarius*)

Jack Common, Christ Church



My project looked at how the foraging behaviour of bumblebees within small resource patches might be influenced by the quality of the surrounding habitat. All the

data were collected at the Upper Seeds experiment in Wytham Woods, so most of my Trinity was spent watching bees and recording flowers in the countryside – hardly the worst way to spend the term! The results were fascinating. Bumblebee behaviour seemed to be more sensitive to within-patch flower abundance when the among-patch abundance is low. This effect disappeared when habitat quality increased, possibly because of changes in the bumblebees' optimal foraging decisions.

Phenotypic characterisation of novel *Arabidopsis thaliana* secretory mutants

Laura Hankins, Magdalen College



Exocytosis impacts many aspects of plant biology, including disease resistance. I aimed to characterise four *Arabidopsis thaliana* lines carrying mutations inhibiting secretion and carrying a

transgene encoding a secretory green fluorescent protein (secGFP). Wild type seedlings secrete secGFP and it degrades, whereas secretory mutants accumulate secGFP so fluoresce more intensely. Mutants identified by this screen were examined using confocal microscopy to observe where secGFP accumulated in cells. One mutation caused vacuolar accumulation in root cells whereas another gave mortality before screening was possible. Finally, two caused hyperaccumulation in hypocotyl cells; I mapped one of these mutations to a region of chromosome 3.

The history in our genes

Chiara Batrni



Collecting DNA

Reconstructing the ancient and more recent history of humans is not a pursuit that springs to mind when you tell someone you trained in molecular biology and genetics. At face value, it appears to be more of a job for adventurous archaeologists digging in remote and exotic regions, or for dedicated historians pouring over indecipherable and mysterious parchments. However, surprising as it sounds, over the last couple of decades genetic tools have provided new and exciting insights into the history of *Homo sapiens*. What is more, some of these discoveries, such as conclusive evidence of an African origin for modern humans and the indication of gene-flow with archaic human forms, could only have been made through the analysis of our genes.

Partner choice in the legume-rhizobia symbiosis

Elsa Field, Magdalen College



I investigated the mutualism between legumes, agriculturally important crops, and nitrogen fixing bacteria (rhizobia). The mechanisms stabilising the symbiosis are

still enigmatic: specifically, it is unknown whether legumes can detect cheater strains of rhizobia that do not fix nitrogen for the plant, prior to infection, and prevent them from forming root nodules (partner choice). I tested if partner choice could occur by co-inoculating pea plants with mixtures of fixing and non-fixing strains of rhizobia. I showed that legumes could not selectively exclude cheating rhizobia, but instead found that plants punished cheaters by only allocating resources to fixing nodules.

The link between us and our past in our DNA should not be unexpected: our genomes are a mosaic of ancestral pieces that we inherited from our ancestors. Not all of our ancestors have left a record in our genome, however, as their number is very large and the amount of DNA in our nucleus is finite. Chance also plays a role in shaping which bits are transmitted from one generation to the next, so each of us carries different fragments of ancestry from our forebears. Nevertheless, by looking at the size and distribution of these fragments across individuals, it is possible to reconstruct a picture of our past and characterise the genetic history of populations.

With colleagues in the Dept of Statistics and at UCL, we recently showed that the vast majority, if not all, human populations bear signals of past encounters between humans groups which exchanged genes and which have shaped the variation present in current populations. This process of genetic exchange – called admixture – appears to be the rule, rather than the exception for our species, and this has been the case across time and space.

With genome-wide data from thousands of individuals we have been able to explore three key questions about human history: who were the groups that met and admixed; when did they admix; and, what was their genetic contribution? Our results have complemented and enriched the picture of our past sketched from other disciplines. For example, while the Roman Empire might have not left any specific Italian genetic signal across Europe, people and their genes moved during its time: from Africa to Southern Europe and from Asia to Eastern Europe. The collapse of that political entity generated a vacuum that instigated the so-called Barbarian migrations, both within the continent and from outside, all of which left signals in the genomes of European

people today. One of the most substantial and widespread events appears to be related to the migration and expansion of Genghis Khan and his Mongols, which left a clear signature of admixture all the way from the Far East to Europe.

The less detailed archaeological and historical record in Africa offers the fascinating opportunity to substantially contribute to the understanding of the past of the continent. Bantu-speaking agriculturalists spread across Sub-Saharan Africa at different speeds over the last few thousand years, assimilating foraging communities when their pace slowed down. Some of these communities have now ethnographically vanished, but their DNA lives on in their contemporary descendants. In Southern Africa, for example, populations that speak languages rich in click sounds are likely to descend, at least in part, from the ancient foragers. When we group individuals from these populations using genetics, there is little correspondence to linguistic classification, however. This pattern suggests extensive gene-flow and/or cultural shifts between their ancestors.

And it is not just the distant past that can be tackled using DNA. In an investigation of the genomes of modern-day American populations, we revealed the complex and fine-scaled recent ancestry to unprecedented levels, identifying subtly different levels of Native American, African and European DNA.

Migration and admixture seem to have played a major role in shaping the diversity of human populations: the exponential accumulation of genomic data now makes it possible to characterise these events in a systematic way and shows a record of the past in the people of the present.

Cristian Capelli

Chiara Batrni



A group of men in the Maloti/Drakensberg mountains of Lesotho, Southern Africa

Instilling new foraging traditions in wild birds

Molly Harwood



Below: Social network for one local area, where circles are individual birds and lines are their foraging associations. The original trained innovator is marked with "D"; black nodes indicate birds that learnt the behaviour over the experiment, while grey nodes are naïve birds

Above: Photograph of a great tit (*Parus major*), showing an individually identifiable metal ring and a plastic leg ring incorporating a passive integrated transponder (PIT) tag

In humans, traditions form when behaviours are transmitted between individuals with high-fidelity learning. When traditions differ between groups they are referred to as cultures, an outcome determined by demographic characteristics such as social network structure, as well as by individual learning processes. A capacity for social learning and complex culture is thought to be vitally important in the success of humans as a species. However we have no comparative understanding in other animals. Can animals have some form of culture? Is it underpinned by similar processes and mechanisms? Under what conditions will innovations spread and persist?

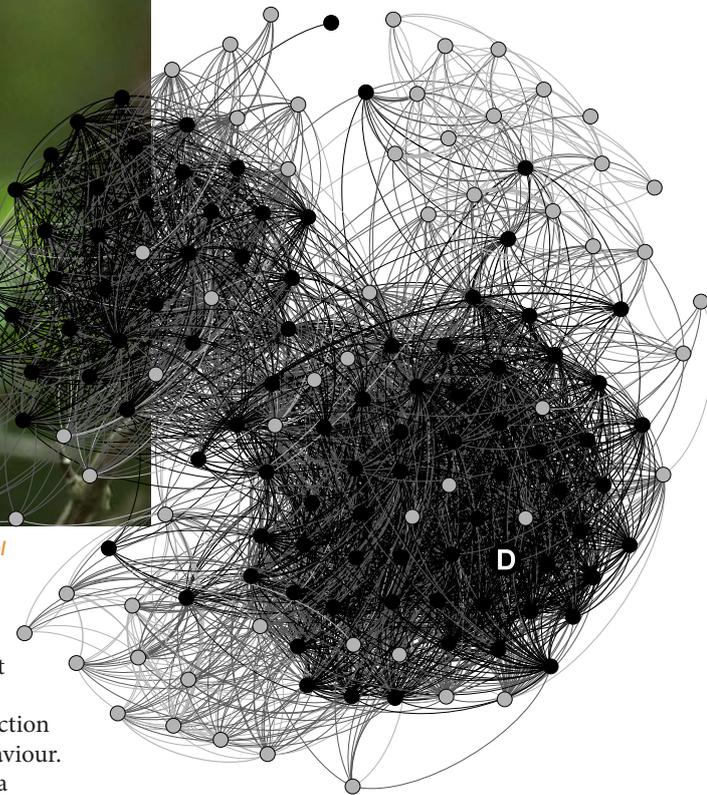
Our research group at the Edward Grey Institute for Ornithology has been investigating these questions in great tits (*Parus major*) at Wytham Woods. The

birds in this population are tagged with transponders that register at antennae, allowing detailed automated data collection on flocking patterns and behaviour. We used this system to build a comprehensive understanding of social structure. We then introduced a foraging innovation, training particular birds from different areas of the woodland to solve novel puzzle-boxes (and gain a food reward). Information about the puzzle-boxes installed across Wytham Woods spread rapidly from these 'innovators', travelling along social network ties to reach approximately 75% of all great tits in each local area. Intriguingly, most individuals copied the solving technique closely, and even after alternative ways of solving the puzzle-box had been discovered, specific local biases to the original technique persisted. Over time,

local networks become increasingly fixed on a single method of solving, with this learnt behaviour persisting over multiple generations.

This research demonstrates that innovations can spread rapidly in wild birds, forming traditions that are resilient to invasion by alternative behaviours. This reveals an intriguing similarity to human cultural behaviours, the form and function of which depend on population-level processes and individual-level capacities for learning.

Lucy Aplin



Student travel bursaries

Today's undergraduates face challenging financial pressures and many find it necessary to seek paid vacation jobs, often in shops or businesses close to their family home. This means that students can miss out on the opportunity to gain extra research experience while they are still undergraduates, whether that is by staying in Oxford for part of the vacations to undertake lab-based research or travelling to conduct fieldwork projects in the UK or overseas. We have set up a scheme to provide research and travel bursaries to assist students in such cases, and we have been delighted to see this fund start to get off the ground. We have received generous donations from individual alumni and also a collective donation from a group of students who matriculated in 1965 (in various biological subjects). If any alumni wish to contribute to the student research and travel fund, do please get in touch, alumni@biology.ox.ac.uk.

Regeneration

My research colleagues and I are interested in the fundamental processes that control regeneration in response to wounding or amputation. Regeneration is the ability to restore damaged adult structures so that they are functional again. While humans, like the Wolverine, can only do this in comics and films many animals have amazing abilities to regenerate their tissues after physical damage and disease. Understanding the genetic control of these phenomena has proven very difficult, as the animals that could regenerate well were also very difficult to study. This is now changing. In the last decade some key technical advances have been made which allow us to identify and describe the functions of gene networks in animals like planarian flatworms, annelid worms, crustaceans, starfish and newts as they regenerate tissues, organs and limbs. Much of what we are trying to understand revolves around the special cells that are the main contributors to regeneration called 'stem cells'.

In my laboratory work we primarily work with planarian flatworms (Fig 1). These amazing animals can regenerate their whole bodies from small starting fragments. To do this they are reliant on a population of amazing stem cells called 'neoblasts', a term coined by Harriet Randolph in the late 19th century. My group and others around the world have made great progress in understanding how these worms regenerate and describing the properties of neoblasts and their progeny (the cells that contribute to new tissues during regeneration; (Fig 2). Many of these findings may be relevant to human health and disease as we share most of our genes and their basic activities in common with these relatively simple worms.

Currently my group consists of five postdoctoral colleagues, three DPhil students and two Research Assistants, and we are funded mainly by UK Research Council grants, but also by international organisations and funding from Europe. Our goal in the coming years is to add to the body of knowledge explaining the genetic mechanisms that orchestrate different stem cells during regeneration, and to expand our work to other model systems. For example, we have recently started to work with an amphipod crustacean called *Parhyale hawaiiensis* (yes, it was first described in Hawaii!). This marine animal is about 1.5 cm when fully grown (Fig 3), can be kept in the lab easily and is capable of regenerating all of

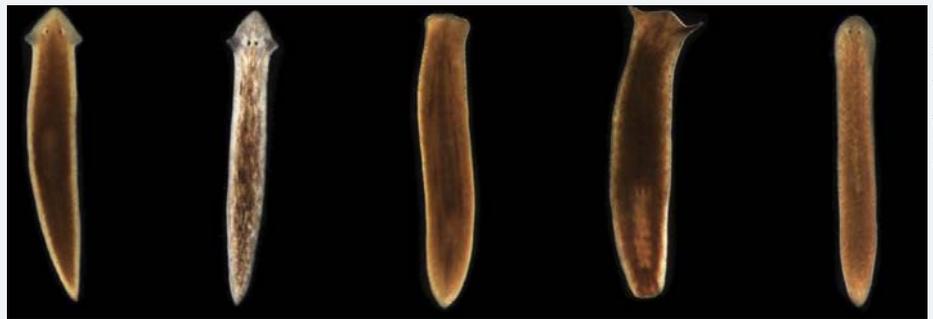


Fig 1: Ellen Aboukhatwa

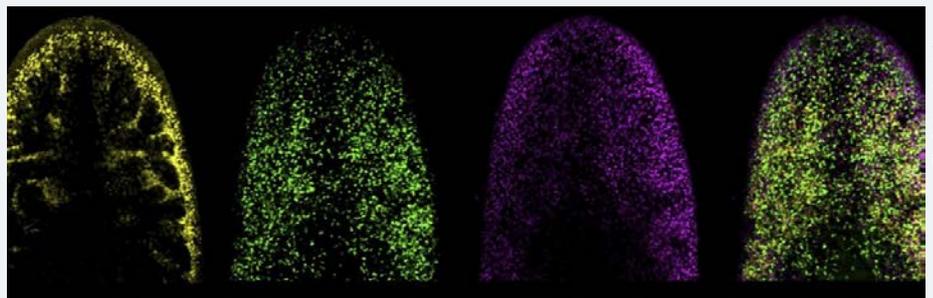


Fig 2: Katerina Johnson

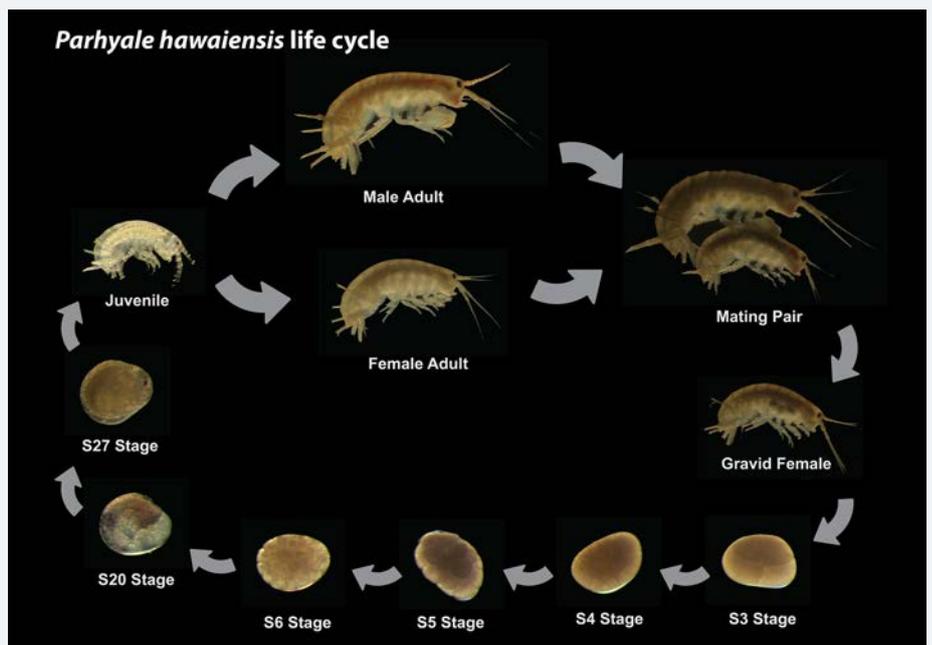


Fig 3: Alvina Lai and Damian Kao

Fig 1 (top), Fig 2 (middle), Fig 3 (bottom)

its limbs. We know almost nothing about how it does this. As a starting point we are sequencing its genome, which will not only help our research but many other groups with questions about this animal's other exciting capabilities (such as digesting wood as a food source, which may be of interest to next generation biofuel production).

Aziz Aboobaker

Alumni reunions

If you would like to catch up with former students, and see more about current teaching and research, please come to our Annual Alumni Day on 17 September (see back page for details). This is organised as part of the University's alumni weekend, so you can combine your visit with attending other events for alumni (see <https://www.alumni.ox.ac.uk/weekend/meeting-minds-alumni-weekend-oxford> for details). If you are organising other reunion events, please do let us know.

Why did more than 200,000 saiga antelopes die in less than two weeks?

In May 2015 an extraordinary scene unfolded on the steppes of central Kazakhstan. Female saigas gathered in their usual huge numbers to give birth on the open plain over a period of just 10 days, a spectacle thought to be a predator-swamping mechanism and a way to hit the peak of forage availability during lactation and calf growth. But this time, the females quickly became weak and uncoordinated, dying in a matter of hours. Soon a vast area stretching over hundreds of kilometres was littered with corpses. The calves followed soon after; within any given aggregation of tens of thousands of animals, it appeared that every single animal died over a period of a few days.

I have been working on the ecology and conservation of saigas for 25 years, during which time I have seen the species decline by 95% from over a million individuals to a few thousands, due to heavy poaching following the break-up of the Soviet Union, and then rebound. This population in central Kazakhstan had got back up to around 240,000 individuals, and was the engine of the species' recovery. So this mass die-off was a terrible tragedy for me and my fellow saiga ecologists. However it was also a fascinating scientific puzzle.

We quickly got to work to form an international, interdisciplinary team to study the disease and its causes. Led by Richard Kock at the Royal Veterinary College, with colleagues from the Kazakh government's Research Institute for Biological Safety Problems and the Association for the Conservation of Biodiversity of Kazakhstan, Bristol, FAO,

Steffen Zuther



A view over the calving ground, showing females lying dead; the regular spacing suggests that they died very quickly, wherever they were grazing or giving birth, when they got sick

Umea and other institutions, we include ecologists, rangeland scientists, vets and spatial modellers. I am focussing particularly on the ecology and life history of the saiga, and exploring the evidence from previous mass mortalities in saigas and other species, to determine how and why an event like this might have occurred.

We quickly raised money to send a team into the field and analyse a range of samples from the environment and the dead saigas. It soon became clear that the cause is not obvious, and that we would have to piece together a complex jigsaw to get the full story. On one level, we already have the answer; the proximal cause of death was toxicity from infection by opportunistic bacteria found naturally in the animals' respiratory tract or in the environment (*Pasteurella multocida* and in some cases *Clostridium perfringens*). But the question then is – why did these

commensals become virulent? What was the environmental or internal trigger, either reducing the animals' immunity to these bacteria or triggering virulence in the bacteria, or both?

We are now exploring these questions. Our research includes going back to old field notes from the Institute of Zoology in Kazakhstan, particularly from 1988 when a similar mass mortality occurred, looking for evidence of events like this in other species, looking at differences in the vegetation composition in die-off and control sites and years, and exploring changes in temperature and rainfall over a range of different temporal and spatial scales. We are also testing tissue and environmental samples for a wide range of toxins, as well as other disease-causing agents in case some other underlying infection was involved. So far, the evidence points towards a combination of short-term but landscape-scale weather variation and physiological stress from calving, but there is still a long way to go until we can be sure.

There has been huge public interest in this event, both within Kazakhstan and globally, with wild and not-so-wild theories circulating, and a call for quick answers and assurances that this will never happen again. It seems, however, that we won't be able to give the comfort that people need; in fact it is likely that with climate change this type of event will become more rather than less common. Our strong message is that resilient and abundant populations are required, with strong protection from poaching, so that the species can do what it does best when catastrophe strikes: bounce back.

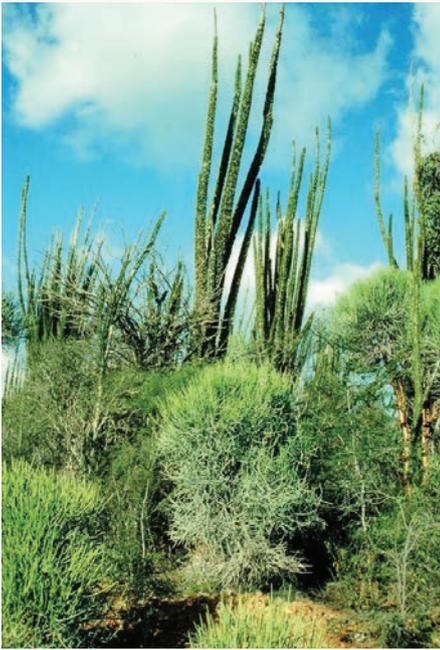
E.J. Milner-Gulland

Steffen Zuther



The field team carrying out a post-mortem on a dead saiga, showing Richard Kock from the Royal Veterinary College (right) and Mukhit Orynbayev from the Research Institute for Biological Safety Problems (left)

The value of succulence



The spiny thicket of southern Madagascar, dominated by succulent members of the families Didiereaceae and Euphorbiaceae

Succulent plants, whose leaves and stems have a reduced surface area to volume ratio that aids in water conservation, are one of the distinctive life-forms of semi-arid regions. The fleshy tissues also act as very effective storage capacitors, filling up with water when rainfall is abundant, and drawing on this reservoir during times of drought. Underpinning this lifestyle is the remarkable biochemical adaptation known as crassulacean acid metabolism (CAM). As discovered by De Saussure in 1804, CAM plants have the unusual ability to absorb carbon dioxide from the atmosphere at night rather than during the day. This minimizes the concurrent transpirational loss of water from the shoot surface by restricting stomatal opening to the cooler, more humid night-time. Of course, the drawback is that the light energy needed to drive photosynthesis is not available at night. So CAM plants fix their absorbed carbon dioxide into malic acid, which is stored overnight and then decarboxylated during the day, releasing carbon dioxide behind closed stomata for photosynthetic carbon assimilation.

Research in recent years has shown that CAM plants are much more widespread, both taxonomically and geographically, than previously supposed. Once caricatured as mere curiosities, we now know that CAM photosynthesis is found in 35 families, accounting for about 5% of all flowering plants. Most biologists will be familiar with the cacti and agaves that characterize arid regions of the Neotropics, or their analogues such as the succulent

euphorbias, crassulas and asclepiads of the Palaeotropics. But we have discovered that there are similarly large numbers of CAM species amongst the epiphytic plants of tropical rain forests, where the outer reaches of the forest canopy can be micro-climatically arid. Here we find an abundance of plants such as orchids and bromeliads, their root systems reduced to the function of a holdfast, experiencing regular cycles of wetting and drying while exposed to full-intensity sunlight and the evaporative effects of winds.

Our research is exploring the biochemical properties of CAM plants that underpin this metabolic adaptation. We estimate that CAM photosynthesis has evolved independently more than 60 times, so we are using genomic tools to investigate whether this complex trait has arisen on separate occasions by the same or different molecular pathways. This will be aided by the recent sequencing of the genome of the bromeliad *Ananas comosus*, the pineapple plant, which occupies an intriguing evolutionary position as an early-diverging member of the order Poales that includes the grass family and all our cereal crops.

Pineapple also gives the lie to the notion that CAM plants are intrinsically slow-growing plants of little commercial value, as it is cultivated as a profitable crop in 80 countries in the tropics and subtropics, with an international trade value approaching 9 billion US dollars per year. Other CAM plants cultivated as crops also show high growth rates, such as the sisal and tequila agaves, prickly pear cactus and aloe vera, which are of major importance to the economies of several developing nations. Indeed, the ability of such plants to grow in semi-arid conditions with little or no irrigation or fertilization suggests they might provide a valuable bioenergy feedstock for cultivation on marginal or abandoned agricultural land, thereby avoiding competition for the better-quality land required for food crops. Understanding how CAM plants can be so productive under conditions of water limitation and high temperatures will thus provide valuable lessons for agriculture, faced as it is with the challenges posed by global warming and more extreme weather events in the future.

Andrew Smith



Upper reaches of the forest canopy in lowland tropical forest in Panama, 30 m above ground level. Note the tree limbs festooned with epiphytic ferns, bromeliads and orchids

Widespread mistaken identity in tropical plant collections

Insects and flowering plants are the most species rich clades of terrestrial organisms, comprising two thirds of all biodiversity so far described, yet our taxonomic knowledge of these groups remains poor particularly for tropical biodiversity. For example, 90% of tropical plants are invisible to modern ecological modelling techniques as they have been collected so infrequently, fewer than 20% of all flowering plants have been the subject of IUCN conservation assessments, less than 10% of all crop wild relative germplasm exists in global repositories, and 65% of all published names are synonyms. The need for improved taxonomy is paramount.

The obstacles to improving the taxonomy of species-rich tropical taxa include a lack of taxonomic capacity, the doubling of the world's plant collections over the last 50 years and a voluminous scattered literature leading to a massive burden of historical information that needs to be assembled, synthesised and reinterpreted. For example, there are ~200,000 specimens of *Ipomoea* (morning glories), a group we are revising, in the world's herbaria. The lack of taxonomic capacity is illustrated by the average lag of 35 years between the collection and recognition of a new species.

Our recent research addresses these issues from two perspectives. First, to understand more fully the spatial, temporal and sampling dynamics that underlie species discovery and taxonomic revision. Secondly, to develop a realistic, accelerated pipeline to overhaul the taxonomy of species-rich poorly known tropical taxa, an approach we call 'foundation monographs'.

To understand the dynamics of the taxonomic process we identified a group that had been recently monographed, *Aframomum*, a genus of 63 species of African ginger. We assumed the taxonomic monograph to be essentially correct and examined the 4500 *Aframomum* specimens for the name associated with each specimen over time between when it was collected and named in the recent monograph. We found that 58% of all specimens did not have a correct name before being named in the current monograph.

We wanted to place our results in a broader context so conducted two further studies to measure the extent of incorrect names associated with specimens. We

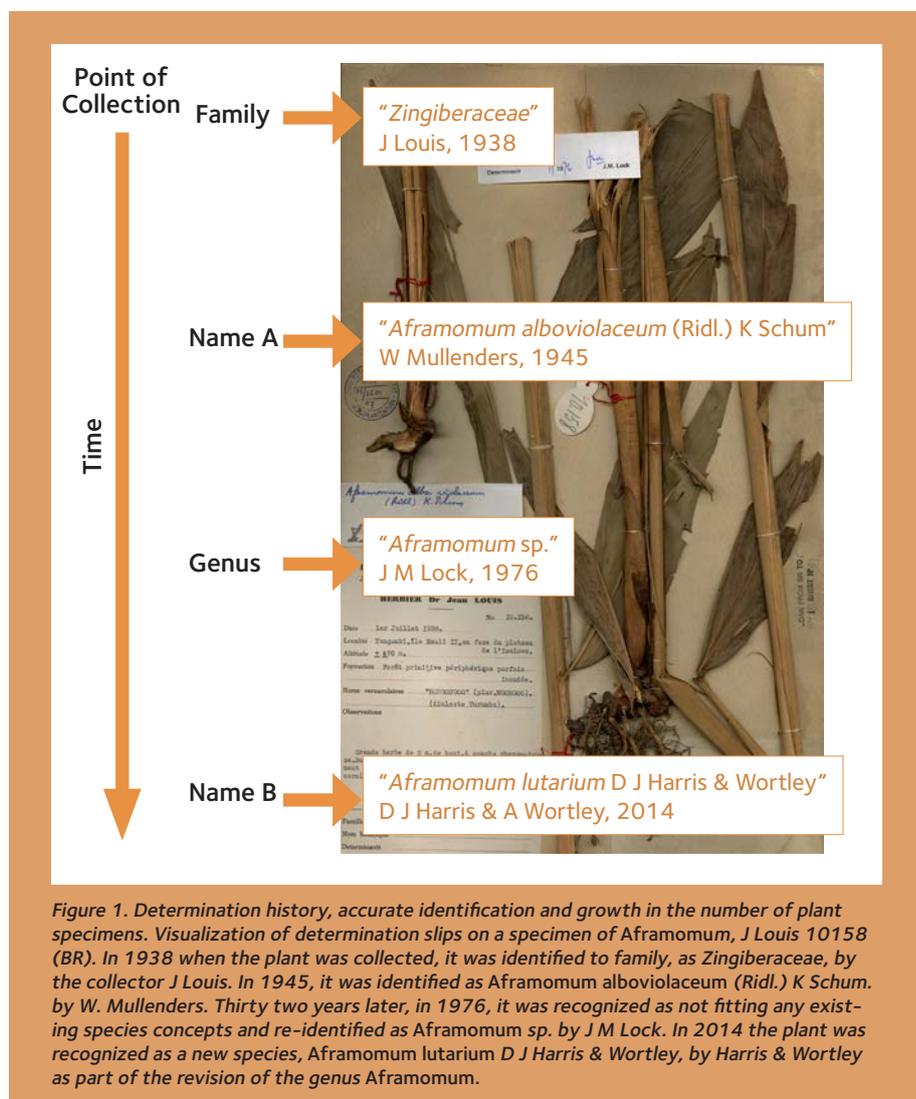


Figure 1. Determination history, accurate identification and growth in the number of plant specimens. Visualization of determination slips on a specimen of *Aframomum*, J Louis 10158 (BR). In 1938 when the plant was collected, it was identified to family, as *Zingiberaceae*, by the collector J Louis. In 1945, it was identified as *Aframomum alboviolaceum* (Ridl.) K Schum. by W. Mullenders. Thirty two years later, in 1976, it was recognized as not fitting any existing species concepts and re-identified as *Aframomum* sp. by J M Lock. In 2014 the plant was recognized as a new species, *Aframomum lutarium* D J Harris & Wortley, by Harris & Wortley as part of the revision of the genus *Aframomum*.

considered how duplicated specimens from the same plant might be given different names in different herbaria. It is common practice for plant collectors to distribute specimens of a single plant to museums and herbaria around the world. Once distributed, they are often independently named by an in-house expert. Analysing the *Dipterocarpaceae*, a family of rainforest trees from Asia, we found that 9,222 collections had been divided into two or more duplicates, making a total of 21,075 specimens. Of these, 29% had different names in different herbaria.

Lastly, we considered mistakes contained within aggregated records stored in online repositories such as Global Biodiversity Information Facility (GBIF). We examined the records of *Ipomoea* – a large and diverse genus that includes the sweet

potato – in GBIF. Examining the names of 49,500 specimens from the Americas, we found that 40% were outdated synonyms rather than the current name, and 16% were unrecognizable or invalid. In addition, 11% of the specimens were only given the name of the genus.

Our results highlight a serious disconnection between the rapid accumulation of tropical plant collections and the capacity to accurately identify them. We assume that the situation for flowering plants is also true and possibly worse for insects, given that the number of described insects is three times that of flowering plants. This led us to extrapolate that more than half of the world's natural history collections have an incorrect name.

Robert Scotland

Exploring antagonistic interactions in the plant apoplast

The extracellular space of leaves (apoplast) is one of the largest biotic interfaces on earth. Many microbes have adapted to live in the apoplast, and many of them cause disease. These extracellular antagonistic interactions between host plants and pathogenic microbes are an intriguing but largely unexplored battlefield that has captured our interest.

Using tomato as a model plant, we discovered that unrelated microbes (a fungus, bacterium and oomycete) secrete unrelated inhibitors that target the same secreted proteases of the host. This is associated with a protease-inhibitor arms-race, testified by variant residues in proteases in natural populations of wild tomato plants. Depletion of these proteases by reverse genetics causes hypersusceptibility to these diverse pathogens, highlighting the universal relevance of these enzymes and their manipulation.

Interestingly, inhibition of one of the proteases (Rcr3) by the fungal protein Avr2 in tomato plants carrying the *Cf-2* resistance gene, leads to localized hypersensitive cell death, providing full immunity. *Cf-2* encodes for a receptor-like protein that is able to sense the Rcr3-Avr2 complex at the cell surface. So in this case, protease inhibition acts like a trap that leads to pathogen recognition and defeat. Understanding the evolution and

molecular mechanism of this indirect perception mechanism will enable us to engineer proteases that evade manipulation or confer recognition of protease inhibitors of relevant crop pathogens.

The discovery of protease-inhibitor interactions has inspired us to seek more of these interactions and study their relevance in pathogenicity and immunity. We therefore investigate the interaction between the wild tobacco plant *Nicotiana benthamiana* and various strains of the bacterial model pathogen *Pseudomonas syringae*. Both organisms can be easily manipulated and robust infections lead to large quantities of secreted proteomes for further studies. We found that the apoplast contains a few hundred hydrolytic enzymes, many of which accumulate upon infection. We discovered that several of these hydrolases are inactivated during infection, often by inhibitors of both metabolite and protein origin. Identification and depletion of these inhibitors and their targets is a major current research effort.

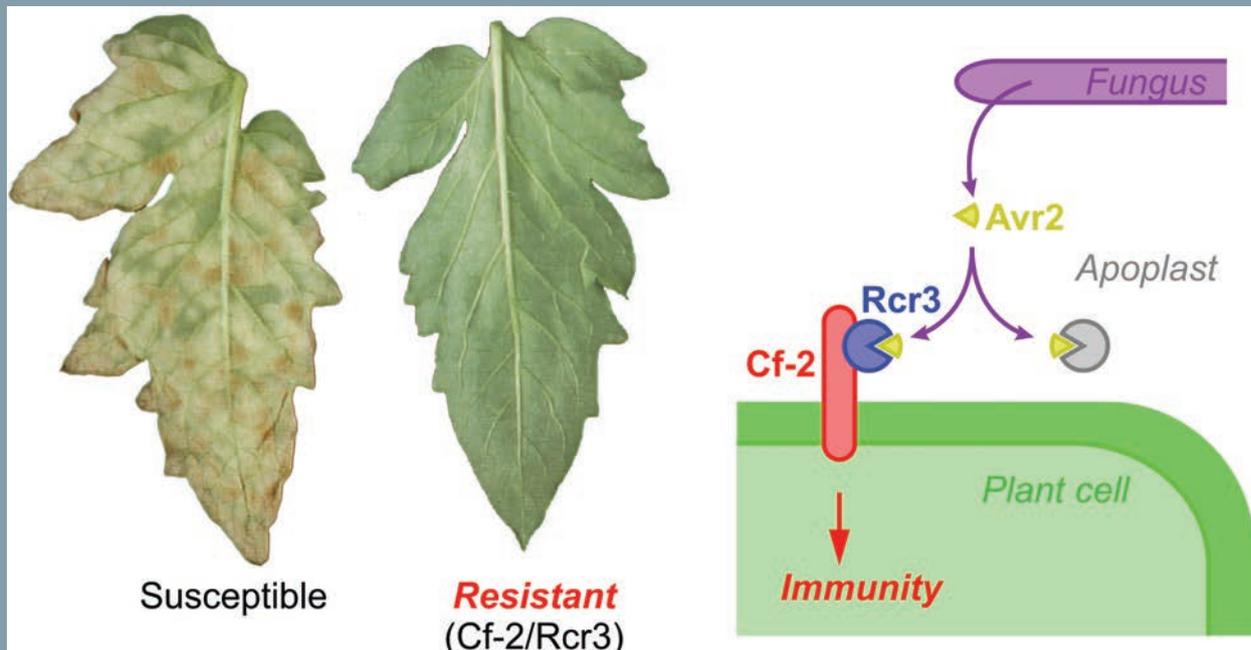
By working on secreted proteases of *N. benthamiana*, our research lab is in the unique position to solve a key bottleneck in the molecular pharming industry. Plants are increasingly used for the production of pharmaceuticals because this is cheap, safe, fast and flexible. Transient expression in *N. benthamiana* by

infiltration of *Agrobacterium tumefaciens* (agroinfiltration) is now used to produce 10 million influenza vaccines per month, and also ZMapp against Ebola was produced through this system. Unfortunately, however, the production of other recombinant proteins is limited because of processing by plant proteases, many of which accumulate upon agroinfiltration. The aim of our ERC-funded research program is to control these harmful proteases and study their endogenous roles.

Unique to the identity of the lab is our ability to monitor active hydrolases and other enzymes using activity-based protein profiling (ABPP). This functional proteomics technology is based on the use of chemical probes that react with the active site of enzymes in a mechanism-dependent manner, leading to labeled proteins that can be purified, identified and quantified by mass spectrometry. By pioneering ABPP in plant science, the lab is visited by a stream of scientists that wish to apply ABPP to different biological systems.

Thus, we are operating in the fields of plant pathology, molecular pharming and chemical proteomics. Please do not hesitate to find us to discuss science and find exciting areas for projects and collaborations.

Renier van der Hoorn



Mining the active apoplast

OXFORD UNIVERSITY ALUMNI WEEKEND SEPTEMBER 2016



AFTERNOON EVENT FOR BIOLOGY ALUMNI AND FRIENDS

See our website (www.biology.ox.ac.uk/alumni), and
email us on alumni@biology.ox.ac.uk

OXFORD UNIVERSITY ALUMNI WEEKEND

The Departments of Plant Sciences & Zoology
invite you to our Open Afternoon on

SATURDAY 17th SEPTEMBER 2016
12 NOON TO 4PM

ATTRACTIONS WILL INCLUDE

TALK:

12.30pm –1.30pm Prof Lord John Krebs
"Do science and politics mix?"

TOURS AND DISPLAYS from 2pm

Oxford University Herbarium, Department of Plant Sciences
Biological Sciences Open Day Exhibits, Department of Zoology
Interactive Research Exhibits
Refreshments from 1.30pm

TO REGISTER PLACES, PLEASE EMAIL
sharon.cornwell@zoo.ox.ac.uk

