

# Antenna

Volume 46(1) | 2022



**INCLUDED IN THIS ISSUE:**  
**PHOTONIC COLOURS OF INSECTS**  
**INSECT VENOMS**  
**DNA SEQUENCING**



**Royal  
Entomological  
Society**

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## Author Guidelines

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Submissions are made by email to [antenna@royensoc.co.uk](mailto:antenna@royensoc.co.uk) and reviewed by *Antenna's* editorial team. There are no page charges for publication in *Antenna*, where we encourage use of full colour figures and photographs to accompany text. Standard articles are normally 1,000–3,000 words in length and submitted with four to eight images (file should be original size of image taken and not reduced in size nor cropped heavily).

**Cover Picture:** Tasmanian Eucalyptus beetle, *Paropsisterna selmani*, photographed by James Wong in the Children’s Garden at the Royal Botanic Gardens, Kew. Submitted to the Society’s Insect Identification Service, see article on pages 51–53.

# Editorial

Welcome to this iridescent issue. Rarely has *Antenna* been quite so colourful! By now, you will likely be aware of the Society's new strategy and brand, and I very much hope that you approve. The thinking and processes behind both are explained herein by our Chief Executive Officer, Simon Ward. The articles by Stuart Reynolds and Dominique Vassie are the perfect start to the new-look *Antenna*, dealing as they do with iridescence and other aspects of structural colour from a biophysics and an artistic angle respectively.

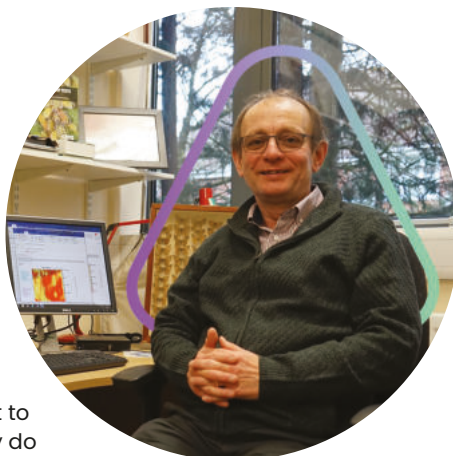
ENTO'21 was a while ago, but some of the excellent talks remain fresh in my memory. Many of the presentations would translate very well into *Antenna* articles, and I asked two speakers if they would be willing to do this. They kindly obliged. Tim Lüddecke's fascinating article on insect toxins and Philip Donkersley's beginners' guide to DNA sequencing are the result.

I was astonished at the AGM to discover the number, diversity and strangeness of some of the specimens sent to the Society by members of the public during 2020 for our Director of Science (now Resident Entomologist) Jim Hardie to identify. The haul for 2021 has been just as impressive and unexpected, as you will see. Jim gave one enquirer their best Christmas present ever, apparently!

Our librarian Val McAtear and administrator Sue Ward have, sadly, left the Society. Both contributed hugely in many ways, including to *Antenna*. Val recently digitised many years of copy and made it available online. Sue supplied the membership schedules like clockwork. I, and many others, will miss them greatly. All readers will also miss Dave George, who has been *Antenna* editor for almost ten years and has decided that the time has come to step down. He has been an absolute joy to work with, full of great ideas, incredibly efficient and always responding quickly and helpfully to queries. Thank you so much Val, Sue and Dave. Many thanks also to Peter Smithers who has stood down as reviews coordinator, and to Richard "Bugman" Jones, who has taken his place.

Much more awaits you, thanks to our excellent contributors.

Richard Harrington



# Antenna

## Bulletin of the Royal Entomological Society

### The Royal Entomological Society

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For *Antenna* 46(2) – 1st April 2022 (RH)  
For *Antenna* 46(3) – 1st July 2022 (RH)

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Printed by Andrew Smith Print Ltd  
Chelmsford, Essex  
email: [andrew@asmithprint.co.uk](mailto:andrew@asmithprint.co.uk)



## Antenna

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# Letter from the President



A new website, new brand and the launch of the Royal Entomological Society Strategy – exciting times. It has been wonderful to have so many members contributing to the development of these important initiatives. The iridescence of the new logo was inspired by one of our early-career researchers through discussions at a small workshop that was the culmination of consultation with the wider membership. So, for me the vibrant design will evoke memories of the many people who make our Society sparkle.

The history of the Society is also to be celebrated. I have enjoyed hearing stories from members about their experiences of the Society over the

years. I can remember attending the Postgraduate Forum as a PhD student in the late 1990s. I felt so pleased and inspired to be amongst other entomologists. My first presentation – a poster describing some studies on the feeding behaviour of *Coccinella septempunctata* in the presence of the aphid-specific fungal pathogen *Pandora neoaphidis* – was at the Royal Entomological Society Queen's Gate headquarters. I awkwardly remember the six panels that I had carefully mounted onto some thick card falling noisily from the poster board during the talks! But mostly I remember the wonderful welcome from others attending the event and the lively atmosphere in the library at the end of the day.

During my time as President I have particularly enjoyed meeting with the early-career researchers. The enthusiasm and commitment they bring to the Society is incredible. The online events that they have organised have been hugely successful – with many people attending and discussions that are inclusive and just as lively as those I remember from the library of Queen's

Gate. Early-career researchers are now widely represented within the Society – their many and varied contributions through publications, Council, committees, workshops and other events have been outstanding. Despite the challenges of the last few years they have shown resilience and compassion – supporting one another and developing the future of our Society. A place where everyone can shine.

There is no doubt that the Society has seen lots of change over the last few years but there are many things that remain much the same. Our shared commitment to advancing entomology and celebrating the wonders of insects in all their guises. The wonderful connections we have with one another. The sense of a thriving and inclusive community. The laughter and enjoyment when we come together. The support and guidance provided when times are challenging. It is a great privilege to work alongside you all. I am honoured to be the President of the Royal Entomological Society. I feel incredibly excited for the future of the Society and I hope you do too.

**Helen Roy**  
President  
Royal Entomological Society

# The ‘fantastical’ photonic colours of insects: iridescence and more



*Chrysolina herbacea* Photo credit: pjt66: CC BY-SA 3.0



## RESEARCH SPOTLIGHT

It has become clear that insects are masters of light engineering, and maybe we can learn something from them

### Stuart Reynolds

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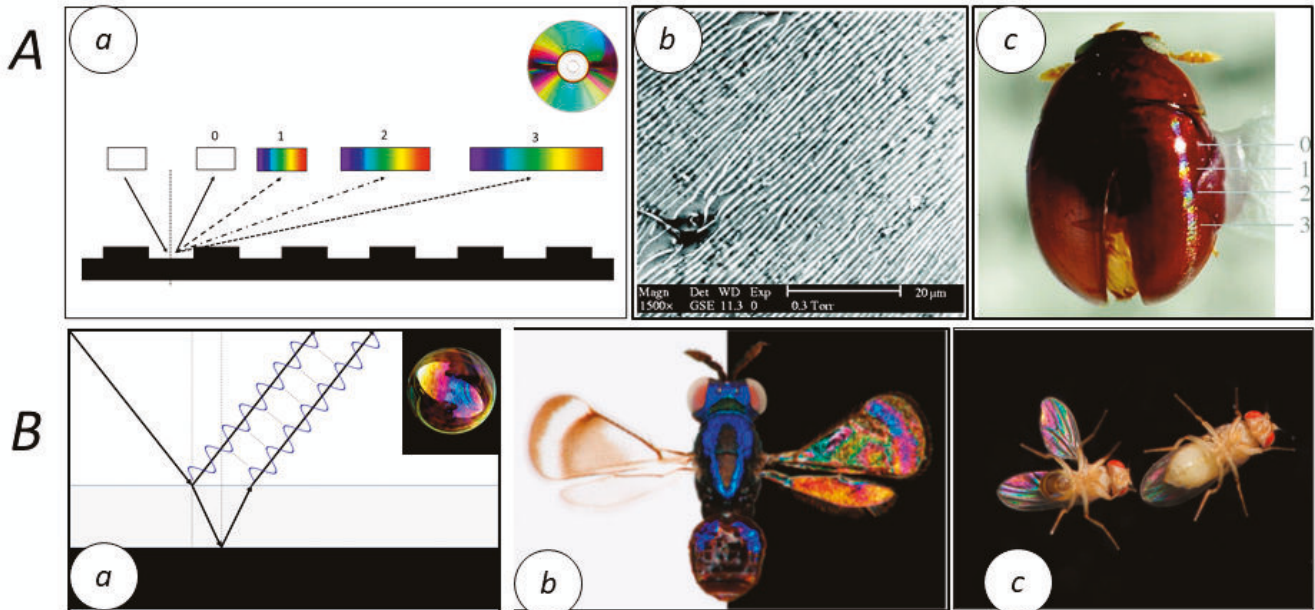
### The flashy photonic colours of insects

Every summer, the patch of garden mint by my back door becomes infested by a host of the brilliant metallic green chrysolid beetle, *Chrysolina herbacea*. I await the event with pleasure; the shining beetles are beautiful, and I don't begrudge them a share of the crop at all. It interests me as a scientist that the insects' colours result solely from the selective reflection of sunlight. Despite their brilliance, when viewed from the 'wrong' vantage point such colours may not only change, but in some cases vanish altogether. This is *iridescence* (it means that the colour changes according to the angle of observation). It seems a bit like magic. More than three hundred and fifty years ago the scientific polymath and early microscopist Robert Hooke (1665) thought so too. He referred to such animal colours in his wonderful book *Micrographia*, as 'fantastical' (*i.e.*, imaginary) because the colour is not due to a pigment.

One of the great heroes of natural history, explorer-entomologist Henry

Walter Bates, chased the spectacular iridescent blue butterfly *Morpho rhetenor* (Lepidoptera, Nymphalidae), which inhabits sunny patches in the otherwise shady Amazon tropical forest; he said: "When it comes sailing along it occasionally flaps its wings, and then the blue surface flashes in the sunlight so that it is visible a quarter of a mile away" (Bates, 1864, p.63). Like Bates, I find the brilliance of these structurally-coloured insects extremely *noticeable*. Perhaps that is indeed its evolved function. But that will be a story for another day; in this Research Spotlight I'm just going to review the phenomenon.

In recent years, such colours have been the subject of intense research interest. It has become clear that insects are masters of light engineering, and maybe we can learn something from them. Already technologists are creating devices for human use that mimic those of our hexapod friends. Here, I'll present the background to this exciting nexus between entomology and the physics of light, indicating some areas where



**Figure 1. A. Diffraction gratings.** (a) diagram of how a diffraction grating works. The inset in the top right corner is an image of a familiar object with this kind of optics – a digital compact disk or CD. (b) Scanning electron microscope image of the diffraction grating of a water beetle (Fam: Hydrophilidae, Subfam: Sphaeridiinae), and (c) the beetle itself. Note the four orders of reflected light; the zero order is white light, while orders 1, 2 and 3 are Newtonian spectra. **B. Thin film reflectors.** (a) diagram of how thin films work. The inset in the top right corner is an image of a familiar object with this kind of optics – a soap bubble. (b) montage of dorsal views of a tiny parasitic wasp, *Closterocerus coffeellae* (Fam: Eulophidae), seen against a light background (left) and a dark background (right). (c) Mating display of a male (left) in the presence of a female (right) fruit fly *Drosophila melanogaster* (Fam: Drosophilidae). Sources and image credits: A(b-c), Seago et al. (2009) [used by permission]; B(b), Shevtsova et al. (2012) [used by permission]; B(c) photo by Qinyang Li, University of Lund, Sweden.

we understand the subject fairly well, and others where there are still unanswered questions. It's clear to me that there is a lot of room for insect scientists to make an important contribution. In taking you on this rapid tour of the fantastical structural colours of insects, I will avoid going into the physics of light in too much detail (there will be no equations!), but for those who wish to dig deeper, an excellent review by Kinoshita et al. (2008) is helpful; if you're really keen, try the introductory textbook by Waldman (2003).

#### Diffraction gratings: directional colour sequences

First, some insects use **diffraction gratings** to create colour. This is how they work. When light falls on a surface with a regularly repeating array of surface projections or indentations (usually called 'lines') it is reflected to produce a pattern of diffracted light, a series of bands of different colour in reverse Newtonian sequence (i.e., in the opposite order to the spectrum formed by a prism). The colours are oriented at right angles to the axis of the lines, most often aligned either in the insect's long axis or at 90° to it. The sequence of colours is repeated in multiple orders of reflection (Order 0, 1, 2, etc.), each projected at a greater angle than the previous one (Seago et al., 2009) (Fig. 1Aa).

## Diffraction gratings

Diffraction gratings have been well understood since the early nineteenth century, but it remained uncertain until 80 years ago that insects use them to make colour. Hagen (1882) confidently asserted that gratings are present in insects but wasn't able to prove it in any particular case. Michelson (1911) examined a specimen of a 'diamond beetle' that was probably *Entimus imperialis* (Coleoptera, Curculionidae) and concluded that the striations on its scales were indeed a diffraction grating. But in fact, we now know that the iridescence of this species is due not to a grating, but to the presence of 3-D photonic crystals (see below) located in cuticular scales on the wing surface (Mouchet et al., 2013; Wilts et al., 2012).

The problem at that time was that the line spacing on optically useful gratings (which must be in the order of the wavelength of light,  $\lambda=400-700$  nm) is too small to be accurately measured using a light microscope (maximum resolution ~ 200 nm). Thanks to the invention of the electron microscope in the 1930s, it became possible to check a grating's line spacing against the observed colours. Anderson et al. (1942) were first to use transmission electron microscopy (TEM) to show that a grating is present on the elytra of the scarabaeid beetle *Serica sericea*, and that its dimensions are consistent with

the colours of the intact beetle. In the 1960s and 70s, H.E. Hinton and his collaborators used the more recently introduced scanning electron microscope (SEM) to study diffraction gratings in insects (e.g., Hinton et al., 1969) and catalogued a large number of species with grating-derived colours. A nice example of an insect that is now confirmed to use a grating to produce colour is the water beetle (Fam: Hydrophilidae; Subfamily, Sphaeridiinae) seen in Fig. 1Ab-c. According to Seago et al. (2009) diffraction gratings are now known to occur in at least 15 different families of beetles, and they appear to have evolved (and probably been lost too) on multiple occasions.

In almost all cases, grating-derived colours are flashy colours; they are not seen as a uniform colouration over all of the body surface and are often glimpsed only as evanescent highlights. Mason (1927) in criticising Michelson's (1911) proposal that gratings might be responsible for insect colours, pointed out that gratings are ill-suited to generating body-wide colour because it is hardly conceivable that the highly accurate alignment of the necessary diffracting lines could be maintained over extensive distances on the insect's body surface. This is true, but I think his criticism is wrong. Mason fails to recognise that when insects see each other, they are often very close together. Decisions about friend and foe, predator and prey need not be

based on looking at all of the other insect's body all at once. Presumably an insect may actually be on the lookout for flashes of colour, visible on only small patches of the body surface. Gratings are (sorry for the pun) great for this.

### Interference colours: thin layer reflectors on insect wings

Interference between light reflected from structures within the cuticle is far more important than diffraction from superficial gratings as the physical basis for producing insect structural colours. The simplest kind of device is the **thin layer reflector**, as in the well-known colours of soap bubbles. This is how a thin layer reflector works (Fig. 1Ba): as light approaches the 'front' surface of the thin layer, some fraction of the light will be reflected, while the rest enters. The extent of reflection is dependent on this difference of refractive index (RI), because RI is in effect a measure of the resistance of the material to the passage of light. The unreflected light passes through the thin layer, a further fraction being reflected from the 'back' surface before exiting at the 'front'. The front- and rear- reflected components of the light now interact either constructively or destructively (*i.e.*, they 'interfere' with each other) according to the relative phases of the two waves – this depends on the difference in path lengths they have just experienced. To generate colours, the difference in the distance travelled must be that of the wavelength of light or some integral fraction or multiple of it, and this means in turn that the thickness of the film needs to be roughly 0.5  $\mu\text{m}$ . Only in the smallest insects will an entire wing be sufficiently thin to act as a useful reflector, so insect wings are not universally iridescent. Variation is to be expected because wing cuticle is thicker (*i.e.*, stiffer) in some parts of the wing blade than others for aerodynamic reasons – hence the existence of their colour 'patterns'.

Thin single-layer reflectors made of cuticle occur at the surfaces of the wings of many small insects (Fig. 1Bb–c), as was established long ago by Goreau (1843) and later confirmed by Mason (1927); these layers are responsible for the characteristic transient iridescent colours of insect wings. A relatively recent, high-profile paper (Shevtsova *et al.*, 2011a) reported the (re-)discovery of these wing interference patterns (WIPs) without any apparent knowledge of

their 158 year-old history. People really should read more! Nevertheless, I mustn't grumble because the newer study beautifully documents a wide range of colour and pattern due to thin film reflection in the wings of small Diptera and Hymenoptera. A point worth noting is that often the WIPs of small insects can only be seen when viewed against a dark background (Fig. 1Bb). Have WIPs evolved? It seems likely that insects (especially the smallest ones) just can't help reflecting the light in this way. But that doesn't mean that the interference colours are unimportant in evolution. For a WIP to be subject to selection it's necessary that the pattern should be heritable. As long as wing thickness or wing-cuticle chemistry are under genetic control, evolution, whether by natural or sexual selection, has something to work on.

## Thin layer reflector

So what exactly is the nature of the thin film reflector? Although Goreau (1843) thought that a thin layer of air in between the upper and lower surfaces of the wing was the only important component, Mason (1927) asserted that there are two independent thin layer reflectors, one being the upper layer of wing cuticle while the other is the lower layer. By contrast, Shevtsova *et al.* (2011a) suggested that the entire thickness of the wing constitutes a single reflector. This may differ between species.

One obvious evolutionary hypothesis is that WIPs could be the subject of sexual selection within species. In many insects, including *Drosophila melanogaster*, courtship involves wing display behaviour (Fig. 1Bc). Although this involves sound signals too, it will also display the WIP. Possibly it is being shown off as evidence of fitness (*i.e.*, 'good genes')? Katayama *et al.* (2014) have shown that adult female flies are able to distinguish and prefer WIPs of certain types. In a very nice paper, Hawkes *et al.* (2019) found that WIP patterns can be selected. They found that when male flies were forced to compete for females under polyandry conditions for many (68) generations, their WIP displays were intensified in brightness and as a result the flies became more attractive to females. Butterworth *et al.* (2021) found that WIPs are species-specific in blowflies in the genus *Chrysomya* (Calliphoridae) and that both sexual dimorphism and sex-specific variation exist. All of this is strong evidence that WIPs can be the subject of sexual selection. Since such

traits are involved in assortative mating, it is therefore possible that WIP displays are actually evidence of species identity. This suggests that in at least some species, WIPs will prove helpful in taxonomy. Although some early work indicates that this is true in at least some cases (Shevtsova *et al.*, 2011b; Simon, 2013; Pielowska-Ceranowska *et al.*, 2020; Hosseini *et al.*, 2021), it isn't yet clear that WIPs are sufficiently useful to become a normal part of species descriptions. WIPs may also provide traits that can be used in phylogenetic analysis (Buffington *et al.*, 2011). And then of course there is always the possibility of cryptic species. But care is needed before concluding that WIPs are a new and essential taxonomic tool; this is because bigger insects are likely to have thicker wings, and it's distinctly possible that a change in WIP might be more related to a change in size than to be an independently-evolving morphological trait (Ament, 2021).

WIPs might prove to be important in applied entomology in an entirely different way. Gebru *et al.* (2014) have fabricated electronic devices to detect WIPs in flying insects, and plan to use this information, in conjunction with wing beat frequency analysis, to detect the presence and movement patterns of particular species of insect (mosquitoes seem like a good place to start).

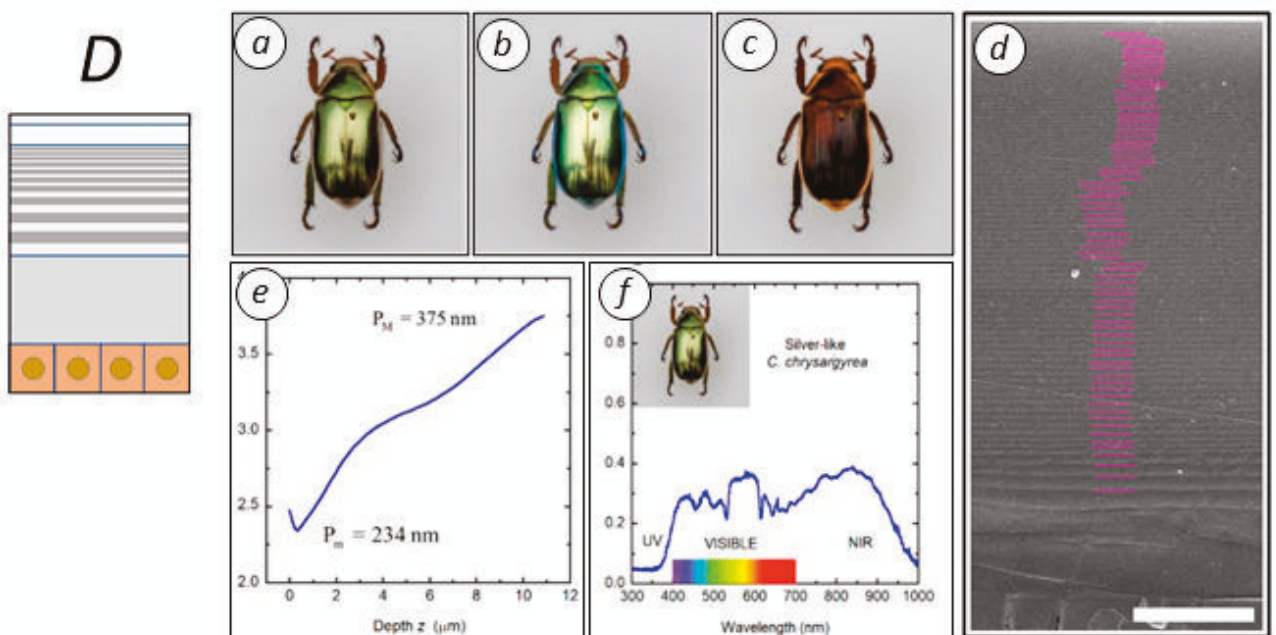
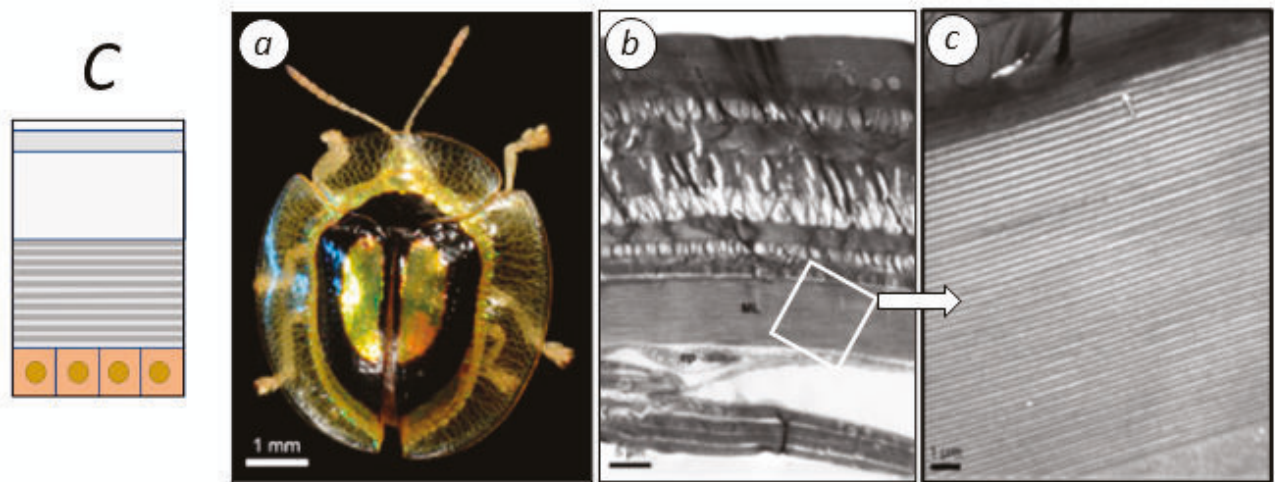
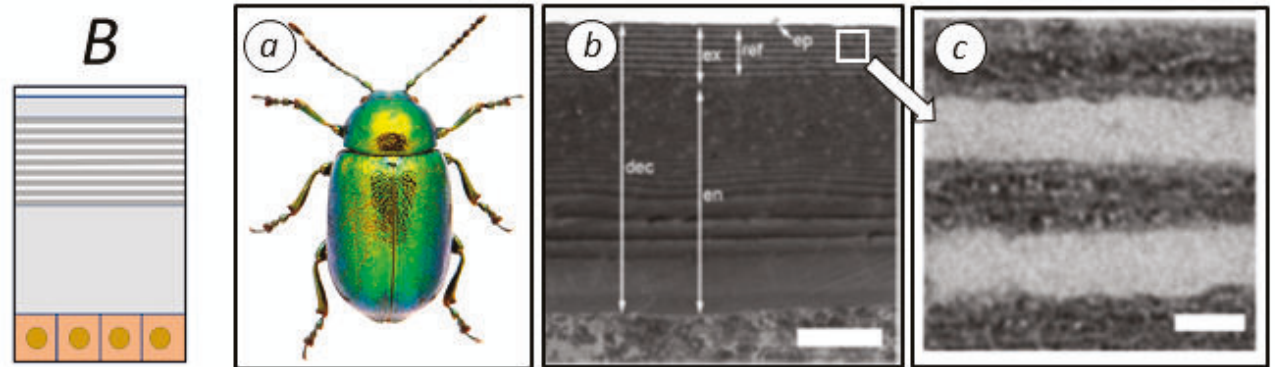
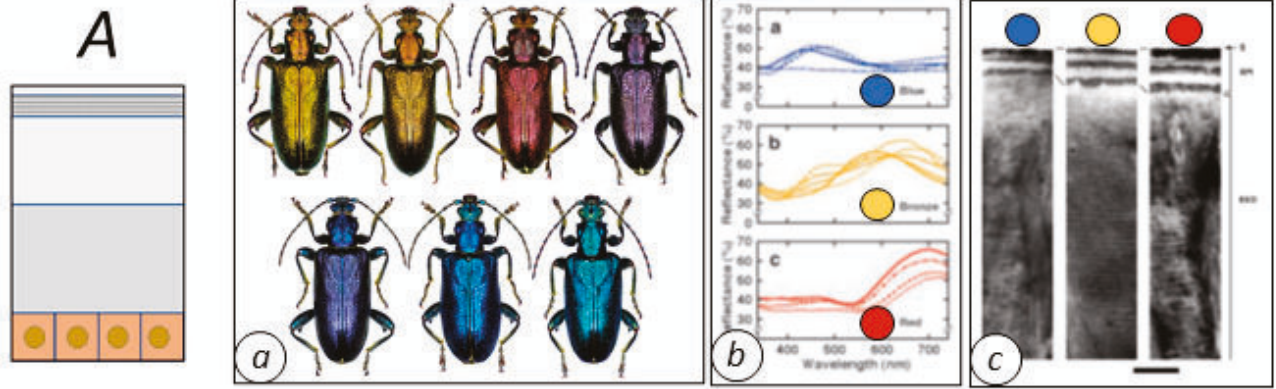
Thin film reflectors also occur in other insects in different phenotypic contexts. In particular, in some butterfly wings the lower surface of the scale is a thin film that reflects iridescent coloured light upwards through the rest of the scale, which may contain coloured pigment chemicals. Thus, the final colour seen is due to the combined effects of the pigment illuminated by incident white light from above and the structurally-coloured light reflected from below (Stavenga, 2014). In some butterfly wing scales, colour has evolved by tuning the thickness of this lower surface thin film (Thayer *et al.*, 2020).

By the way, not all structural colours on insect wings are due to thin films. In larger insects (for example in many damselflies), wing colouration is due to the cuticular multilayer reflectors that we will meet in the next section (Nixon *et al.*, 2012).

### One of the many brilliant ideas of the Braggs: multilayer reflectors

It has been useful to introduce thin layer reflectors first, because we can now use the same optical theory to understand the more complex light-







**Figure 2. Multilayer reflectors. A. Epicuticle.** (a) Colour variants of the leaf beetle *Plateumarium sericea* (Chrysomelidae). (b) spectral content of light reflected from blue, bronze and red beetles (colour indicated by dots). (c) insect colours are due to differently spaced epicuticular layers, scale bar, 500 nm. **B. Exocuticle.** (a) Metallic green colouration of the green dock beetle, *Gastrophysa viridula* (Chrysomelidae). (b–c) reflective layers in exocuticle, bars (b) 2  $\mu\text{m}$ ; (c) 100 nm. Dec, dorsal elytral cuticle; ep, epicuticle; ex exocuticle; en, endocuticle; ref, reflector. **C. Endocuticle.** (a) The golden tortoise beetle, *Charidotella ambita* (Chrysomelidae, Cassidinae). (b–c) golden areas of dorsal cuticle are broadband reflectors due to a multilayer reflector located in the endocuticle, bars (b) 5  $\mu\text{m}$ ; (c) 1  $\mu\text{m}$ ; (d) layer thickness declines progressively with cuticle depth. **D. A broadband chiral reflector in the exocuticle.** Silver-like form of *Chrysina chrysoargyrea* (Coleoptera, Scarabaeidae). (a) viewed in ordinary white light. (b) through a left-circularly-polarising filter. (c) through a right-circularly-polarising filter (reflectivity and green colouration are lost). (d) TEM section through exocuticle, purple lines highlight helicoidal lamellar boundaries, bar 5  $\mu\text{m}$ . (e) lamellar thickness vs depth, PM = maximum, Pm = minimum. (f) spectrum of reflected light (high reflectivity across entire visible range plus infra-red); Sources and image credits: Aa photo by Gubin Olexander; Ab,c from Kurachi *et al.*, (2002); B, Onelli *et al.*, (2017); C, Pasteels *et al.* (2016); D, Vargas *et al.* (2018). All images used under Creative Commons (CC-BY 4.0).

reflecting devices seen within the body cuticle of the most brilliant iridescent insects, such as the charismatic metallic-green chrysomelid beetles with which I began this story. When many thin layer reflectors are stacked one upon the other, we have a **multilayer reflector** or distributed Bragg reflector, so called because the potential of periodic structures to reflect electromagnetic radiation was originally recognised by William and Lawrence Bragg (father and son), who then used the same discovery to more or less invent modern crystallography (Bragg *et al.*, 1913). I'll note here that multilayer Bragg reflectors are often nowadays considered as a special 1-dimensional case of the general class of **photonic crystals** (Yablonovitch, 1993), because the periodicity of the device (and therefore the axis of light reflection) is present in only one dimension (more on photonic crystals below).

The multilayer reflector is probably the most common type of photonic device in insects; they are seen in many hexapod orders and have presumably evolved on many occasions. Their layered structures can be present at any level of the cuticle and can clearly be seen in stained TEM images of the cuticle. The optical properties of multilayer devices are basically the same as those of thin layer reflectors, only more so. As before, the key requirement is that in each lamina of the multilayer, refractive index (RI) is different from the material in between the layers. The presence of many reflecting layers, however, means that the proportion of incident light reflected by the whole structure is amplified. 'Tuning' of the spectrum of the reflected light is accomplished by adjusting the thickness of the repeated layers. Moreover, repeated episodes of reflection and interference as light meets each of the reflector's layers mean that the opportunity for light to follow consistently low angles of incidence in entering and leaving the layers is greatly reduced, and as a result the range of colours reflected (the 'bandgap') has a much narrower spread of wavelengths than in a

proper thin layer. The greater the difference in RI between the alternating layers of the reflector, the fewer layers are needed, and the more narrowly the reflected light is tuned. These principles are nicely explained for biological structures by Land (1972).

Multilayer reflectors are found in iridescent insects from a number of different orders, but most notably in the elytra of beetles (Fig. 2 A–D). Cuticular multilayers that have a uniform lamellar spacing throughout their depth reflect a relatively narrow band of wavelengths (*i.e.*, they generate a single, more or less pure colour), but even so this colour may appear iridescent when viewed at a steep angle. But if lamellar spacing varies over a wider range (usually in the form of a 'chirped' structure in which the lamellae become further or nearer apart with depth) then the resulting reflector reflects a wider range of wavelengths, and in the most extreme cases has a metallic mirror-like appearance (sometimes called 'specular' reflection). This is called a **broadband reflector**; Fig. 2D illustrates such a device for the scarab beetle, *Chrysina chrysoargyrea*, in which the exocuticular layers increase continuously in thickness as we travel further from the surface. The measured reflectance spectrum shows that a wide range of wavelengths is reflected (the beetle looks silver) and the model shows that different colours are reflected at different cuticle depths. In fact, 50 years ago, Neville *et al.* (1969) had described crude experiments in which the cuticle was progressively abraded to reveal exactly this pattern of colour at different depths.

These apparently simple multilayer structures are constructed entirely within the ordinary body cuticle; importantly, they differ from some of the photonic structures that we will meet later, in that they are entirely made of cuticle, with no air gaps between layers. We know that the layers are there because we can see them in stained microscopic sections (look at Fig. 2B), and in most cases the

layers have alternate light and dark staining bands. But there's something about these structures that we don't understand: optical theory is insistent that in order to act as reflectors, the alternating lamellae must have different refractive indices; the reflective optics of cuticular multilayers can be modelled quite successfully provided that we make assumptions about the RI values in the alternating layers, but there are very few cases indeed where RI has been measured empirically, and in most models either dubious assumptions are made about the RI used to model

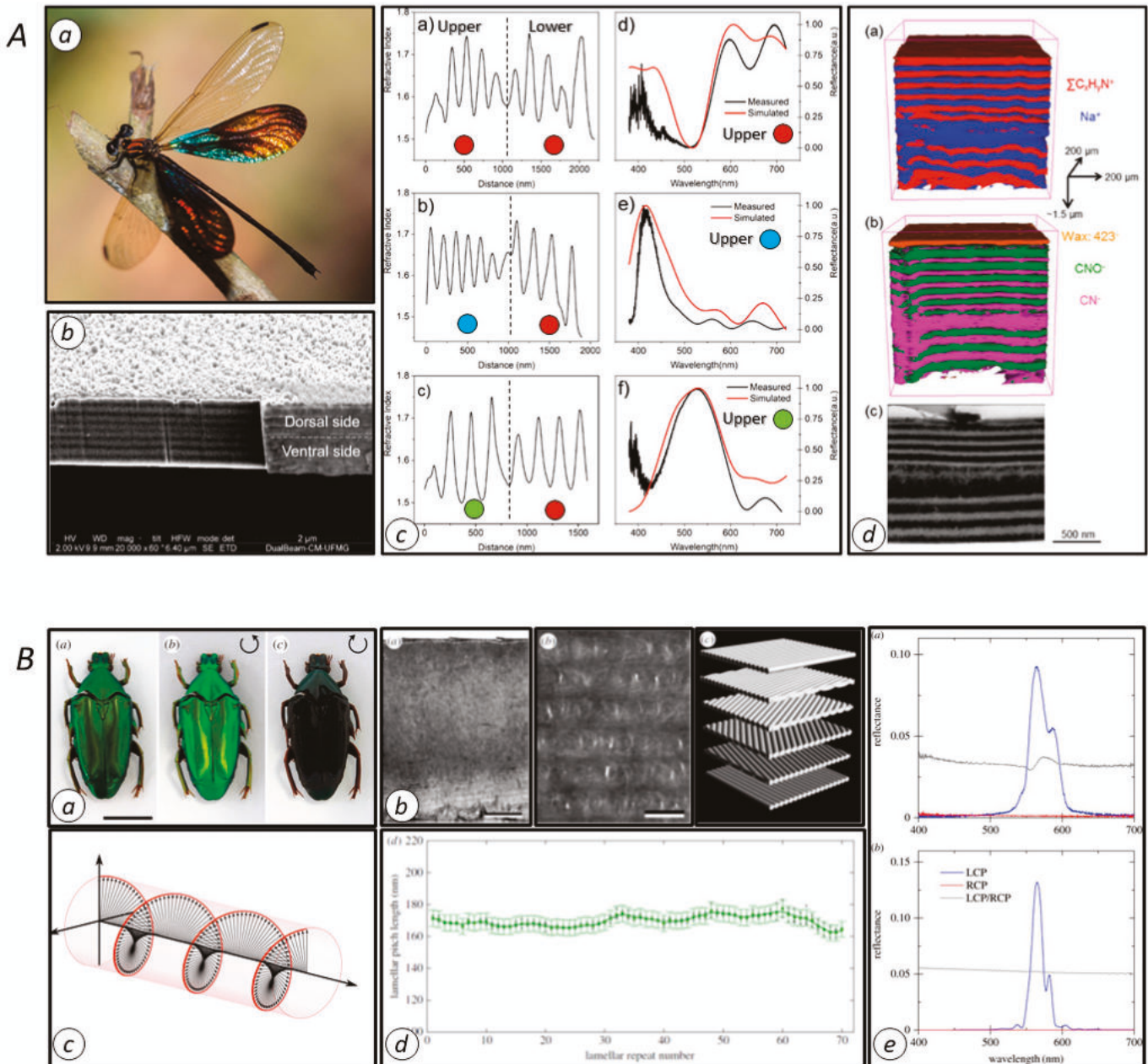
## Broadband reflector

cuticle components, or the RI values actually used in the model are chosen by fitting the parameters to the results.

Because we don't know enough about the actual materials of which the cuticle is made, we don't know what the value of RI should really be.

With this in mind, it is encouraging that Valeriano *et al.* (2021) have now devised a method using electrostatic force microscopy (EFM) to directly measure the relative permittivity  $\epsilon_r(\omega)$  (sometimes called the dielectric constant) of insect cuticle within the layered structure itself. Relative permittivity is a physical property of a material that affects the ability of electromagnetic radiation, including light, to penetrate it. It is thus directly related to RI. The authors followed the spatial variation of relative permittivity across the thickness of the wing in the sexually dimorphic damselfly *Chalcopteryx rutilans* (Fig. 3Aa). This spectacular insect has transparent uncoloured forewings but has iridescent hind wings, which are red on both the underside and the upper side in both sexes, but (only in males) the upper surfaces also have patches of iridescent blue and yellow-green. The difference between the two sides tells you straight away that separate Bragg reflectors are present in the upper and lower cuticle surfaces, even though they are very closely apposed (Fig. 3Ab). In SEM pictures, the cuticle has a layered structure that corresponds exactly to laminae of differing relative permittivity (and thus RI). The upper side of the wing cuticle





**Figure 3. A. Measuring refractive index (RI) in situ and identifying melanin in a damselfly cuticular multilayer reflector.** (a) Male *Chalcopteryx rutilans* (Zygoptera, Polythoridae). Forewings are uncoloured in both sexes; in the female, hindwings are uniformly red on both lower and upper surfaces, in the male, upper wing surfaces have blue and yellow-green patches. (b) SEM of wing; shattered area reveals closely appressed cuticles of upper and lower surfaces. (c) resistive permittivity of cuticle was determined using EFM, allowing calculation of actual RI values. Left panels, plots of RI vs cuticle depth in different colour cuticle areas. Peaks represent layers of alternating low and high RI; note differing number of peaks in different panels, and between left (upper) and right (lower) wing surfaces, corresponding to wing colour (red, blue and green dots indicate colour of overlying cuticle). Right panels, calculated reflected spectra of red, blue and green areas. Pairs of panels show data for red (top), blue (middle) and green-yellow areas (bottom). (d) false-coloured plots indicating relative strengths of various different TOF-MS signals in different cuticle zones. Top panel shows positive ions; middle panel, negative ions, it has been suggested that the blue/green layers in the diagram correspond to high melanin zones. **B. Reflection of polarised light in scarab beetles.** (a) *Chalcothea smaragdina* (Scarabaeidae, Cetoniinae) (left) as it appears in ordinary white light, (centre) through a left-circularly-polarising filter, and (right) a right-circularly-polarising filter (almost all reflectivity and green colouration are lost). The insect's dull appearance in ordinary light is due to a superficial layer of light-scattering wax. (b) (left) TEM image of whole depth of elytral reflector (scale bar 3µm); (centre) typical Bouligand structure within reflector (scale bar 200 nm); (right) schematic helicoidal architecture within exocuticle (a lamellar stack with successively rotated chitin microfibril layers). (c) rotation of e-vector in left-circularly polarised light is anticlockwise when viewed from the origin. (d) in *C. smaragdina*, lamellar pitch (i.e., depth for 180° rotation) does not change with depth - this is why *C. smaragdina* is green and not gold or silver (contrast Fig. 2D). (e) measured (upper) and modelled (lower) spectra of reflected light from *C. smaragdina* elytra, LCP (blue) is left-circularly polarised light, RCP (red) is right-circularly polarised light. (LCP/RCP is cross-polarised light, a phenomenon not considered here). See original papers for more information. B. McDonald et al. (2017) images used with permission.

under the blue patches has a larger number of thinner layers than in other cuticle regions, and the number of layers in red areas is lower than elsewhere. The absolute values of RI obtained from EFM (it varies from ~1.5 to ~1.75) can be plugged into a standard Bragg reflector model and this yields simulated colour spectra for each region of the wing that are very

similar to those of the damselfly itself, with restricted blue and yellow-green patches on the upper wing surface of male wings only (Fig. 3Ac). This is a great advance on what has been possible before, because optical modelling of the iridescent cuticle can now be properly parameterised using empirical data. But it leaves unsolved the biochemical nature of the layers.

It happens that the reflective layers in the damselfly wing cuticle are in the exocuticle. But as shown in Fig. 2A–C, in various iridescent insects multilayer reflectors can be found in epicuticle, exocuticle and endocuticle. All these locations are suitable as long as the overlying material is transparent. The molecular composition of these varying locations in the cuticle is

diverse, and we should notice the complete absence of chitin from the epicuticle. This fact effectively disposes of the idea (all too frequently mentioned in biomimetic papers about structural colours) that chitin is in some way fundamental to cuticular colour-generating devices. (It's annoying that so many papers from biomimetics- and physics-based researchers seem to think that 'chitin' is the same material as 'cuticle!'). It could be argued (especially by physicists!) that it doesn't matter what is the chemical nature of the reflecting layers, but I say that it *does* matter if we want to know how and from what precursor structure an insect multilayer reflector evolved. In other words, the physics of structural colour is a good start, but we need more chemistry.

Valeriano *et al.* (2021) suggest that in damselflies, the reflector is constructed from alternating layers of cuticle and melanin. Melanin is a pigment made by polymerising precursors synthesised from the amino acid tyrosine. It has been known for a very long time that insect cuticle is sclerotised (chemically stabilised and made permanently hard and stiff) by incorporating these tanning precursors. So it is not unreasonable to suppose that local deposition of such materials might also contribute to the cuticle's optical properties. Valeriano *et al.*'s proposal is supported by Carr *et al.* (2018) (it's actually the same research group) using focussed ion-beam SEM combined with time-of-flight (TOF) mass spectrometry to show that the coloured hindwing cuticle yields signals that are apparently derived from appropriately spaced layers of eumelanin, while these signals are absent from the transparent forewings (Fig. 3Ad). The chemical identification is not completely watertight, but it looks good so far. Having said that, we have absolutely no idea how such very thin layers of melanin could be produced in the cuticle.

### Multilayer reflectors and polarised light: 2-D photonic crystals

In some insects, light reflected from a cuticular multilayer is left-circularly polarised. This means that its electric field not only vibrates in one axial plane (the 'e-vector') more than the other, but also that the preferred e-vector rotates anticlockwise as the light travels through space. Since the incoming light contains an equal proportion of left- and right-circularly polarised light, the reflector must

selectively turn away left-circularly polarised light, while right-handed light is allowed to pass. That insects can use chiral selectivity of this kind to generate iridescent colours was first demonstrated experimentally by Michelson (1911) using the elytra of the golden scarabaeid beetle *Chrysina (=Plusiotis) resplendens*. This unexpected finding was subsequently confirmed by Gaubert (1924) and Matthieu *et al.* (1937).

Only much later was the structural basis of this beetle's chiral reflectivity explained by Neville *et al.* (1969) in terms of the anticlockwise helicoidal array of chitin nanofibers in the exocuticle of which the reflector is made. In Fig. 3B, I have shown more recent data from another scarab, *Chalcothea smaragdina*. This is green, not golden, but its reflected light is circularly polarised, as is shown by the complete disappearance of its colour and metallic lustre when seen through a right-circular polarising filter (Fig. 3Ba(a-c)). This type of supramolecular architecture, long known to exist in certain chemical polymers when in the liquid crystalline state, and which is known to reflect left-circularly polarised light (Fig. 3Ba), was discovered to characterise all arthropod cuticles by Yves Bouligand (1972), an outstanding discovery that was greatly extended and developed by Charles Neville (1975). The exocuticle of *C. smaragdina* is continuously helicoidal with a constant pitch (Fig. 3Bc-d). The spectrum of its reflected light is closely matched by a simulation based on its dimensions (Fig. 3Be).

A particularly interesting suggestion that arose from this work was that insect cuticle might be self-assembled; *i.e.*, its macromolecular components – chitin and protein – would be synthesised by underlying epithelial cells, but the precise orientation of the molecules within the cuticle would not need to be specified by the cells. Today, there is widespread agreement that this is almost certainly what happens, but it can't be considered completely certain. As we shall see, this has important implications for the way in which cuticular materials are assembled into photonic structures.

In the language of today's photonics, the cuticular reflector of scarab beetles must represent a photonic crystal with at least a 2-dimensional bandgap (Solli *et al.*, 2003). Basically, a 2-D photonic crystal must have materials of different refractive index (*i.e.*, permittivity to

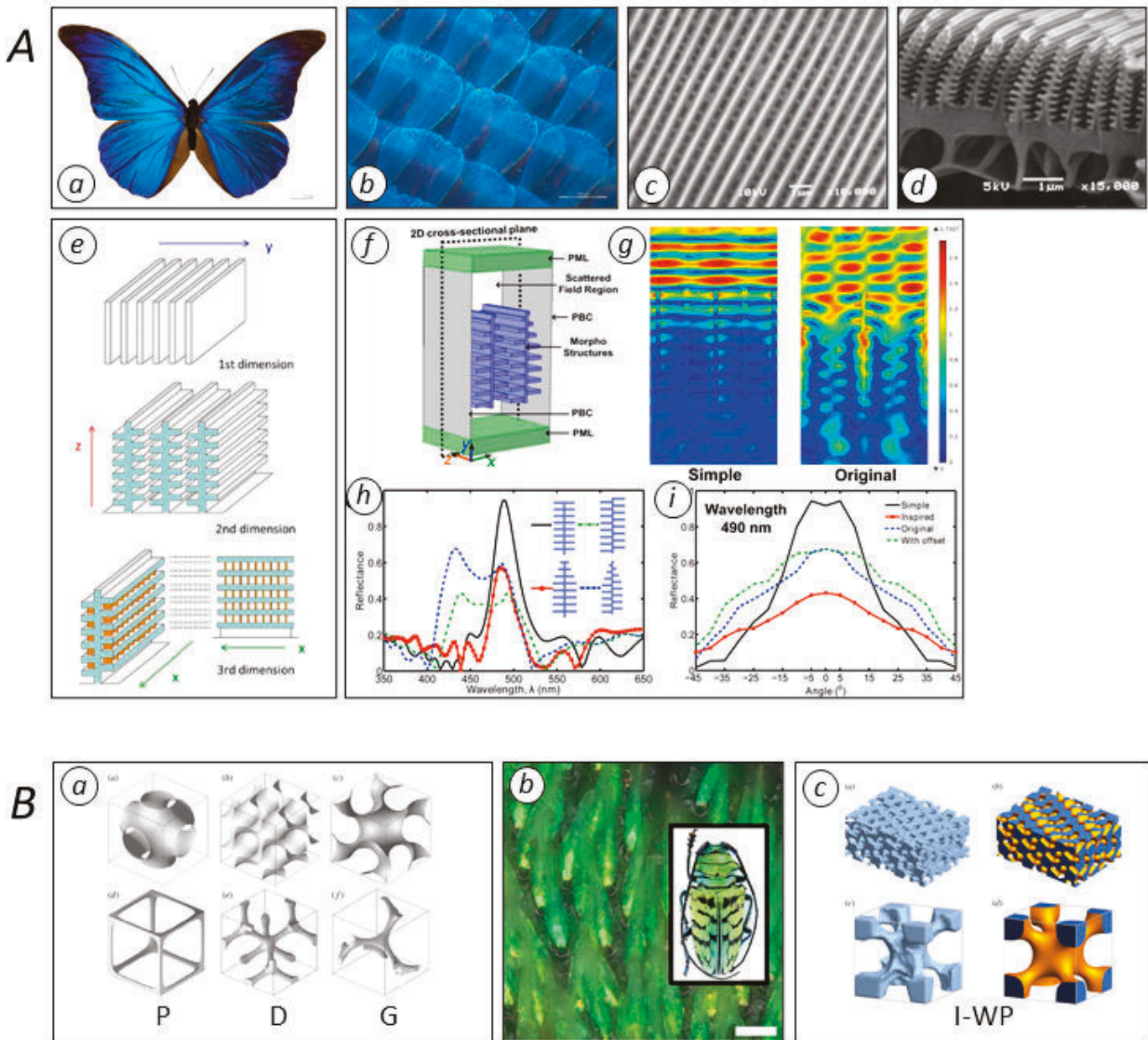
electromagnetic radiation) arranged periodically in 2 dimensions. The helicoidal Bouligand structure of a scarab's elytra exactly satisfies this requirement. Many studies of scarabaeid beetle structural colours have now confirmed that the reflected spectrum is well-modelled by a chiral multilayer reflector with the same lamellar spacing as that of the 360° pitch of the chitin helicoid (*e.g.*, Azofeifa *et al.*, 2015; Arwin *et al.*, 2016; Finlayson *et al.*, 2017; McDonald *et al.*, 2017; Bagge *et al.*, 2020).

At this point, however, despite all these papers in which theory so satisfactorily meets observation, we have to recognise a problem. It isn't only the cuticle of scarabaeid beetles in which chitin nanofibers are helicoidally organised, but that of *all* insects, indeed of all arthropods (Neville, 1975). Despite this universality, it turns out that the selective use of circularly polarised light is so rare that, of all insects, only beetles in the Scarabaeoidea are able to reflect circularly-polarised light. Not even all scarabs have circularly-polarising reflectors of this kind, and the trait seems to have evolved within the clade on multiple occasions (Pye, 2010). So, asked Neville (1975), when the ordinary everyday cuticle of all insects ought to be able to reflect coloured circularly-polarised light, why is that only scarab beetles do it?

Forty-seven years later, Neville's question remains unanswered. Obviously, something is missing from this scientific story. The problem is that we don't know for sure what it is in the cuticle that is actually doing the chirally-selective reflecting. Although almost every modelling paper assumes that chitin is the birefringent cuticle component that is responsible, this isn't at all certain. Typically, chitin represents less than half of the dry mass present in the cuticle (Richards, 1952); most of the rest is protein, but other components are also present. In order to selectively reflect circularly-polarised light, the beetle's optically-active device needs to have a chiral array of a substance that has a markedly different refractive index from the rest of the cuticle. Although it is helicoidally organised in the cuticle, chitin's RI is not markedly different from other cuticular components.

In line with this way of thinking, Caveney (1971) showed that in the most intensely reflecting mirror-like scarabs, *C. resplendens* and other species of the same genus, high levels of crystalline uric acid (UA) are incorporated into the cuticle, and that





**Figure 4 A: Wing scales of *Morpho* butterflies.** (a) *Morpho rhetenor* (Lepidoptera, Nymphalidae), upper wing surface. (b) overlapping wing scales, scale bar 100 $\mu$ m. (c) SEM view, scale ridge tops, bar 1 $\mu$ m; (d) SEM view, lateral decorations (lamellae) of ridge bars in shattered scale. Note air gaps between lamellae, bar 1 $\mu$ m. (e) 3-D structure of scale ridges and their decorations. Note asymmetric positioning of lamellae on ridge, and presence of micro-ribs between lamellae. Periodicities are differentially arranged in each of 3 spatial dimensions, as is required for a photonic crystal unit cell. (f) orientation for (g), which shows a finite element method (FEM) simulation of light reflection from scale structures shown in (f); ‘original’ means actual structure of lamellae, while ‘simple’ refers to a simplified structure without the taper towards the ridge tip, and without the asymmetry between the two sides of the ridge. (h) shows these two features are required to broaden the reflected spectrum, and (i) the angle over which reflected light is propagated.

**B. Photonic crystallography and a new type of photonic crystal in insects.** (a) Three distinct types of photonic unit cell, the P-, D- and G-nodal surfaces (left to right). Top row shows the unit cell, while lower row shows skeletal surfaces to illustrate how air-filled channels intercommunicate between cells. (b) *Sphingnotus mirabilis* (Coleoptera, Cerambycidae). (Main panel) scales on the surface of the elytra; (inset) the insect itself. The scale cuticle is made of I-WP photonic cells. (c) the novel I-WP unit cell, top left shows actual cuticle architecture reconstructed from milling and SEM imaging, top right shows a modelled idealised structure, lower left shows the cell’s skeletal surface from actual images, lower right an idealised version. Sources and image credits: Aa, Didier Descouens (CC-BY-SA 4.0), Ab, Frederik Nijhout (NISE), Ac-d, Shinya Yoshioka (NISE); Ae, Thomé et al. (2020); Af-i, Siddique et al. (2013), images used with permission; Ba, Michielsen et al. (2008); Bb-c, Kobayashi et al. (2021), images used with permission.

this greatly enhances the reflection of circularly-polarised light. Crystalline UA has a very high value of RI that varies in different crystalline planes (i.e., it is strongly birefringent) (Ringertz, 1965); Caveney’s suggestion was that the orientation of UA crystals follows the underlying helicoidal array (this is likely since it is incorporated into the cuticle matrix after adult eclosion, when the cuticle is already fully formed) and, as a consequence, it is really the UA that actually does the reflecting of circularly-polarised light,

not the chitin. The less intense reflection of circularly-polarised light by the elytra of other scarabaeid species might then be due to the presence in the cuticle matrix of lower levels of UA, or perhaps of a similar but less intensely birefringent substance. Those species that don’t reflect circularly-polarised light at all, might completely lack such substances. Caveney’s hypothesis has been supported by a recent study that models the circularly-polarising reflectors of two scarabs, *Chrysina*

*chrysargyrea* and *C. optima*, which also incorporate UA (or something very like it) into their multilayer reflectors (Vargas et al., 2018) (Fig. 2D).

This leaves unanswered the question of why (as far as we know) no other insect family has hit upon the trick of generating circularly-polarised colours. One possibility is that when the aim is to communicate with other members of the species, there’s no adaptive advantage in displaying a circularly-polarised colour signal unless they can see it. There is some

evidence that scarabs are indeed able to distinguish left- and right-circularly-polarised light (Brady *et al.*, 2010), but we know very little about circularly-polarised vision in other insects. Now there's an opportunity!

### 3-D Photonic crystals: colour-generating networks in the cuticle

The multilayer reflectors that I have described so far are structurally simple. In the simplest case, the periodicity of a simple Bragg reflector exists in only one dimension, in the same direction as that of the propagated light. Thus it is a 1-D photonic crystal. Even in the chirally-active reflectors of some scarabs, which appear to be photonic crystals with at least 2-D periodicity, the overall structure of the cuticle is relatively straightforward.

But some other insects have more structurally-complicated reflectors, which involve layers of optically-active materials arranged in complex three-dimensional arrays; these are the wing scales of butterflies. Their structures are so complicated that it's hard to know how to even start to understand their ability to reflect coloured light. But in fact, in many cases, they are just special examples of Bragg multilayer reflectors. We'll begin with the amazing *Morpho* butterflies studied so long ago by Bates (Fig 4A). The wing surface is decorated with overlapping layers of flat scales that are made of cuticle. On the surface of the scales there are long, thin plates of cuticular material separated by air, which are themselves decorated further with side projections, also separated by air (*i.e.*, a gap with very low RI). Viewed in transverse section, this surface ornamentation has an amazing Christmas-tree-like topology (Fig. 4Ad). The dimensions of the smallest cuticular side-projections and the intervening air gaps are in the same order as the wavelength of light, and so it is here that the Bragg reflector resides. The big difference in RI between the air gap and the cuticular material means that a modest number of layers is sufficient to reflect light with strong (saturated) colours.

The developmental processes that result in the formation of these scales have been intensively studied, but they are not yet completely understood. Initially, underlying epidermal cells from the wing surface become invaginated and secrete cuticular materials (presumably chitin and protein) into a complex scale precursor shape. The sheer complexity

of the final scale morphology led to the suggestion that later steps in the process are probably achieved by self-assembly, perhaps involving an origami-like self-folding of the final scale shape (Ghirardella, 1974) but more recent work has revealed that these final stages of the process may be organised from within the secreting epidermal cell by processes that involve actin bundles (McDougal *et al.*, 2021). It's not yet evident how such complicated developmental processes could have evolved; as always, the key will probably turn out to be thinking about how a topologically simpler scale structure could nevertheless have brought useful adaptive fitness to its owner. But, as we will see in a moment, it is now beginning to look as though most if not all photonic materials are formed through some sort of crystallisation process.

To understand the evolutionary origin of insect structural colours, we need to know the identities of the genes that control the development of photonic structures in the cuticle. It is becoming evident that many interacting loci involved in multiple interacting gene-regulatory networks are likely to be involved (McMillan *et al.*, 2020; van Belleghem *et al.*, 2021). With the decreasing cost and increasing technical ease of massive parallel DNA sequencing, comparative transcriptomics appears to be the best bet to cast light on the problem. Many studies of this type are currently under way on butterfly species that not only display structural colours subject to sexual selection, but which are also subject to natural selection through mimicry (*e.g.*, Piron-Prunier *et al.*, 2021). Thus, data collected to solve one evolutionary problem may also shed light on another. This area of research has recently been ably reviewed by Lloyd *et al.* (2021). I think that we may be confident that rapid progress will be made in discovering the genes that are ultimately responsible for the structural colours in butterfly wings.

The generation of colour by the wing scales of *Morpho* butterflies appears, however, to be much less difficult to understand. Models that compare the spectral content of reflected light with the topology and dimensions of ridge decorations are quite successful in reproducing the optical performance of the wing scales. Interestingly, some at first puzzling aspects of structure, like the tapering of side projections toward the top of the ridge, and the marked asymmetry between the

arrangement of the projections on one side of the ridge compared to the other, are found to be essential to extend the photonic bandgap from its main peak in the green towards the blue end of the spectrum (see Fig. 4Ai).

But increasingly it is being found that the highly complex architectures of the surface decorations of butterfly wing scales appear to be examples of 3-D photonic crystals; these are structures in which all three dimensions have periodically repeated alternations in RI, and which can thus reflect light in all three dimensions. This is such a complicated subject that I have chosen to illustrate the point with only a single example (Fig. 4B).

Photonic crystals are three-dimensional objects in which space is partitioned between two phases, each with a different permittivity. It is generally the case that one of the two phases is filled with air, the other with some solid material. As light passes through the material it passes from one phase to another and is reflected in the same way on multiple occasions, just as occurs in a Bragg reflector, except that the periodicity of the transitions from one phase to the other is repeated in three dimensions. To imagine an object like this, think of a block of material with holes drilled in it (this is in fact how the earliest physical models of photonic crystals were made). It is the pattern of holes that determines how the light will behave.

Such objects are described as 'crystals' because this partitioning of space between phases is achieved in a regular way, such that there are regularly repeating unit cells within the material. These unit cells can combine to produce continuous interpenetrating networks of the two phase-spaces. It is at present uncertain whether the photonic crystals of living systems self-assemble as do conventional molecular crystals, but at least some fabricated ones have been shown to do so, and it is generally supposed that this is the case in living systems too, despite the known involvement of cells in the developmental processes that lead to their formation.

Three distinct types of unit cell are known that have equal volume fractions of two phase-spaces: these are designated as P-, D- and G-nodal surfaces ('primitive', 'diamond' and 'gyroid') (Fig. 4Ba). All these structures have been found to exist in the photonic crystals of insect cuticles. The P-surface and D-surface types



have rather simple structures and could in principle be crudely modelled by drilling linear holes in a block of material; the P-type unit cell has sixfold symmetry while the D-surface cell has fourfold symmetry. The G-surface cell, however, is not so simple; the ‘holes’ in the unit cell follow sinuous trajectories through the solid matrix. They divide to produce triadic junctions, and the cell is therefore intrinsically chiral (*i.e.*, left-handed and right-handed versions of the gyroid unit cell exist). ‘Double’ versions of the gyroid unit cell exist that are not chiral; these have been observed to occur during the development of butterfly wing photonic crystals that subsequently collapse to become single gyroids. Interestingly, it seems that when butterfly wing scales are made of G-surface photonic crystals, extensive domains occur that are composed of one or the other chiral forms of photonic cell. Just last year, an additional type of unit cell was recognised to occur in photonic crystals from elytral scales of the cerambycid beetle *Sphignotus mirabilis* (Kobayashi *et al.*, 2021) (Fig. 3Bb); this previously unknown type of photonic unit cell has been named the I-WP cell, an arrangement in which the volume fractions of the two phases within the unit cell are unequal (see Fig. 3Bc). The functional significance of all this complexity is not yet known. But if we believe in natural selection then we have to suppose that there are functional consequences of the varying types of photonic cell construction.

Where will all this lead? Photonics is currently a booming area of research that promises to create new biomimetic materials and devices, based to a very considerable extent on the ‘fantastical’ colours of insects. Possible uses for these products include data handling devices for ultrafast computational networks, ultra-real 3-D-simulating video displays, paints, smart fabrics and materials, cryptography (*e.g.*, for banknotes and certificates of ownership), and so on. Will this new research area raise the profile of insects in the world? It already has! It is astonishing how many of the papers that I have cited in writing this article originate from Departments of Physics and were published in non-biological journals. Will the new science of biomimetics prove to be a good thing for human lives? We’ll see. As for the insects, I’m keen to see this year’s visitation of *Chrysolina herbacea* in my garden. I might just do some experiments.

**Acknowledgement:** I thank Professor Bob Fosbury (Institute of Ophthalmology, University College, London) for really helpful discussions on the colourful physics of light (but if I have made any mistakes here, they are mine not his). Almost 50 years ago, as a postdoctoral Fellow in the Department of Zoology at the University of Bristol, UK, I worked alongside both Charles Neville and Howard Hinton, both now sadly deceased; as the years have gone by, I have appreciated their respective outstanding contributions to insect science more and more. I thank them for the initial push they gave to my career as an entomologist.

Photonics is currently a booming area of research that promises to create new biomimetic materials and devices, based to a very considerable extent on the ‘fantastical’ colours of insects

## References

- Anderson, T.F. *et al.* (1942) *Journal of Applied Physics* **13**, 748–758.
- Ament, D.C. (2021) *Journal of Zoological Systematics and Evolutionary Research* **59**, 1951–1961.
- Arwin, H. *et al.* (2016) *Optics Letters* **41**, 3293–3296.
- Azofeifa, D.E. *et al.* (2015) *Journal of Quantitative Spectroscopy & Radiative Transfer* **160**, 63–74.
- Bagge, L.E. *et al.* (2020) *Applied Optics* **59**, 85–93.
- Bates, H.W. (1864) [https://www.google.co.uk/books/edition/The\\_Naturalist\\_on\\_the\\_River\\_Amazons/EwEMAAAAMAAJ](https://www.google.co.uk/books/edition/The_Naturalist_on_the_River_Amazons/EwEMAAAAMAAJ)
- Boulligand, Y. (1972) *Tissue & Cell* **4**, 189–217.
- Brady, P. *et al.* (2010) *American Naturalist* **175**, 6140620.
- Bragg, W.H. *et al.* (1913) *Proceedings of the Royal Society of London A* **88**, 428–438.
- Buffington, M.L. *et al.* (2011) *Invertebrate Systematics* **25**, 586–597.
- Buttenworth, N.J. *et al.* (2021) *Evolutionary Biology* **34**, 558–570.
- Carr, D.M. *et al.* (2018) *Biointerphases* **13**, 03B406.
- Caveney, S. (1971) *Proceedings of the Royal Society of London B* **178**, 205–225.
- Finlayson, E.D. *et al.* (2017) *Journal of the Royal Society Interface* **14**, 20170129.
- Gaubert, P. (1924) *Comptes rendus hebdomadaires des séances de l’Académie des Sciences Paris* **179**, 1148–1150.
- Gebru, A.K. *et al.* (2014) *Journal of Applied Remote Sensing* **8**, 083503.
- Ghiradella, H. (1974) *Journal of Morphology* **142**, 395–409.
- Goreau, M. (1843) *Annales de la Société Entomologique de France* **2**, 201–214.
- Hagen, H.A. (1882) *Proceedings of the American Academy of Arts and Sciences* **17**, 234–267.
- Hawkes, M.F. *et al.* (2019) *Proceedings of the Royal Society of London B* **286**, 20182850.
- Hinton, H.E. *et al.* (1969) *Nature* **221**, 953–954.
- Hooke, R. (1665) *Micrographia: or some physiological descriptions of minute bodies made by magnifying glasses, with observations and inquiries thereupon*. 246pp. London: Royal Society.
- Hosseini, F. *et al.* (2021) *Journal of Zoological Systematics and Evolutionary Research* **59**, 1481–1490.
- Katayama, N. *et al.* (2014) *Proceedings of the National Academy of Sciences USA* **111**, 15144–15148.
- Kinoshita, S. *et al.* (2008) *Reports on Progress in Physics* **71**, 076401.
- Kobayashi, Y. *et al.* (2021) *Journal of the Royal Society Interface* **18**, 20210505.
- Kurachi, M. *et al.* (2002) *Naturwissenschaften* **89**, 295–298.
- Land, M.F. (1972) *Progress in Biophysics and Molecular Biology* **24**, 75–106.
- Lloyd, V.J. *et al.* (2021) *Current Opinion in Genetics and Development* **69**, 28–34.
- Mason, C.W. (1927) *Journal of Physical Chemistry* **31**, 321–354.
- Matthieu, J.P. *et al.* (1937) *Comptes rendus hebdomadaires des séances de l’Académie des Sciences Paris* **205**, 1378–1380.
- McDonald, L.T. *et al.* (2017) *Interface Focus* **7**, 20160129.
- McDougal, A.D. *et al.* (2021) *Proceedings of the National Academy of Sciences USA* **118**, e2112009118.
- McMillan, W.O. *et al.* (2020) *Frontiers in Ecology & Evolution* **8**, 221.
- Michelson, A.A. (1911) *Philosophical Magazine* **21**, 554–567.
- Michielson, K. *et al.* (2008) *Journal of the Royal Society Interface* **5**, 85–94.
- Mouchet, S. *et al.* (2013) *Optics Express* **21**, 13228–13240.
- Neville, A.C. (1975) *Biology of the arthropod cuticle*. 448pp. Berlin: Springer.
- Neville, A.C. *et al.* (1969) *Biological Reviews* **44**, 531–562.
- Nixon, M.R. *et al.* (2012) *Optics Express* **21**, 1479–1488.
- Onelli, O.D. *et al.* (2017) *Scientific Reports* **7**, 1373.
- Pasteels, J.M. *et al.* (2016) *Arthropod Structure & Development* **45**, 509–518.
- Pielowska-Ceranowska, A. *et al.* (2020) *Zootaxa* **4868**, 389–407.
- Piron-Prunier, F. *et al.* (2021) *Journal of Evolutionary Biology* **34**, 1704–1721.
- Pye, J.D. (2010) *Biological Journal of the Linnean Society* **100**, 585–596.
- Richards, A.G. (1952) *The integument of arthropods*. 411pp. Minneapolis: University of Minnesota Press.
- Ringertz, H. (1965) *Acta Crystallographica* **19**, 286–287.
- Seago, A.E. *et al.* (2009) *Journal of the Royal Society Interface* **6**, S165–S184.
- Shevtsova, E. *et al.* (2011a) *Proceedings of the National Academy of Sciences USA* **108**, 668–673.
- Shevtsova, E. *et al.* (2011b) *Zookeys* **154**, 9–30.
- Siddique, R.H. *et al.* (2017) *Optics Express* **21**, 14351–14361.
- Simon, E. (2013) *Zookeys* **319**, 269–281.
- Solli, D.R. *et al.* (2003) *Optics Express* **11**, 125–133.
- Stavenga, D.G. (2014) *Materials Today: Proceedings IS (2014)* 109–121.
- Thayer, R.C. *et al.* (2020) *eLife* **9**, e52187.
- Thomé, M. *et al.* (2020) *Applied Physics A* **126**, 778.
- Valeriano, W.W. *et al.* (2021) *Bellstein Journal of Nanotechnology* **12**, 139–150.
- van Belleghem, S.M. *et al.* (2021) *Current Opinion in Genetics & Development* **69**, 72–81.
- Vargas, W.E. *et al.* (2018) *Biomimetics* **3**, 30.
- Waldman, G. (2003) *Introduction to light: the physics of light, vision and color*. 228pp. New York: Dover Publications.
- Wilts, B.D. *et al.* (2012) *Proceedings of the Royal Society of London B* **279**, 2524–2530.
- Yablonoitch, E. (1993) *Journal of Physics, Condensed Matter* **5**, 2443–2460.



# Iridescence in art

Cicada shell coated in particles of iridescent opal.  
Photo © Tyler Thrasher

Iridescence offers  
truly innovative  
artistic  
possibilities, most  
of which are as yet  
unexplored

## Dominique Vassie

Featuring artists  
Franziska Schenk  
and Tyler Thrasher

### What is iridescence?

People around the world have long been attracted to the shifting colours of iridescent objects, a word derived from the Greek *iris* meaning 'rainbow'. Iridescence occurs when a material gives the impression of changing colour as it moves relative to the viewer or light source. So alluring is the effect of changing colours that the technology now exists to make even chocolate iridescent (McGreevy, 2020).

Colour itself comes in two main forms: pigmentation and structural colour. Pigmented objects simply absorb some colours of light and reflect others and most materials available to artists are this type of colour. Structural colour, including iridescence, occurs when an object's surface has microstructures fine enough to interfere with the reflection of light. As the light is reflected in different directions, some waves of light amplify each other and others cancel each other out, resulting in colours of varying vibrancy depending on the angle from which the object is viewed (Indralingam, 2013).

Structural colour is also responsible for the vivid pure colours that are hard to replicate in traditional paint, such as the colour of a kingfisher's blue feathers. Techniques to recreate pure structural colour are gradually being refined. The company *Lifescaped*, led by scientist and artist Andrew Parker, has been taking direct inspiration from biological structures to replicate structural colour and bring those intense colours more widely to human-made objects (Charara, 2021). Using structural colour might also have environmental benefits as it requires no chemical pigments, unlike traditional paints which have historically contained many harmful substances (Christensen, 2018).

The difficulty of replicating structural colour and iridescence has likely helped naturally iridescent objects capture the imagination of artists and artisans for thousands of years. Consequently, people have devised many methods for incorporating iridescence into art, using both natural and artificial materials.

## The shifting colours of these objects allowed people to bring light and colour into even the darkest corners of their homes

### Using the iridescence of natural objects in art

There are many examples of people borrowing the iridescent natural materials that arise from their surroundings to add colour, light and drama to clothing and fabrics. The Shuar people of Ecuador and Peru create ear ornaments called *akitiai* using the iridescent elytra of beetles from the Amazon rainforest (NHM LA, 2021; RAMM, 2021). Similarly, the men of the Huli people of Papua New Guinea adorn wigs with a colourful array of feathers belonging to local bird species, the centrepiece of many being the iridescent blue breastplate feathers of the superb bird-of-paradise (*Lophorina superba*) (Anywayinaway, 2019a). Along the north coast of Papua New Guinea, the Kalam use the metallic green heads of thousands of beetles to decorate their huge headdresses with iridescence (Anywayinaway, 2019b; Gneh, 2021).

The use of iridescent beetle elytra to decorate fabric has occurred widely across India for at least 200 years (Libes, 2021). Such garments are most associated with the Mughai era (1526–1857), with elytra being used as decoration on pieces such as robes, fans and door hangings. As elytra are delicate, they were cut into tiny sequins for use in patterns on clothing to help them survive the wear-and-tear of use (Libes, 2021).

Following the expansion of the East India Company and eventual establishment of the British Raj in 1858, beetle wings began to appear in English clothing too (Libes, 2021). Such items were only ever popular among the upper-class, a symbol of having the wealth or social status to travel. Unlike the Indian designs, they featured whole beetle elytra stitched into depictions of beetles and insects themselves, a style undoubtedly influenced by the Victorian colonial fashion of collecting wildlife for social currency and displaying authority over the natural world (Libes, 2021). Actress Ellen Terry famously wore a striking beetle-wing dress when playing Lady Macbeth, immortalised in a painting by John Singer Sargent now residing at the Tate Britain.

Another major source of natural iridescence is nacre or mother-of-

pearl from certain molluscs, a substance used widely in art and jewellery worldwide. Nacre is formed from extremely thin iridescent layers of aragonite 'bricks', a crystal of calcium carbonate (Chasteen, 2007). It is a tough material which reinforces the molluscs' shells and envelops debris to protect their soft tissues from parasites and injury.

Lacquerware objects decorated with nacre have been produced in countries such as India, China, Japan, Korea and Thailand. Such objects, from small boxes to large screens, are made by coating objects in the viscous resin of the lacquer tree (primarily *Toxicodendron vernicifluum*) where it sets into a water-resistant, plastic-like coating upon exposure to air. Nacre in lacquerware goes back to before the 8<sup>th</sup> century in China and was used to create shining illustrations of animals, people and landscapes contrasting the dark colours of the lacquered wood in which it was inlaid (The Met, 2021). In Māori culture, the colourful iridescent shells of pāua abalones (primarily *Haliotis iris*) have long been used in sculpture to represent eyes. They are symbolic of the stars which are considered to be the eyes of the ancestors looking down from the night sky (Brooke, 2013).

### Adding iridescence artificially in design

People have developed and refined the technology for artificially creating iridescent materials for over a thousand years and some of the earliest examples are found in the fragile glazes of decorative ceramics known as 'lustreware'. The origin of such objects can be traced back to the 8<sup>th</sup> and 9<sup>th</sup> centuries in Mesopotamia, now Iraq, where the first techniques were developed (Driehaus Museum, 2021). To achieve the lustre, two firings of the object are required. The first firing

sets the base colours and the second firing occurs in a furnace which transforms the metal-oxide glaze into an extremely thin layer of iridescent metal on the surface of the pottery (De Morgan, 2021).

After its origins in Iraq, Egypt then became the primary centre of lustreware production followed by Persia and Syria. From here, its popularity spread around the Mediterranean to Spain and Italy where iridescent pottery was produced well into the 15<sup>th</sup> century. Lustreware later had a revival in England by makers such as Wedgwood in the 19<sup>th</sup> century leading to further developments of the technology (De Morgan, 2021).

At the end of the 19<sup>th</sup> century, fine glass manufacturers such as Louis Comfort Tiffany in New York began producing handmade iridescent glassware in the Art Nouveau style. Tiffany achieved iridescence in his glassware, known as 'favrite', through treating molten glass with metal oxides in a way similar to the ceramic process (Invaluable, 2020). However, handmade glass from famous designers was expensive and so cheaper, mass-produced 'carnival glass' gained popularity as an affordable iridescent alternative. The shifting colours of these objects allowed people to bring light and colour into even the darkest corners of their homes in a time when electric lighting was still relatively expensive in the USA and Europe (Carnival Glass Society, 2021).



Favrite bowl overseen by Louis Comfort Tiffany in 1895–96 – Cooper Hewitt Collection.





## Adding structural colour to artwork still requires creativity, curiosity and a fair helping of science

### Iridescence in contemporary art

Despite there being many modern methods of synthesising the micro-structures which produce iridescence artificially, these techniques are largely confined to industrial processes and are ignored by most artists. Therefore, adding structural colour to artwork still requires creativity, curiosity and a fair helping of science and it is being achieved by determined artists around the world through a variety of methods. Here, we will hear from two such artists about their work in bringing iridescence to both 2D and 3D artworks.

### Franziska Schenk – bringing iridescence to painting

Franziska Schenk is an award-winning artist based in the UK whose fascination with natural iridescence led her to explore deeply the ways in which it can be reproduced on a canvas. Her work often centres on life-like depictions of insects and invertebrates with a focus on accurately portraying their complex colours and vibrant beauty through using biologically-inspired structural colour techniques.

She is a lecturer in Fine Art at Birmingham City University and has been funded to work on a number of different art-science projects on topics such as iridescence, chemistry and working with colour-shifting pigments. One of her most recent projects investigated in detail how structural colour can be brought to the artist's palette, resulting in large-scale paintings of the lesser purple emperor butterfly (*Apatura ilia*) complete with iridescence (Schenk *et al.*, 2020).

Franziska kindly agreed to answer a few questions about her work and process for *Antenna*.

#### What inspires you to use iridescence/structural colour as an artist?

**FS:** Having focused, from the outset of my artistic career, on trying to capture

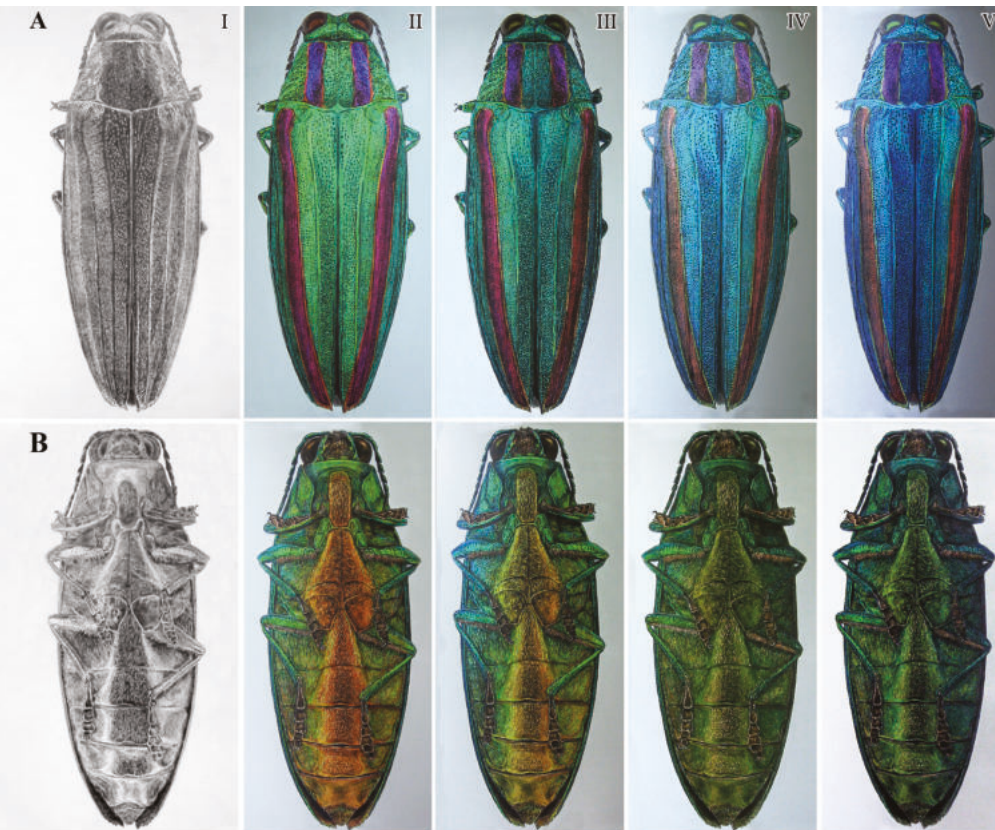
on canvas dynamic natural principles – namely evolution, fossilisation and camouflage – iridescence seemed a most appropriate vehicle. Hence, my sustained attempts to introduce the fluctuating rainbow colours of iridescence into painting – traditionally a static medium. This, in turn, has enabled me to probe the fluid boundaries between representation and abstraction: dovetailing the romantic and scientific, the ancient and modern, old-masterly techniques and latest paint technology.

#### How did you find a way to incorporate structural colour into your art?

**FS:** In 1999, this technology came to my attention in a chance conversation at the opening of 'Beginnings' (my group show at the Whitworth Gallery, Manchester). At the time I was working on a series inspired by the chameleon's subtleties of transformation. A representative from a leading pigment manufacturer suggested that the latest colour-shift flakes might be pertinent. Having been provided with the flakes by the manufacturer it took me several years to gain a basic understanding of the optical principles involved and transform the raw material, ironically a grey powder, into a medium suitable for painting. Faced with manifold technical challenges, crucially, studying



Franziska Schenk. The Lesser Purple Emperor, *Apatura ilia*, painting, iridescent medium on paper, close up. © F. Schenk.



Franziska Schenk. Japanese Jewel Beetle, mixed media on board, 90x60cm. © F. Schenk. Two stages of the painting process shown: Stage 1 - Carbon drawing (panel I) and Stage 2 - Introduction of iridescent colour and angle-dependency for different illumination (panels II-V). A - upperside; B - underside.

the ingenious ways in which iridescent displays are generated by insects has provided me with vital clues on how to adapt and adopt these challenging optical nano-materials for painting. Indeed, after years of meticulous and painstaking research, both in the lab and studio, the desired effect was achieved. The resulting paintings, like an iridescent insect, do in fact fluctuate in perceived colour – depending on the light and viewing angle.

#### **Why are you drawn to insects for artistic inspiration?**

**FS:** Since childhood I have been captivated by the ephemeral beauty, fragility and capacity for continuous transformation of butterflies. Crucially in their race for survival, many of these short-lived creatures dazzle with vibrant displays of iridescent colour. Unlike, and unmatched by, the chemical pigments of the artist's palette, the effect is generated by layered microstructures that refract and reflect light to make colour visible. Therefore, in my attempt to capture iridescence on canvas, I turned to butterflies for inspiration. Adopting a biomimetic approach, my scientific study of the insects' colour-generating mechanisms helped me understand the optical principles underlying iridescence and provided essential technical ground rules for the colour's incorporation into painting.

#### **What are your artistic plans for using iridescence in the future?**

**FS:** There are many further subtypes of iridescent materials (all with distinctively different optical signatures) yet to be explored as well as further creative methods of application. So far, I have only just scratched the surface. As regards positioning iridescence within the wider multidisciplinary discourse on colour, this is an area yet to be explored. Potentially an active, 'living' colour that changes with every shift of light or angle of view; that vanishes and reappears; that advances with an intensity never seen in art before, might simply refuse to be rationalised and pinned down. It is iridescence's more mysterious, metaphorical and philosophical dimensions that I would like to focus on in the future.

#### **Where do you see synthesised structural colour going as an artist's material?**

**FS:** Iridescence offers truly innovative artistic possibilities, most of which are as yet unexplored. There is huge untapped potential. By introducing an element of change, movement and transience into a traditionally stationary medium, iridescent technology has all the credentials to revolutionise fine art painting. In adapting and adopting latest novel iridescent materials to the canvas, my

My scientific study of the insects' colour-generating mechanisms helped me understand the optical principles underlying iridescence and provided essential technical ground rules for the colour's incorporation into painting

intention has not been to prescribe a definite formula for success, a particular subject matter or style, but rather to counteract a widespread lack of understanding, often coupled with disinterest, scepticism, even prejudice. As demonstrated, latest iridescent technology offers manifold innovative artistic possibilities, together with a unique aesthetics – yet to be fully explored, exploited and endorsed. Indeed, colour has changed, and will continue to do so.

#### **Tyler Thrasher – sculpting with nature and chemistry**

Tyler Thrasher is a multidisciplinary artist from Tulsa, Oklahoma, whose work fluidly combines both science and art, varying from intricate drawings to photography and crystalline sculptures. Through employing the beauty and unpredictability of nature and its processes, he creates works of art using chemistry which evoke thoughts about life and death and also simply about the spectacle of nature. He has used his art to raise significant sums for charitable causes and his work has been shown widely around the USA.

One of his current artistic projects involves developing methods to create iridescent sculptures using laboratory-grown opal. Opal is a mineral made from silica particles possessing a microstructure that

naturally scatters light in an iridescent display (Thrasher, 2018). He has devised techniques to deposit opal onto natural objects as a shimmering glaze and to create a cast of a form in pure opal. Many of Tyler's opal experiments so far have focused on turning empty cicada shells into colourful works of art bringing wonder to an object many would be quick to dismiss as ugly or creepy. No animals are killed to make his artworks.

Tyler kindly agreed to answer a few questions about his iridescent opal works.

***As an artist, what inspires you to use iridescence and structural colour?***

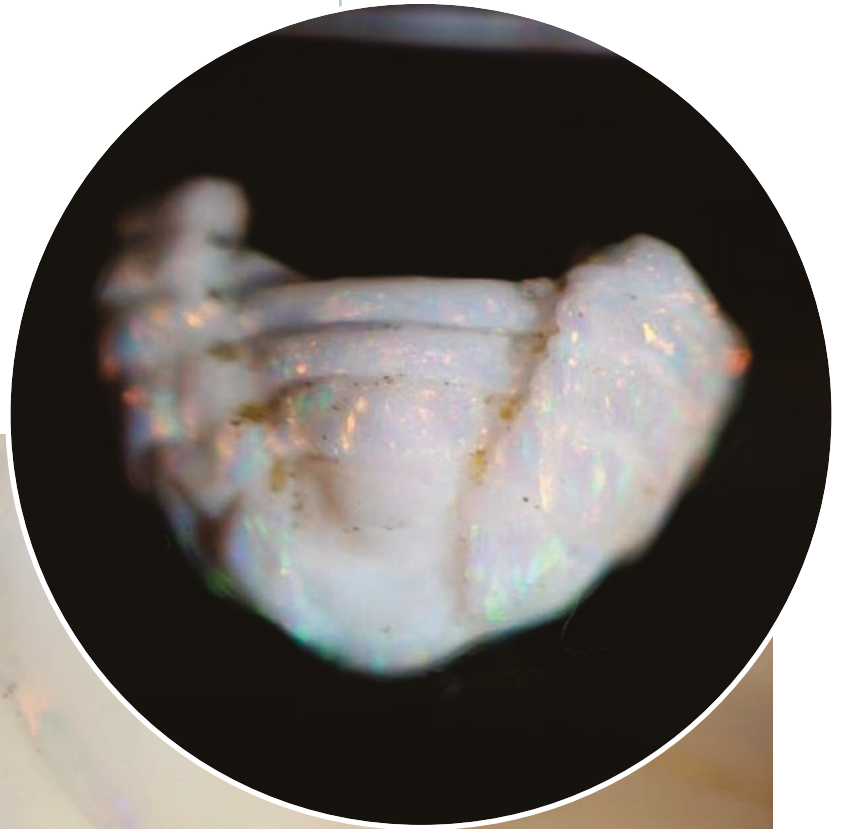
**TT:** The idea of using new and "exotic" materials is always alluring to creatives, especially materials that interact with the physical world in such a unique way as lab grown opals.

***How did you discover a way to synthesise opal onto objects?***

**TT:** A lot of time went into reading and poring through journals and essays on structural colours and the synthesis of silica nanoparticles. I essentially tweaked a protocol that worked for my purposes and found a way to apply it to foreign objects such as insect exoskeletons.

***What are your artistic plans for using opal in the future?***

**TT:** I plan on making photonic and light diffracting flowers and insects; essentially coating them in silica nanoparticles and letting the light dance around the specimen.



Solid cast of the abdomen of a cicada shell made in synthesised iridescent opal.  
Photos © Tyler Thrasher

**Where do you see synthesised opal going as an artist material?**

**TT:** It's a very tricky and finicky process. The particles can't be disturbed so any process that involves too much movement is a no go. Any art piece that is "self-growing" and light-interactive would be an obvious route for the material, but I would assume the artist can't be too precious about the end result. This would be a wonderful avenue for microscopic art as well and any intersection where art and technology meet.

**Where do you source the insects you opalise?**

**TT:** My wife and I climb trees in Tulsa during the summer to collect the exoskeletons. People also send me bundles of dead insects frequently, as do taxidermists and entomologists I correspond with regularly! Typically, the dead insect bodies find me somehow!

**Insects feature quite widely in your art; what draws you to using and depicting insects?**

**TT:** They're so incredibly intricate and interesting. You can't observe an insect up close and not be enamoured and wildly curious. The breadth in structure and form alone provides endless ideas and inspiration. Nature in my opinion is the best source to draw from (pun intended).

Many thanks to artists Tyler Thrasher and Franziska Schenk for their contributions and permission to share their iridescent work here.

## The future of iridescent art

Inspired by birds, insects, minerals and plants, artists and artisans will continue to attempt to capture the shifting beauty of iridescence in their art. We are now at an interesting point in the history of artificial structural colour as it may soon become more accessible to artists in a way it hasn't been in the history of art. The ethics of using real dead animals, animal parts and natural objects in art is a complex subject far too large to delve into deeply here, yet it is certainly something any artist must question and research. Natural materials have been used creatively since humans first began making art, as nature provides endless inspiration and means to do so. However, in a time when the natural world is facing a multitude of pressures from human activities, care must be taken to reduce our impact on wildlife and artists and artisans must be responsible about where their materials originate, both natural and artificial. There is a benefit to all people, including artists, to have a world brimming with biodiversity for years to come and also a benefit in sharing Earth's beauty through art.

As ever, we will continue to be dazzled by iridescence, either in works of art, craft or in nature, being reminded of the important reality that looking at something from another angle can provide an entirely new perspective.

You can't observe an insect up close and not be enamoured and wildly curious. The breadth in structure and form alone provides endless ideas and inspiration. Nature in my opinion is the best source to draw from

### Sources

- Anywayinaway (2019a) <https://anywayinaway.com/photography/papua-new-guinea/huli-tribe/>  
 Anywayinaway (2019b) <https://anywayinaway.com/photography/papua-new-guinea/kalam-tribe/>  
 Brooke, C. (2013) <https://featuredcreature.com/paua-abalone-the-spectacular-mollusc-reveared-by-the-maori-of-new-zealand/>  
 Carnival Glass Society (2021) <https://www.thecgs.co.uk/concise-guide-2>  
 Charara, S. (2021) <https://www.wired.co.uk/article/nike-air-jordan-3-rtna-structural-colour>  
 Chasteen, S. (2007) <https://physics.aps.org/story/v20/st1>  
 Christensen, I. (2018) <https://www.artsy.net/article/artsy-editorial-paints-toxic-chemicals-avoid-harming-environment>  
 Cooper Hewitt (2021) <https://collection.cooperhewitt.org/exhibitions/1158829409/>  
 De Morgan Collection (2021) <https://www.demorgan.org.uk/lustreware-a-short-history/>  
 Driehaus Museum (2021) <https://driehausmuseum.org/blog/view/the-origins-of-lustreware-recapping-over-ten-centuries-of-aesthetic-pottery>  
 Gneh, C. (2021) <https://postcourier.com.pg/the-green-beetle-giants-of-simbai/>  
 Hindmarsh, G. (1998) <https://www.nzgeo.com/stories/passionate-about-paua/>  
 Indralingam, R. (2013) <https://www.yalescientific.org/2013/05/qa-what-causes-iridescence/>  
 Invaluable (2020) <https://www.invaluable.com/blog/favrile-glass/>  
 Libes, K. (2021) *Dress* 47(1), 79–94.  
 McGreevy, N. (2020) <https://www.smithsonianmag.com/smart-news/iridescent-chocolate-safe-eat-180974967/>  
 Natural History Museum Los Angeles County (NHM LA) (2021) <https://nhm.org/unexpected-animal-parts>  
 Royal Albert Memorial Museum & Art Gallery (RAMM) (2021) <https://rammcollections.org.uk/object/103-2003-8/>  
 Schenk, F. et al. (2020) *Faraday Discussions* 223, 145–160.  
 The Met (2021) <https://www.metmuseum.org/exhibitions/listings/2006/mother-of-pearl>  
 Thrasher, T. (2018) *Wisdom of the Furnace*. Self-published.



# The venoms of insects – often overlooked chemical arsenals



Figure 1. Venoms of some larger or more dangerous arthropods, such as scorpions (here *Buthus occitanus*), are quite well studied.  
(photo: Tim Lüddecke)

Venom research represents a promising source for novel bioresources and for many lineages we have only just started to open up this natural “treasure trove”

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## Venom in the animal kingdom

When thinking about nature, most people tend to imagine a peaceful and friendly world where species coexist harmoniously. However, for naturalists it is obvious that this perception is far from reality. On the contrary, nature, and in particular the animal kingdom, is more comparable to a battlefield where species are essentially trapped in everlasting fights for survival. Over millions of years, predatory and prey species hence evolved a wide toolkit of behavioural and morphological adaptations that support them in this ongoing battle. While some of these adaptations, such as sharp teeth, horns, armoured skin, or claws, are fearsome and effective weapons, several animals adopted a much more subtle weaponry. They evolved into true master chemists that utilise toxic secretions to mount chemical attacks on their opponents.

It is estimated that more than 100,000 animal species are capable of toxin usage (Fry *et al.*, 2009). Animal toxin cocktails tend to be outstandingly complex with some species harbouring thousands of components. Thus, they belong to the

chemically most diverse mixtures known in nature. Toxic animals can be subclassified into two classes based on the mechanism of toxin application. The first class is that of poisonous animals, which secrete their toxins onto their body surface. These lack any injection system and rely on physical contact with their opponent to transfer their toxins passively via resorption. The other class is that of venomous animals. In contrast to poisonous animals, they have evolved an injection system (typically modified teeth, spines or ovipositor) and are capable of delivering an active injection of their toxin cocktail (Nelsen *et al.*, 2014). The type of toxin delivery system has direct repercussions on the chemical arsenal that is present within a given species. Because poisonous animals lack an active delivery system and rely on passive resorption, molecular size is a major determinant for uptake efficiency and thus the functionality of the toxins. Passive resorption works much faster for small molecules than for large ones, and therefore leads to quicker effects. Hence the toxin arsenal of poisonous animals is mostly composed of small organic

molecules such as alkaloids, biogenic amines or steroids. However, as an actively injected weapon, venom components are not size-restricted. Consequently, they are typically dominated by macromolecules, mostly proteins and peptides, that are at least an order of magnitude larger than the compounds that constitute a poison. Another key difference lies in the function of both systems. While poisons are almost fully restricted to a defensive function, the active delivery of venoms grants them a multifunctional nature. Venoms are used for three main purposes: defence, predation and competitor deterrence. In addition, at least eleven secondary purposes have been described from different venomous animals, which include roles in the immune system, sexual communication and prey-tracking (Schendel *et al.*, 2019). This multi-purpose character of venoms may also explain their tremendous evolutionary success. Venom evolved convergently up to 100 times among animals, making it one of the most abundant features among them. Lastly, while poisonous animals are very seldom of medical significance given their passive toxin delivery, venomous animals are of major relevance in several parts of the world. Mostly snakes, but also some scorpions, spiders, insects and jellyfish, are accountable for millions of envenomations and cause hundreds of thousands of deaths plus permanent disabilities every year.

### Understanding insects as understudied venomous master chemists

One of the lineages that culminated in the highest diversity of venomous animals is the phylum Arthropoda. It comprises several groups that are widely recognised for their venomous nature. For instance, spiders, scorpions and centipedes are widely known by the general public to be venomous, partly because of their coverage in the media (which usually exaggerate their threat potential). However, arthropods also include several groups that are much less known to be venomous. For instance, some pseudoscorpions carry functional venom systems and this is probably unknown to almost all non-toxinologists.

Insects are the most prominent group of arthropods and the evolutionarily most successful group of all terrestrial animals given their age, abundance and diversity (Misof *et al.*, 2014). Unsurprisingly, different insect

lineages evolved venom systems and some of these are quite well-studied. For instance, the venom systems of *Apis mellifera* (Western honey bee) have been widely investigated, which is mostly explained by the species' abundance and its coexistence with people, but also by the medical importance of bee-sting allergy. The evolution of the aculeate stinger, and its subsequent modification from an ancient ovipositor towards a venom injector that developed sting-autotomy to maximise its defensive potential for the hive, has also been of great interest. Insect venoms have in recent years aroused substantial interest from the general public because of the "Schmidt sting pain index", established by the American entomologist Justin O. Schmidt. This index, for which the author was awarded the Ig Nobel Prize, ranks the stings from venomous insects based on the strength of the resulting pain. In recent years, the index has been covered widely in the media and led to an increased recognition of venomous insects, especially those with extremely painful venoms. Species frequently covered include *Paraponera clavata* (Bullet ant), *Pepsis grossa/Pepsis formosa* (Tarantula hawk), *Dasymutilla occidentalis* (Cow killer) and *Polistes carnifex* (Executioner wasp). The overwhelming majority of less enigmatic venomous insects received miniscule attention and the chemical landscapes within their venoms remain largely unexplored. At the time of writing, the bioinformatic databases that store taxon-specific data on animal toxins only include *ca.* 360 toxins identified in insect venoms compared to *ca.* 2,400 from snakes, *ca.* 300 from jellyfish and anemones and *ca.* 1400 from cone snails – all of which are much less diverse. Also, although thousands of insect species carry venom systems, only a small fraction has been investigated for venom so far. For instance, the "venomzone" database currently lists only 100 insect species for which toxin data have been deposited. This illustrates how little we know about venom compositions across the class Insecta and how much remains to be learned. However, it also raises the question of the reasons for this knowledge deficiency.

### The rise of venomics and the current revolution in venom research

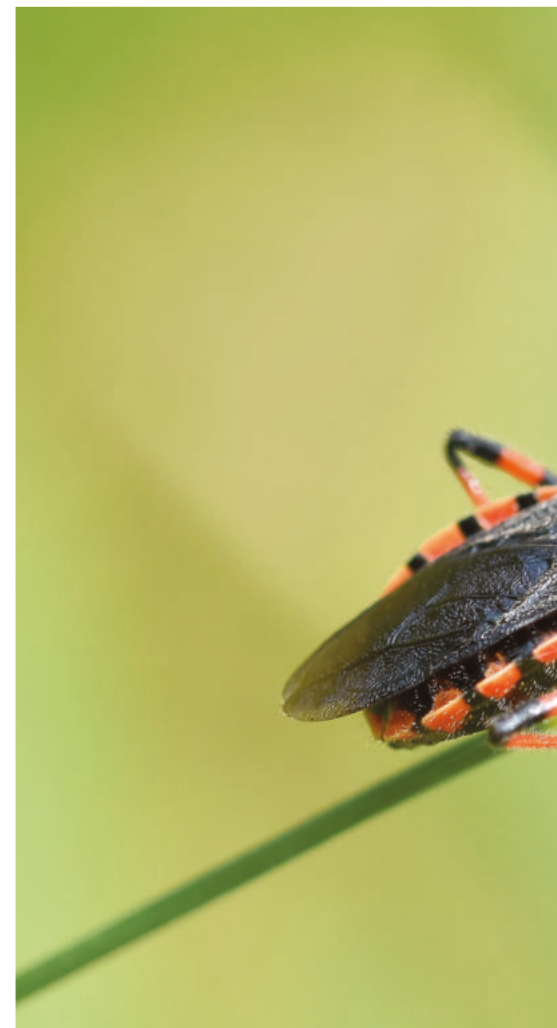
This knowledge deficiency regarding insect venoms, which is paralleled in other arthropod groups, is explained



Figure 2. Among insects, the honeybee *Apis mellifera* represents the species with the best characterised venom (photo: Robin Schmidt).

by a combination of two components: an anthropocentric bias and methodological limitations.

The issue of anthropocentric bias refers to the fact that studies on animal venoms have mostly emphasised taxa that are of medical significance. As a result, the venoms from dangerous lineages (mostly snakes) are well understood, but most



venomous animals which pose no threat to people have only been sporadically investigated, if at all. Another aspect of anthropocentric bias is that venom researchers have favoured large and easy to access taxa over the small and difficult to find ones. Accordingly, some taxa represent a much larger fraction of the venom-wise studied representatives of their lineage than they account for species-wise. Therefore, they over-proportionally influence our assumptions on venoms from some lineages. The most prominent examples here are certainly tarantulas, which only account for two percent of all spiders but represent a third of all known spider toxins (Lüddecke *et al.*, 2019). The problem of anthropocentric bias has been discussed a great deal within the venom community and several researchers have now started to investigate venoms in neglected groups. However, more often than not, the second problem of methodological limitations has hindered their research efforts.

The traditional way of studying a venom is to first catch a certain number of individuals from the

species of interest and to collect their venom. From here, investigations are guided by biofractionation. This means that the obtained material is injected into a chromatographic system that uses the physicochemical interactions of the toxins with co-injected solvents and the coating of the chromatographic platform to isolate and purify the singular components. The toxins obtained are then tested for their biochemical properties, their structure and activities. After this cumbersome process, a fairly complete image of the composition from a given venom and the activity of each component is gained. The problem with this approach lies with its demand for large amounts of sample material. Usually milligram amounts of venom are required, which can be obtained easily from larger species, but which cannot be realised efficiently for the many small ones. In those, hundreds or even thousands of individuals are required to perform even exploratory studies, and quite commonly the venom collection fails completely. Consequently, it was almost impossible to study venoms from the smallest animals, such as most

insects, for a long time. It is only very recently that technological advancements in chemical analytics, bioinformatics and sequencing have provided the sensitivity needed to access these taxa. This culminated in the rise of “venomics”, a novel, integrative field of research, that applies modern technologies of systems biology (referred to as -omics methods) to venom systems and has revolutionised venom research. The ability to detect the smallest numbers of molecules, to sequence the expressed genes from dissected venom glands, or even to mine toxin genes from genomes, is providing the means to study venoms from all animal species in a reasonable time frame. Moreover, after the components are identified by venomics, synthetic biology can be used to engineer genetically-modified bacteria that produce these components in the lab and thus enable functional studies. Venomics has dramatically expanded our understanding of the venoms of many previously understudied animals, including insects. In the following three paragraphs, I summarise some of the most recent and most fascinating insights on insect venoms gained via this approach.

### Venom modulation in assassin bugs

One of the insect lineages that has received the most attention in recent years is the predatory assassin bugs of the family Reduviidae. As members of the hyperdiverse Heteroptera they belong to one of the most speciose families of insects. In contrast to most of their relatives, reduviids evolved a venom system to subdue prey. Their venom injection apparatus is incorporated into their proboscis to which complex venom glands are attached. From this proboscis a venomous stab can be employed that is able to paralyse and liquefy prey items and which is also quite painful to humans. Some species are even capable of long-range attacks, as they can spit droplets of venom towards potential threats. The defensiveness of many assassin bugs is often flagged by aposematic colour patterns displayed by many species. Despite their enigmatic appearance, diversity and wide abundance, the assassin bugs had seldom been studied in terms of their venom before modern venomics approaches emerged. However, since this toolkit gained more momentum, reduviids have repeatedly been studied.



Figure 3. Some assassin bugs (here *Rhynacoris annulatus*) are able to employ different venoms in a context-dependent manner (photo: Robin Schmidt).

Consequently, quite exhaustive data on venom composition have been generated for several species. In particular, representatives from Africa, which are commonly kept as pets (such as *Platyeris rhadamanthus*, *Platyeris biguttatus* and *Psytalla horrida*), and some species from Australia (*Pristhesancus plagipennis* and *Havinthus rufovarius*) have been investigated. From Europe only a single species (*Rhynocoris iracundus*) has been investigated in detail. The in-depth analysis of venom and venom systems from assassin bugs has not only shed light on the chemical arsenal of this lineage but also revealed a previously unrecognised versatility in assassin bugs.

Venom systems of most taxa only consist of an injector, a sack-shaped venom gland and a connecting venom duct. In contrast, the injection apparatus of assassin bugs displays a great structural and functional diversity, as recent work on *Pristhesancus plagipennis* has shown (Walker *et al.*, 2018). The gland of this aquatic assassin bug is subdivided into three sections (anterior main gland, posterior main gland and accessory gland). Venomics revealed that the anterior and the posterior main glands produce and store different venoms with distinct chemical profiles and display different activity patterns. The venom of the posterior main gland displays foremost a neurotoxic, paralysing effect and is mostly used as an offensive weapon to overpower prey. On the other hand, venom produced in the anterior main gland lacks such paralysing effects and is commonly used in a defensive context. Since its discovery in *P. plagipennis*, this context-dependent utilisation of distinct venoms and the presence of several gland sections has been demonstrated in other assassin bugs. Therefore, it seems that such modulation strategies that multiply the chemical profile of a given species are quite common in reduviids and likely contribute significantly to the evolutionary success of this family.

### Multimodal venom gene evolution in robber flies

Robber flies of the family Asilidae are venomous members of the Diptera, another hyperdiverse insect lineage. Unlike most other members of their lineage, robber flies maintain a predatory lifestyle on reaching adulthood. This is especially remarkable as they are capable of



Figure 4. The evolution of venom in robber flies, such as *Laphria gibbosa*, is characterised by an interplay of different mechanisms (photo: Robin Schmidt).

subduing much larger and potentially dangerous prey, such as wasps and bees. This ability provoked the interest of several entomologists and it was hypothesised early that Asilidae may utilise some form of toxin on their dangerous prey (Drukewitz *et al.*, 2018). However, it was also speculated that they instead kill their victims via a forceful mechanical sting from their proboscis. Intrigued by these hypotheses, Whitfield (1925) performed stinging experiments with needles and showed that paralysis by robber fly attacks sets in much faster than paralysis after needle stings and thereby validated the presence of a toxic agent. He identified several gland systems that may be responsible for toxin production. Subsequent studies by others demonstrated that, indeed, the contents of these glands cause the paralysis and hence robber flies are now undisputedly recognised as venomous Diptera. However, similar to the venoms of assassin bugs and other insects, it is only recently that their venom compositions could be inferred thanks to venomics. Species studied so far include European taxa (*Eutolmus rufibarbis*, *Machimus arthriticus*, *Dasypogon diadema*) and a giant robber fly from Australia (*Dolopus genitalis*).

Among the most exciting findings that stem from studies on robber fly venoms is the multimodal nature by which venom genes seem to evolve, as revealed by recent work on *Dasypogon diadema* (Drukewitz *et al.*, 2019). In many venomous animals a single mechanism is largely driving the evolution of venoms. For instance, in snakes venom genes are usually

duplicated and accumulate mutations that alter their function in a process commonly referred to as neofunctionalisation or “weaponisation”. In parasitoid wasps, single-gene co-option is the principal mechanism and in centipedes horizontal gene transfer of toxin genes from bacterial symbionts to their hosts’ genome is important. In contrast, robber fly venoms seem to evolve in multimodal fashion where different processes are equally relevant. While some components emerge via neofunctionalisation, others evolve by co-option and others may even evolve *de-novo*. The latter refers to a rare and heatedly discussed mechanism whereby a random mutation makes a previously non-coding part of a chromosome coding and thereby gives rise to a novel gene.

### Hijacking of host immunity by parasitoid venoms

The last group of venomous insects that I want to highlight is unique in the sense that its members use venom as a tool in their reproductive biology. Parasitoid wasps are, again, a very diverse group within the Hymenoptera. Female



Figure 5. *Hedychroma rutilans* belongs to the diverse array of parasitoid wasps that utilise their venom to paralyse hosts for egg deposition (photo: Robin Schmidt).



parasitoids carry an ovipositor which, over the course of their evolution, has been weaponised into a stinger. Although the presence of a venom apparatus is quite common in female hymenopterans, parasitoids differ from their relatives in the utilisation of this weapon. In most hymenopterans, the venom serves a predominantly defensive role and is used to defend the hive in social species, or the individual itself in solitary species. In parasitoids, on the other hand, venom is the principal means to subdue suitable hosts for their offspring. The adult wasp delivers a venomous sting to its victim, which is then paralysed. The immobilised body is next brought to a previously prepared burrow, an egg is deposited within or adjacent to it (depending on the wasp species) and then left alone. After emerging from the egg, the larva feeds on the paralysed insect. The venom of parasitoids has been of great interest because of its ability to cause long-lasting paralysis and because of its very painful nature. However, with a few exceptions, parasitoid venoms have been studied only

sporadically in the past.

Thanks to venomics, this situation has changed throughout the last decade or so.



Since then,

venoms of many parasitoids have been investigated including some of the large and enigmatic ones (e.g., *Pepsis*), those specialised on important insect pests (e.g., *Aphidius*) but also less prominent ones (e.g., *Pimpla*). The most-studied venom so far of any parasitoid wasp, however, comes from *Nasonia vitripennis*, where a broad range of toxins has been identified via venomics and where even a genome has been sequenced. Several components from parasitoid venoms have now been identified, and we have learned that their venoms are composed of a variety of unique proteins (e.g., “venom protein Y”) but that some species also synthesise small neurotoxic peptides similar to those present in spiders. The most astonishing insight, however, is that the venom of parasitoids is not only a chemical attack that paralyses the host, but it is also capable of hijacking the immune system of the host to protect the deposited eggs against infections (Özbek *et al.*, 2020). This is achieved by small pieces of nucleic acids (micro RNAs) that are present in the venom and co-injected with the toxins. While the toxins facilitate rapid paralysis, these micro RNAs interact with the genetic machinery of the host and induce the activation of immune genes. As a consequence, the paralysed host produces a variety of components that defend it and the attached egg against microbial colonisation.

### The value of venom

The many insights into venoms of insects are certainly of great intellectual value to anyone interested in insects. That said, for most people these findings are of little significance and the question about the value of venom research to humanity may appear justified. Fortunately, this question is easily answered.

The toxic molecules that are present in a venom achieve their devastating activity by highly selective interactions with target molecules involved in vital physiological processes in their victim. While these toxins cause damage to a healthy metabolism, some of the targeted molecules are likewise pivotal components of some disease states. In such cases, venom toxins can be used as templates to generate artificial compounds that modulate these targets, and to treat the disease. For instance, the venom of *Bothrops jararaca* (Jararaca pit viper) acts on the blood-clotting cascade and the



Figure 6. Members of the genus *Ammophila* belong as well to this group. Parasitoids supplement their venoms with co-secreted DNA fragments that modulate host immunity and increase the fitness of the larvae (photo: Robin Schmidt).

blood vessels, and a key symptom of envenomation is a rapid drop in blood pressure. When investigating the venom of *B. jararaca* in the 1960s and 1970s, Brazilian researchers isolated the peptide teprotide that specifically inhibits a protein called Angiotensin-converting enzyme, an important mediator of blood pressure, and hence was responsible for the observed blood pressure drop. A team of scientists developed teprotide further into a novel biomolecule, which was eventually patented as Captopril (Cushman *et al.*, 1991). This drug was the lead component for the therapeutic class of ACE-inhibitors that has, since the 1980s, been used for the treatment of high blood pressure and congenital heart disease. It advanced to become one of the most commercially successful therapeutics ever developed and saved millions of lives. Similar to Captopril, several other venom-derived drugs have been generated in recent decades. Among others, an anti-diabetic peptide from *Heloderma suspectum* (Gila monster) and an analgesic from *Conus magus* (Magical cone snail) are important to mention. In addition, many venom components that may be used as therapeutics in future are currently undergoing preclinical examination. For instance, a venom peptide from *Hadronyche infensa* (Australian funnel-web spider) was able to impose neuronal protection after stroke in mice and could be repurposed for therapy after stroke. Another promising compound is chlorotoxin from the venom of *Leiurus quinquestriatus* (Deathstalker scorpion), which binds very specifically to cancer cells. This toxin

has been modified via biotechnology to be fluorescent and could be used as a marker protein that guides physicians during tumour excision. As for insects, melittin, the major toxin from Western honey bee venom should be mentioned. This small peptide displays promising activities against several microorganisms and cancer cells. It may therefore serve as a template for the development of an antibiotic or anti-tumour drug. However, melittin is very toxic to human cells, so substantial engineering of this toxin will be required. Nevertheless, melittin represents a promising drug candidate. Given that only a small proportion of insect venom has been studied, and facing the sheer diversity of venomous species that will be investigated in the future, it must be concluded that insect venoms are extremely promising sources for novel drugs (Herzig *et al.*, 2020).

Another important area in which venoms, and in particular those from insects, may generate value lies in the agricultural sector. In the age of a growing world population, ever higher yields of agricultural crops are needed to produce food. Pest insects that feed on these crops are hence major problems. Due to global warming and migration, several pests are undergoing range expansion and are about to become major threats in even more areas. In the past, chemical insecticides have been used to defend crop plants against pest insects, but due to tremendous over usage, resistance against such chemicals is spreading in several species. Also, given the unselective nature of most chemical insecticides and their great stability, they pose a major environmental burden as they affect beneficial insects and accumulate in the environment. Insect venoms appear to represent an excellent source to lead the design of biology-inspired, sustainable pesticides. Notably, the venoms of most insects evolved to overpower other insects and thus they are evolutionarily refined for this purpose. Also, as they are composed of peptides which are biodegradable, these molecules shouldn't accumulate in the environment. Conceptually, by studying the venoms of insects that are specialised to prey on pest insects, it should be possible to identify molecules that only cause a toxic effect against these pests while being non-toxic to other insects. Such highly specific and sustainable insecticides hold the promise of

**With every species that we lose to extinction before having the opportunity to explore its venom, we lose the hundreds of venom biomolecules that are encoded within their genome, any of which may represent the cure for a disease or be the basis for a sustainable insecticide**

revolutionising global agronomy. First steps in this direction have already been taken, *e.g.*, some ant venom peptides that display promising activities against *Acyrtosiphon pisum* (Pea aphid) have been identified and tested. Apart from insects, spider venom peptide-based insecticides that are non-toxic towards bees recently entered the market.

### Loss of species means loss of bioresources

As I've hopefully outlined sufficiently, venoms are extremely fascinating. Unlike any other biological systems, they incorporate an unprecedented chemical complexity that one can explore and provide the means to understand the fundamentals of some key aspects of the biology of the species of interest. Given the wide abundance of venom in the animal kingdom, it is quite possible that anyone who is seriously interested in an animal has to consider venom at some point, either because the focal species is venomous itself or because it has to deal with venomous predators or prey. Venom also provides the opportunity to connect basic and translational research and thereby to provide significant value to humankind. It is particularly the

pharmaceutical and agrochemical sectors where venom research represents a promising source for novel bioresources and for many lineages we have only just started to open up this natural "treasure trove". Owing to recent developments in venomomics, it is now possible to study venoms from virtually all species known to science.

While all this sounds rather promising, it is critical to emphasise that venom research is facing a tremendous threat in the current biodiversity crisis. In the Anthropocene, humans have turned into a global driving force that alters the geosphere and impacts all terrestrial and aquatic environments. Several animal lineages, as a consequence, are threatened or have already been extirpated. Important causes are habitat loss and fragmentation, invasive species, emerging infectious diseases, climate change and pollution. While this biodiversity crisis poses a substantial threat to the integrity of many (or even all) ecosystems, it poses an independent threat to venom discovery. To study the venom of species and to derive potential products from them, their venoms must have been collected. With every species that we lose to extinction before having the opportunity to explore its venom, we lose the hundreds of venom biomolecules that are encoded within their genome, any of which may represent the cure for a disease or be the basis for a sustainable insecticide. It is therefore in our own interest that, beyond protecting global biodiversity, research on venoms becomes emphasised, and that we study as many venoms as we can before they are lost forever. This is especially true for insects, which constitute one of the most diverse yet threatened animal lineages and thus should be prioritised in venom research.

### References

- Cushmann, D.W. *et al.* (1991) *Hypertension* **17**, 589–592.  
 Drukewitz, S.H. *et al.* (2018) *Toxins* (Basel) **10**, 29.  
 Drukewitz, S.H. *et al.* (2019) *Gigascience* **8**, gjz081.  
 Fry, B.G. *et al.* (2020) *Annual Review of Genomics and Human Genetics* **10**, 483–511.  
 Herzig, V. *et al.* (2020) *Biochemical Pharmacology* **181**, 114096.  
 Lüddecke, T. *et al.* (2019). *Toxins* (Basel) **11**, 488.  
 Misof, B. *et al.* (2014) *Science* **346**, 763–767.  
 Nelsen, D.R. *et al.* (2014) *Biological Reviews of the Cambridge Philosophical Society* **89**, 450–465.  
 Özbek, R. *et al.* (2020) *Proceedings of Biological Sciences* **287**, 20200704.  
 Schendel, V. *et al.* (2019) *Toxins* (Basel) **11**, 666.  
 Walker, A.A. *et al.* (2018) *Nature Communications* **9**, 755.  
 Whitfield, F.G.S. (1925) *Proceedings of the Zoological Society of London* **95**, 599–638.



# DNA sequencing, meta-barcoding and applications in entomology and taxonomy – a beginner's guide

The basic science underpinning molecular approaches is still ultimately reliant on classic taxonomy

Global insect declines are putting ecosystem services at risk [1]. As any conservationist would doubtless concur, without a system in place to accurately measure and contextualise losses, geographic trends and species migrations, a comprehensive understanding of the extent of such apparent declines can be misleading [2,3]. One critical issue is that our ability to monitor and record these declines is highly dependent on taxonomic expertise [4]. Consequently, there is a growing acknowledgement of the breadth and depth of data needed, and the decreasing number of entomological taxonomists [5–7]. Of course, these trends are not occurring in isolation; there has been a growing trend in taxonomic research employing molecular methods – eschewing morphological identification in preference for those that determine species based on DNA.



DNA sequencing in particular has become a central component of the modern diagnostic toolbox. DNA barcoding – a subset of sequencing technologies – involves comparing the genetic code of a part of the animal genome that appears in the same place in every species but, owing to a universally occurring mutation rate, differs very slightly between species [8]. Owing to the ability to compare a single unknown specimen against many potential species in a single assay, and standardised protocols that allow transparent and objective

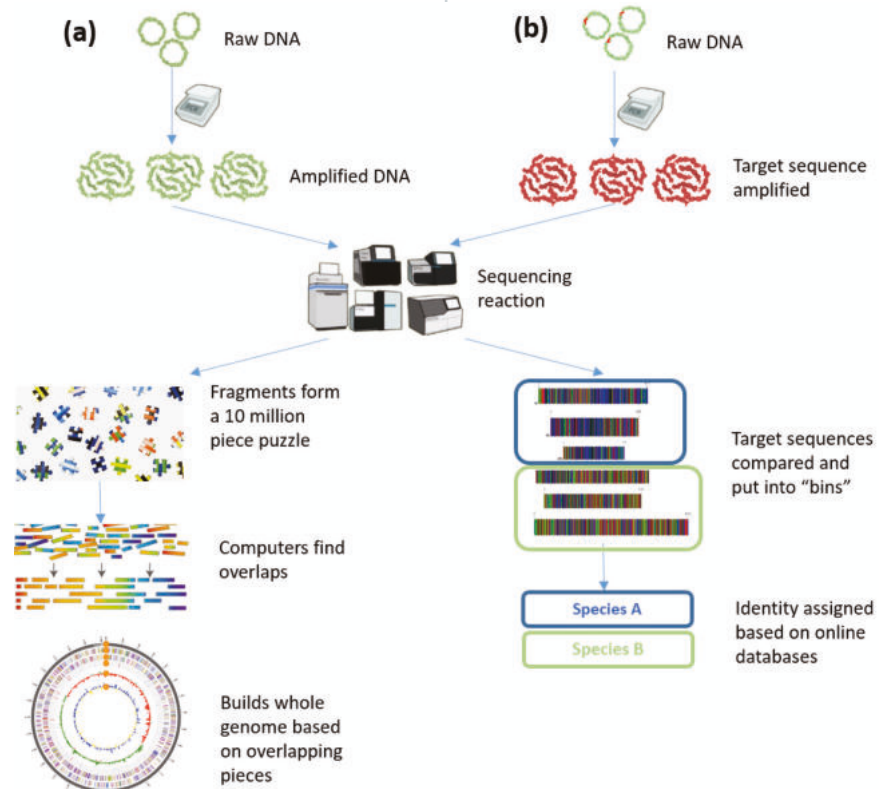


Figure 1. Sequencing approaches take DNA samples extracted from insects, make millions of copies of (a) random fragments, which are then paired together based on overlapping sections for genome sequencing or (b) copies of targeted parts of the genome (a barcode) that are compared based on dissimilarity between fragments, then compared to databases to describe the community composition.

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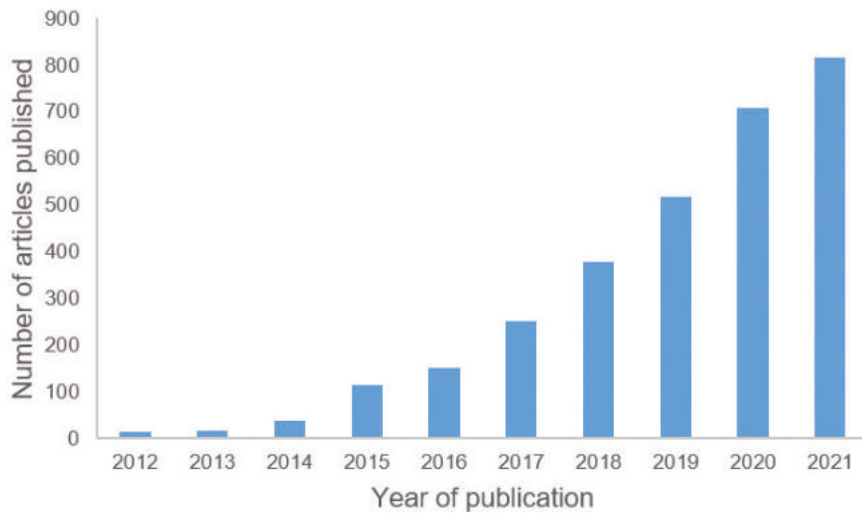


Figure 2. Metabarcoding in the literature. Published articles obtained from Scopus, Crossref, and PubMed databases on 09 Nov. 2021 for all metabarcoding studies.

comparison of specimen identifications between laboratories, barcoding is becoming more and more popular [9]. Despite these advantages, the time-consuming processes of extracting DNA and conducting sequencing reactions on individual specimens have mostly limited DNA barcoding for specimen identification to life stages where a taxonomic key may not be available or important diagnostic structures are degraded or missing [10].

Large numbers of samples are part and parcel of ecological monitoring, the reality of which has so far limited the use of DNA-based approaches; that is, until the recent advent of high-throughput sequencing (HTS) technologies. HTS has allowed DNA barcode-based identification to be conducted relatively cheaply and on a huge number of samples [11]. Thousands of reactions can be done at the same time to produce a huge number of barcode sequences [12], which can in turn be used for genome sequencing (Figure 1a) or “metabarcoding” (simultaneous comparison of different insect species in a mixed sample; Figure 1b).

Due to downstream computer analyses of these sequences, many thousands of individuals can thus be identified rapidly based on comparison to publicly available databases like NCBI Genbank (<https://www.ncbi.nlm.nih.gov/genbank/statistics/>) and the Barcode of Life Database (<https://ibol.org/resources/natural-history-collections/>). The speed and breadth of biodiversity surveying possible through metabarcoding means it has increasingly been employed across numerous fields of applied ecology [13,14]. The number of papers

published that use a metabarcoding approach has been growing nearly exponentially since 2012 (Figure 2), whilst the cost of sequencing has plummeted in that time [15].

Uptake of molecular tools is about more than just cost; it also encompasses important aspects such as the ease of use, accuracy, reproducibility, up-front investment of training and equipment and compatibility within existing policy frameworks, some or all of which may have hindered widespread collaboration between so-called ‘classic’ and molecular taxonomists [9]. Fortunately, many excellent resources like the following published papers [12,14–17] and training workshops (e.g., Edinburgh Genomics; <https://genomics.ed.ac.uk/services/introduction-metagenomic-data-analysis>, or The Earlham Institute; <https://www.earlham.ac.uk/microbial-analysis>) already exist for bridging this gap, but sometimes they miss out on the basics in terms of molecular technological theory and practice.

As for the practical aspects of conducting an ecological survey using metabarcoding approaches, when designing such a survey, the same constraints related to sampling method and collection scheduling that determine the explanatory power of a classic sampling programme apply [18]. Appropriate sampling tool choice is of course crucial, for example: pan trap, blue-vein trap, Malaise trap for flying insects; pitfall trap, suction sampler or soil cores for ground or subterranean insects; and various combinations for aquatic invertebrates, etc. Despite the high number of sequences that metabarcoding can generate, these sequences do not represent an

“individual” animal in the sample pool, and there is some argument over their statistical significance as “pseudoreplicates” [19,20]. Consequently, inadequate sampling and hence insufficient sample replication within a population cannot be “fixed” by intensive sequencing of a small gene pool.

Following sample collection in the field, bulk samples are typically homogenised back in the lab into a “paste” from which DNA can be extracted. Before this stage, various options are open, e.g., preliminary subsampling of trap samples to a taxon of interest (e.g., bees), or “bulking up” sample replicates from sites to reduce sequencing costs. After DNA extraction, the next decision is which barcode to use.

Despite current widespread usage for assessing *intra*- and *interspecific* genetic variation, there is actually a wide choice of different barcodes. Each barcode is limited, with advantages and disadvantages in terms of the level of variation detectable. Barcoding regions represent highly conserved regions, most often found within the mitochondrial genome. The most popularly employed barcode regions are the Cytochrome Oxidase I (COI) and Cytochrome Oxidase II (COII) genes. Similarly, there are structural mitochondrial genes like 12S, 16S, 18S and 28S as well as various inter-gene spacer regions (e.g., ITS2), which are commonly employed in metabarcoding studies of insects [9,15,21,22]. In terms of selecting these genes or genetic regions, different studies may involve selection of different sections of the gene concerned (e.g., COI has at least three regions commonly used in metabarcoding; Figure 3). Importantly, results from a survey that uses one barcode (e.g., COI) will be subtly different from another study in the same region using a different barcode (e.g., ITS2), meaning they cannot be accurately compared.

For sure, appropriate selection of a barcode or taxonomic marker is a critical step, since all downstream species detection and identification will necessarily rely on how conserved this marker is across taxa, and hence the discriminatory power of the nucleotide variation contained within it [18].

In terms of a broad survey of the insect genome and its variance, difficulties arise due to a lack of universal cover across insects by any one barcode region, either across different taxa (Figure 3) or different

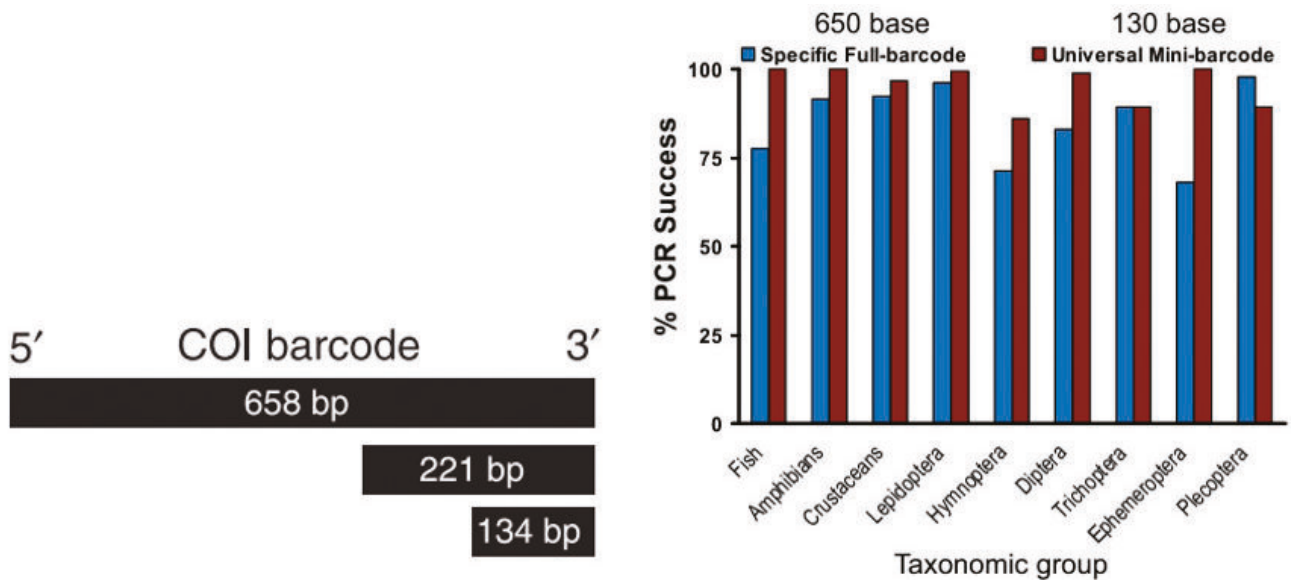


Figure 3. Cytochrome oxidase I gene has three different barcode sections. Longer sections offer greater differentiation between species, but produce fewer reads making them less effective on bigger samples. Data from Meusnier *et al.* [30] (Creative Commons CC BY 2.0).

regions (Figure 4). Although COI is arguably fast becoming the barcode of choice for animals, it has been shown to have limited applicability with certain taxa, such as the Tephritidae, due to its lack of interspecific variation [23]. Multi-locus barcoding, where multiple barcoding regions are sequenced from the same sample, have the advantage of broader and more accurate species identification, but will also double the financial cost of any sequencing endeavour, and make comparison between studies ultimately even more complicated [24].

Even after considering the cost of sequencing, various manufacturers offer different prices, ways of doing the reactions and the types of experiment they are best adapted to. The diversity of sequencing equipment has grown substantially over the past decade; the market is mostly dominated by two companies: Illumina (<https://www.illumina.com/>) and PacBio (<https://www.pacb.com/>). The former employs technology focused on reducing “price per base” sequencing costs and number of reads per sequencing reaction (typically making them the machine of choice for metabarcoding). The latter offers the longest continuous reads of any machine available currently, the company boasting the ability to read an organism’s entire genome in one go, hence eliminating the need for post-sequencing assembly, thereby making these machines more suited to *de novo* genome sequencing. Other small companies produce similar equipment, although most notable of

all, Oxford Nanopore has produced a “portable sequencing machine” called the MinION (<https://nanoporetech.com/products/minion>).

Most sequencing machines use a combination of thermal cycling, DNA polymerase enzymes, spectroscopic lasers and photoreactive DNA markers to replicate the target genome or DNA sequence. From the colour of light given off by the DNA as it replicates the DNA fragment, we can tell what bases are being used, and therefore what the DNA sequence of this new copy of DNA is. The MinION on the other hand uses a passive sequencing approach, rather than a biochemical reaction. This means that it does not replicate the DNA fragments but instead it passes the DNA through a partially-permeable membrane, recording what nucleotides are passing through the membrane in real time.

These machines can work under field conditions, with limited power supply and minimal sample preparation. To date, the MinION has been employed in published studies of microbial ecology using a 16S metabarcoding approach [25], whilst for metabarcoding studies of invertebrates, those involving the COI barcode are just now appearing as preprint manuscripts [26].

In terms of analysing the results obtained from metabarcoding approaches, bioinformatics, the computerised process of converting the sequences into useful information (usually an assembled genome or an ecological community framework) is, despite its complexity, now widely used. These approaches are called pipelines, because rather than being a

simple “put in raw data, get out results” system, the pipelines perform a series of different operations using the results from the previous part of the pipeline. They have many additional functions, including eliminating messy or poor-quality reads from the database, producing scores for the “goodness of fit” onto metabarcoding databases, as well as translating sequencing machine data files into formats that can be analysed on statistical software, like R. The diversity of programs is fortunately small, and most of the commonly-used pipelines (e.g., QIIME2; <https://qiime2.org/>) come with extensive instructional aids. The degree of computer literacy required however, often makes hiring a specialist bioinformatics technician a necessity.

The end result of metabarcoding, ideally, is a complete account of all species in the sampled ecosystem, including ones either difficult to identify accurately under a microscope or extremely locally rare species. Yet, despite the advances and hope of greater things to come in terms of better elucidating functional ecology, the methodology and general approach are far from perfect. New species will always need to be identified initially using microscopy, ensuring the need for maintenance of type specimens and the role of natural history museums [27,28]. Despite ever shrinking costs of sequencing, limited science funding in regions critically understudied for biodiversity will limit the impact of the metabarcoding approach in those regions [29]. Furthermore, because of the relative infancy of the technology

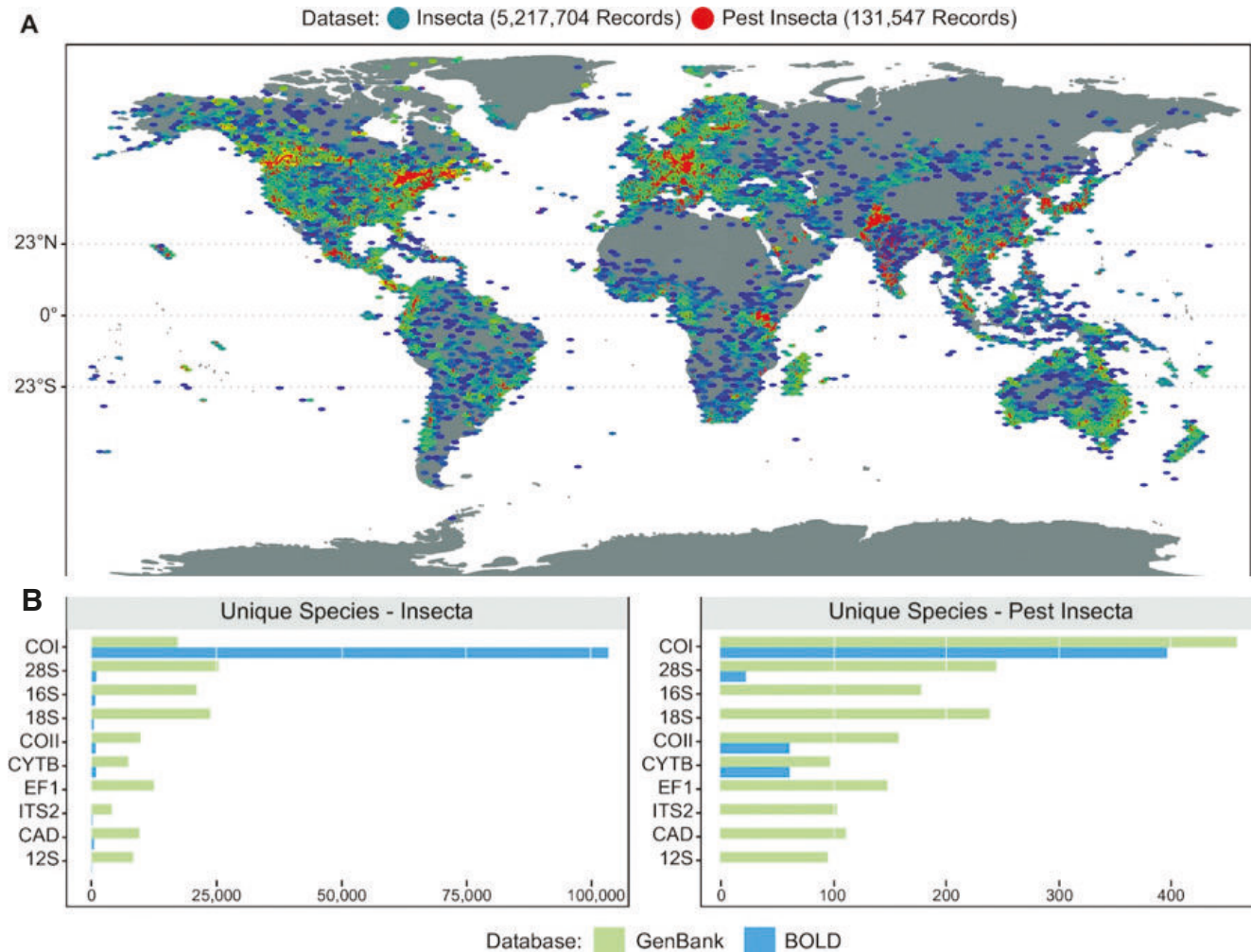


Figure 4. (a) Global distribution of DNA barcodes in public reference databases. (b) Distribution of records and unique species within major public databases for the 10 barcode markers with the most reference information for Insecta. Data from Piper *et al.* [9] (Creative Commons CC BY).

in the eyes of policy makers, standards and guidelines around its use are still evolving and validated protocols do not yet exist. For example, metabarcoding data cannot yet be used for Water Framework Directive (WFD) monitoring of benthic macroinvertebrates. This piece of legislation instead only accepts microscope-based community identification as a record of site biodiversity. Finally, as mentioned earlier, comparison between two studies using different barcoding regions is potentially flawed, meaning that, although there is a huge number of studies already in existence, we are still far away from an accurate global account of insect biodiversity.

Across Europe, several excellent invertebrate monitoring schemes combine classic microscope-based identification with metabarcoding approaches to supplement the breadth and depth of their data. These include the UK Pollinator Monitoring Scheme (PoMS; <https://ukpoms.org.uk/>) and Diversity of Insects in Nature protected Areas (DINA; <https://www.dina-insektenforschung.de/>)

de/insekten-monitoring-evk?lang=en) in Germany. The affordability of metabarcoding approaches has substantially improved over the past decade, as has the robustness of reference databases and data-processing pipelines. Consequently, we appear to be on the cusp of a revolution in both the technology and its application, in effect a fortunate paradigm shift in insect monitoring towards metabarcoding approaches. Having said that, the basic science underpinning molecular-based approaches is still ultimately reliant on classic taxonomy – in other words, you can't assign a barcode to a species without the physical type sample!

### Acknowledgements

The author receives funding from an ESRC Impact Acceleration Account fund at Lancaster University. I would also like to thank Dr Richard Harrington for inviting me to write this article, and for the RES Genomics SIG meeting that originally inspired preparing this material.

### References

- Sánchez-Bayo, F. *et al.* (2019) *Biological Conservation* **232**, 8–27.
- Daskalova, G.N. *et al.* (2021) *Insect Conservation and Diversity* **14**, 149–154.
- Harvey, J.A. *et al.* (2020) *Nature Ecology & Evolution* **4**, 174–176.
- Deng, J. *et al.* (2019) *Insect Conservation and Diversity* **12**, 18–28.
- Hopkins, G.W. *et al.* (2002) *Animal Conservation* **5**, 245–249.
- Cheesman, O.D. *et al.* (2007) *Proceedings of the Royal Entomological Society's 23rd Symposium*; ISBN 9781845932541.
- Orr, M.C.C. *et al.* (2020) *Megataxa* **1**, 19–27.
- Ratnasingham, S. *et al.* (2013) *PLoS One* **8**, e66213.
- Piper, A.M. *et al.* (2019) *Gigascience* **8**, giz092.
- Krehenwinkel, H. *et al.* (2019) *Genes (Basel)* **10**, 858.
- Alberdi, A. *et al.* (2018) *Methods in Ecology and Evolution* **9**, 134–147.
- Taberlet, P. *et al.* (2012) *Molecular Ecology* **21**, 2045–2050.
- Tedersoo, L. *et al.* (2019) *Molecular Ecology Resources* **19**, 47–76.
- Deiner, K. *et al.* (2017) *Molecular Ecology* **26**, 5872–5895.
- Liu, M. *et al.* (2020) *Ecological Entomology* **45**, 373–385.
- Staats, M. *et al.* (2016) *Analytical and Bioanalytical Chemistry* **408**, 4615–4630.
- Elbrecht, V. *et al.* (2021) *PeerJ* **9**, e12177.
- Zinger, L. *et al.* (2019) *Molecular Ecology* **28**, 1857–1862.
- Bush, A. *et al.* (2019) *Frontiers in Ecology and Evolution* **7**, 434.
- Paulson, J.N. *et al.* (2013) *R Packages*.
- Baird, D.J. *et al.* (2012) *Molecular Ecology* **21**, 2039–2044.
- Morinière, J. *et al.* (2019) *Molecular Ecology Resources* **19**, 900–928.
- Jiang, F. *et al.* (2014) *Molecular Ecology Resources* **14**, 1114–1128.
- Zhang, G.K. *et al.* (2018) *Evolutionary Applications* **11**, 1901–1914.
- Kai, S. *et al.* (2019) *FEBS Open Biology* **9**, 548–557.
- Abeynayake, S.W. *et al.* (2021) *Genes (Basel)* **12**, 1138.
- Call, E. *et al.* (2021) *Insect Systematics and Diversity* **5**, 6.
- Salvador, R.B. *et al.* (2020) *Oecologia* **192**, 641–646.
- Simmons, B.I. *et al.* (2019) *Ecology and Evolution* **9**, 3678–3680.
- Meusnier, I. *et al.* (2008) *BMC Genomics* **9**, 214.





# News from Council

## Meetings of Council

Council met on 1st of December 2021. Meetings are now subdivided into matters for decision, discussion and information. At this meeting there were discussions around RES journal publishing and significant numbers of information papers due to the large number of committees that had met in the autumn. The following is a summary of the main points.

## RES Membership for Staff

Employees of the Society are no longer embargoed from being members of the Society following the last AGM, although they are not allowed to have any voting rights. It was agreed that Jim Hardie and Luke Tilley would have their fellowships reinstated. Council also agreed that Simon Ward, Robert Spencer, Fran Sconce and Kate Watkiss would become Members of the RES.

## CEO Report

A summary of activities was presented, including some updates following a review of the workforce. There would be a number of new roles that would be advertised in the coming weeks and months to drive forward the strategy for the RES. An update was also given on the RES application for funding to enter a garden at the RHS Chelsea Flower Show in 2023. An update was given on some of the compliance works that have been taking place at Mansion House including asbestos removal and arboricultural surveys.

## Subscriptions

Membership fees for 2022/2023 were discussed and agreed.

## Library

A paper was submitted from the Library Committee as there were some short- and long-term considerations around storage and how the library would be managed. There are several considerations around Mansion House and its development over the coming months and so it was agreed that this will be further discussed at forthcoming meetings.

## Journal Publishing

A review of the journals through 2021 took place, including a note of the new initiatives that had emerged from Wiley. There was discussion around the future landscape including Open Access, changes to funding models and where new opportunities and challenges may present themselves in 2022 and future years.

## Grand Challenges Project

Work is continuing on the manuscript following the workshop in the summer. This will continue to progress into early 2022.

## The Mansion House

Fire safety, asbestos and underground facilities audits have been commissioned as part of a drive to ensure compliance with relevant legislation. Plans for developing the garden are progressing.

## Website

The new website continues to be developed. The new system includes a membership portal. This will be due for launch in early 2022.

**Simon Ward**  
Chief Executive Officer



# A New Chapter

## - The New RES Strategy and Brand

As I started as CEO in April 2021, it was immediately evident that the Royal Entomological Society is a wonderful organisation with a rich history. It is a real privilege to work alongside a group of dedicated and forward-thinking trustees and staff as well as so many respected Fellows and Members. As we embark on a new chapter, my role is to ensure that the RES builds on its historical foundations by remaining relevant, having a high impact and a sustainable future.

Our correspondence with a large number of our membership, as well as partner organisations, confirmed that the RES is a Society of which people are proud; however, overwhelmingly, people felt that the RES could achieve so much more. Whilst the RES had an aim and charitable objectives, the Society had never had a strategy or a vision that would allow it to realise its full potential. The RES Strategy for 2022–25 reflects the future direction and priorities of the RES. Such strategic planning informs budgets and business plans, which in turn aim to achieve greater investment in insect science, focus on opportunities for entomologists and ensure societal benefit from what we do.

In developing the RES strategy 2022–25, it was imperative that the membership remained at the core of the organisation. Consultation and outreach have been ongoing throughout the process. We ran several workshops, liaised with a number of Members and Fellows via video conference and email, and gathered some of the key points raised from the 2021 membership consultation. Over the last year, our staff examined the feedback in detail, and determined how we can address its challenges.

Our starting point in our strategy development focused on defining our core purpose; being clear why the RES exists. Listening to how so many entomologists talked about the Society, it was straightforward to determine that we want **to show every person how formidable and valuable insects are**. Developing a three-year strategy would enable us to focus on clear and significant targets and provide a suitable time scale to meet them.

From here, we identified our vision: **to enrich the world with insect science**. Finally, we constructed our mission – a

broad statement to outline how we will achieve our vision: **to unite experts across the globe to share and preserve knowledge while engaging audiences everywhere**. We will **invest in meaningful insect science to benefit the people and nature**.

With our purpose, vision and mission in place, we had the foundations upon which we could start determining our strategic priorities between 2022 and 2025. Before we did this staff, trustees and committee members were surveyed to establish the values that they believed should underpin the work of the RES. We were able to determine five key values which remain central to our Society:

### Supportive

We welcome people to our community and encourage everyone to participate, giving help and advice where we can.

### Confident

We pride ourselves in our knowledge and expertise.

### Inclusive

We believe in including everyone. Anyone, from anywhere, who has an interest in insect science is welcome in our community.

### Inquisitive

We ask questions and stay curious. Fascinating subjects and passionate people surround us.

### Collaborative

We stay open-minded and listen, taking everyone's views or experiences onboard to be receptive to different ways of thinking.







With these key elements in place, further discussion and evaluation of feedback enabled us to determine four key strategic priorities that would help us to realise our vision over the next three years.

### **1** Support the study and practice of insect science

Incorporating the development of the RES journal portfolio, the review and development of funding, bursaries and grants, developing strategic partnerships and collaborations, being an independent voice to decision-makers, and developing the annual programme of meetings, special interest groups and conferences.

### **2** Increase public understanding of insect science

Including the sharing of insect science and research with a wide audience, developing high impact outreach, education and resources, and sharing and developing best practice and innovation in communication and engagement.

### **3** Empower and support the entomological community

Including supporting opportunities for our membership at all career stages, growing our global membership with a focus on equality, diversity and inclusivity, developing community activities and events across the globe, and developing our online presence to increase engagement.

### **4** Invest in our workforce and infrastructure

Comprising the development of people and processes to enhance efficiency and success, investing in infrastructure, ensuring financial security to be able to continue investing in insect science and applying compliance and environmental best practice in everything we do.



Guided by these strategic priorities, we can increase the impact, relevance and sustainability of the Royal Entomological Society. We can hope for longer-term impacts from this work:

**Insect science will be at the forefront of research and decision-making**

**We will see wider awareness, more engagement and curiosity around insect science**

**The value and benefits our team and assets bring will be seen throughout the whole organisation**

**The entomological community will feel it's at the heart of the society**



Alongside our strategic development, the Senior Leadership Team considered the RES website, and it became clear that our brand and logo would also need development to make them more present and user-friendly in a digital age. Aside from its logo, the RES had no clear visual identity. The logo itself used a Times New Roman font and the greyscale picture lacked definition when viewed electronically. Furthermore, RES events such as National Insect Week appeared as organisations or brands of their own, and were therefore difficult to link back to the RES.

We engaged with a branding agency, ThreeRooms, who had worked recently with the British Geological Survey. We chose to work with ThreeRooms as they put a strong emphasis on the discovery phase at the start of the branding development.

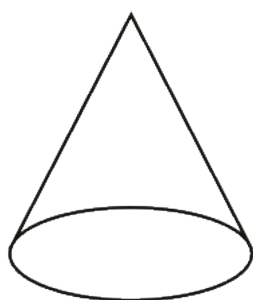
Questionnaires were distributed, telephone interviews took place and a workshop (see photos) in which Fellows, Members, Trustees and Staff took part allowed us to understand what was really important. Feedback and consultation from our strategy development also informed our branding. It was wonderful when Simon Leather finished the branding workshop and told me that, whilst he hadn't been looking forward to it, it was the best workshop in which he had ever been involved! A particularly notable idea came from Dominique Vassie, who highlighted how special the iridescence of insects was and proposed that we capture this in our brand.

Our new brand needed to support the Royal Entomological Society's new vision and strategy, retaining our core values and identity whilst embracing our rich heritage. With a nod to our historic background, we have retained *Stylops* in our new logo and it will remain as the seal of the Society. Our new logo and colour scheme will enable the RES to stand out digitally but will also enable us to complement our brand with fantastic imagery of both insects and entomologists. The feedback about our new brand has been overwhelmingly positive.

As we launch the 2022–25 strategy for the RES, it is a truly exciting time. Whilst Covid has brought many challenges it has also given us new opportunities. The ways in which we can engage with members across the globe has hugely expanded.

When we approach the end of this strategic period in 2025, we will be only eight years from our 200<sup>th</sup> anniversary celebrations. I am truly excited to see what will be achieved in this time through collaboration with our Members, Fellows and Partners.

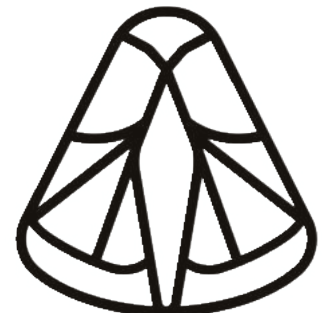
**Simon Ward**  
Chief Executive Officer



SPOTLIGHT



STYLOPS



# Royal Entomological Society



# Staff News

I am pleased to confirm some changes to job titles which took effect from 1 December 2021. Fran Sconce is now 'Senior Outreach and Learning Officer' and Jim Hardie became 'Resident Entomologist'. Kate Watkiss has taken on a new role as 'Facilities Officer'.

After 15 years of dedicated service as the Society's librarian, Val McAtear left on 5 February 2022. Val joined at a pivotal time in the Society's history, coinciding with the decision to move from London to St Albans, during which Val managed the move of the library. Val has provided a high-quality service to the Society's members and many colleagues across the entomological community through her care of our published resources and through the provision of research material from the library's extensive collection.

Sue Ward, after almost 12 years of dedicated service as the Society's Membership Administrator, left us on 5 February 2022. Sue has played a key role supporting our members with their enquiries, maintaining our membership database, managing the administration of subscriptions and the Society's awards programme. She has been in contact with all Society members at some point during their membership. Those who have had the pleasure to be in contact with Sue will know her as helpful, committed and always cheerful.

I am sure you will join me in thanking Val and Sue for all that they have done for the Society and in wishing them all the very best for the future.

**Simon Ward**  
Chief Executive Officer

## Journals and Library

### Pan-African Mosquito Control Association Virtual Conference

20–22 September 2021

Report by Lisa Reimer, Editor-in-Chief Medical and Veterinary Entomology

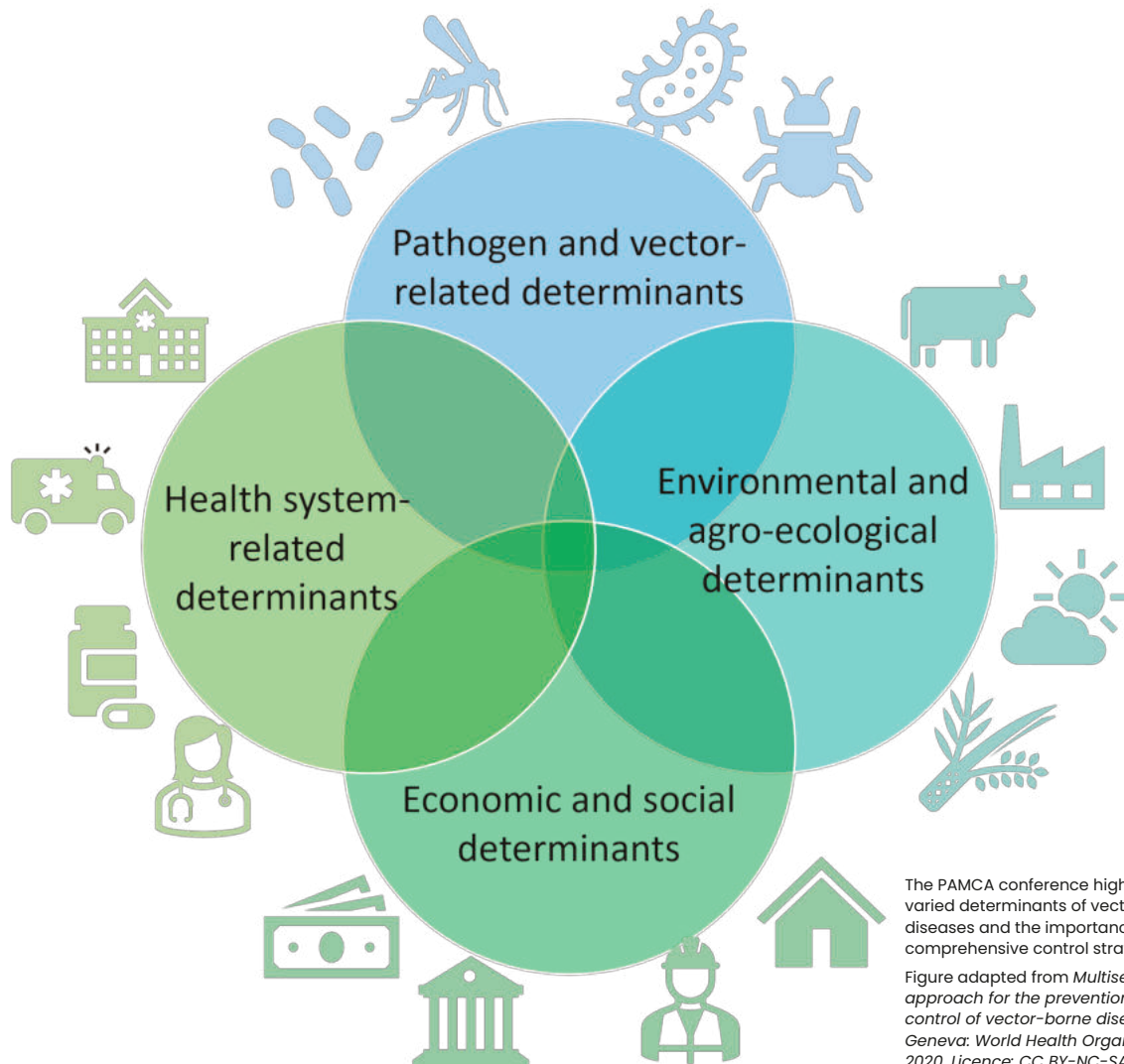
The RES journal *Medical and Veterinary Entomology* was proud to sponsor the Pan-African Mosquito Control Association virtual conference. The theme of the conference was "Empowering local institutions to set the agenda for the elimination of vector-borne diseases". The symposia and scientific sessions over the three days focused on the latest research on vector surveillance, insecticide resistance management and innovative approaches to vector control. Abstracts can be viewed at [www.pamca.org](http://www.pamca.org). Capacity strengthening, data sharing and evidence-based decision making were common themes across all the sessions.

The plenary speakers over the three days delivered a high-level view of the emerging challenges facing national vector-borne disease (VBD) control programmes and shared insightful solutions. Dr Keziah Malm (National Malaria Control Program [NMCP], Ghana) underscored the importance of strengthening capacity for vector surveillance. Surveillance is a core intervention in the fight against malaria; however, vector data are underutilised for decision making. Ghana has achieved success in

producing maps with mosquito breeding habitats, densities and entomological indices since 1911. The NMCP has demonstrated data-based decision making, for example by switching active ingredients following results from the National Insecticide Resistance Monitoring Partnership. Keziah called on donors, governments and stakeholders to build human resource capacity, invest in infrastructure and foster better collaboration.

Dr Audrey Lenhart (Centers for Disease Control and Prevention, USA) highlighted the challenges of vector control in the wake of COVID-19 and called for innovation. While technological innovation may have been sufficient to address many pre-COVID challenges, it's clear that we need innovation across the spectrum in order to make progress on the elimination goals. For example, innovations in engagement and in research practice are needed to address inequality among scientists and unequal power dynamics between external and local institutions. Further innovations in our approach to partnerships which recognise appropriate leadership and enable investment in national institutes are required for resilient disease control programmes.





The PAMCA conference highlighted the varied determinants of vector-borne diseases and the importance of comprehensive control strategies.

Figure adapted from *Multisectoral approach for the prevention and control of vector-borne diseases*. Geneva: World Health Organization; 2020. Licence: CC BY-NC-SA 3.0 IGO

Dr Florence Fuque (WHO/TDR) spoke on global health and the emergent challenges of arthropod-borne diseases in Africa. She highlighted the need for multisectoral action and a population-based approach to protect the most vulnerable. The intersection of poverty, unplanned urbanisation and lack of preparedness, coupled with the adaptability of vectors, can lead to rapid spread of emergent VBDs. Multidisciplinary and multisectoral approaches are needed among departments of water and sanitation, agriculture, housing, education, finance and health. This is the first pillar of the WHO *Global Vector Control Response* programme and the theoretical framework is being implemented to explore links between agriculture, insecticide resistance and malaria transmission.

The *Women in Vector Control (WIVC)* programme led an inspiring symposium on strategic thinking and confidence building in leadership. WIVC's mission is to empower women to combat VBDs by creating an enabling environment and this session was an opportunity to learn from transformative leaders. Only 28% of medical entomologists in Africa are women, yet VBD risk and intervention efficacy differ by gender. Designing solutions to complex VBDs requires diversity of leadership which is representative of society. The WIVC programme prioritises structured mentorship, professional training, networking, collaboration and visibility to achieve this aim. Dr Helen Jamet (Bill and Melinda Gates Foundation) reflected on her experiences in the male-dominated fields of research, industry and funding agencies. Identifying allies among

managers and colleagues is key to creating a safe workplace where self-worth, confidence, and opportunities to grow are supported. Dr Prosper Chaki (PAMCA) credited strong female mentors for encouraging him in his career development. He raised the importance of male ambassadors to take action against gender inequality, by ensuring colleagues feel valued and by fostering transitions into leadership roles. Dr Pamela Mbabazi (WHO) highlighted the importance of a work/life balance, a challenge that cuts across all cultures. All participants agreed that perceptions of leadership are shaped by our relationship with good mentors, and we all have a role to play in mentoring others in order to shift the balance towards effective and inclusive leaders.

While the PAMCA conference delivered excellent scientific talks, this was also an opportunity for the research community collectively to set the agenda for the next year and to reaffirm shared values. There was overwhelming enthusiasm for innovative approaches to VBD control and new multisectoral partnerships to increase the impact. The meeting closed with the WIVC excellence awards which celebrate rising stars and established leaders in the field of vector control: Dr Jessy Goupeyou-Youmsi (early career); Dr Evelyn Olanga (mid career) and Dr Chioma Amajoh (senior).

*Medical and Veterinary Entomology* has produced a virtual issue for the PAMCA conference which highlights recent research on the surveillance and control of the most important mosquito vectors of sub-Saharan Africa: [https://onlinelibrary.wiley.com/doi/toc/10.1111/\(ISSN\)1365-2915.pamca-mosquito-control](https://onlinelibrary.wiley.com/doi/toc/10.1111/(ISSN)1365-2915.pamca-mosquito-control).

# Forest Insects (and their Allies) Special Interest Group Meeting

I wasn't aware of the FAO definition of a forest. It's "land spanning more than 0.5 ha with trees higher than 5 m and a canopy cover of more than 10%, or trees able to reach these thresholds *in situ*". Trees elsewhere are known as 'trees outside forests' (TOFs). In a wide-ranging meeting, Jérôme Rousselet (INRAE, Centre Val de Loire) presented a keynote on the role of TOFs in the dispersal of forest pests in the context of global change. TOFs provide many ecosystem services but can also assist the spread of pests between forests. The trade in ornamental plants has played a large role in a linear increase in the introduction of alien pests since about 1850, and urban trees help to facilitate the establishment and spread of these. French households buy 50 million trees and shrubs each year, roughly the same number as planted by foresters. *Thaumetopoea pityocampa* (Pine processionary moth; PPM) is a useful model species for climate change studies as its larvae are easily visible and mappable. It first appeared in France in the 1970s and is gradually moving north and east. In the 5,000 km<sup>2</sup> Beauce area of northern France between the Seine and Loire rivers, isolated host trees have been mapped. Flight-mill experiments have shown that females can fly up to 11 km but mainly fly less than 1 km. Gradual genetic variation has been shown throughout the region. These



*Enoplognatha ovata* (Candy-striped spider).  
Photo: Sam Rogerson

Online 21<sup>st</sup> October 2021

Convenors: Anne Oxbrough  
and Kirsty Godsman

Report by Richard Harrington



*Agrilus biguttatus*  
Photo: Gareth Thomas  
(copyright Rothamsted Research)

geographical, behavioural and landscape genetics studies have shown TOFs to provide functional connectivity for spread of PPM as the climate warms and more northerly areas become suitable for its establishment. Jérôme will be working with social scientists to understand household demand for ornamental plants and whether there is scope to limit their potential for spread of PPM.

*Operophtera brumata* (Winter moth) is very abundant in the UK and is an important source of food for birds. Experimental manipulation has shown synchrony between egg-hatch and budburst in English oak to be very important. Hatching as little as five days early or late can reputedly push caterpillar fitness to zero. Winter moth larvae can feed on at least 31 genera in 15 families, but the possible role of these other hosts in buffering against phenological mismatch due to climate change has been hitherto ignored. Jamie Weir (University of Edinburgh) reared 4,000 larvae on nine common host plants and measured fitness in terms of survival to pupation, duration of development and final pupal mass. Survival was higher on five tree species compared to Oak. Pupal mass was less variable across host species, but was lowest on Oak. White willow and Birch stand out

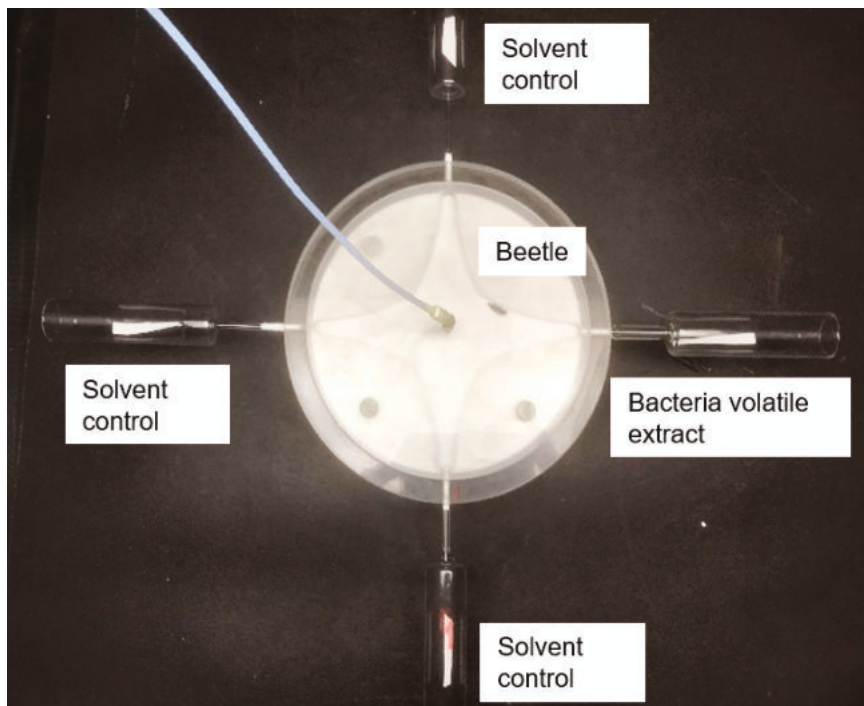
as good hosts for survival, but their wider ecological significance for this species and potential role in buffering against climate change requires further investigation.

*Ips typographus* (Eight-spined bark beetle) is the most serious pest of Spruce in Europe and Asia. It develops on weakened or dead trees. Susceptibility of Norway spruce has been well studied, but susceptibility of Sitka spruce has not, even though the latter makes up 50% of forest in the UK. The beetle first appeared in Kent, and Katy Reed (Forest Research) conducted pheromone-lure experiments which suggest that migration across the English Channel/La Manche probably occurs. Experiments using 4-arm olfactometers showed no difference in attraction of the beetle to the two species, but preliminary trials suggest reduced breeding success on Sitka spruce.

Sophie de Becquevort (Aberystwyth University) is applying morphological and molecular genetic approaches to understanding the ecology and impact of wood-boring and bark-feeding beetles for her PhD. She wants to improve knowledge of their origin, diversity, pest status, distribution and spread, and to reduce damage of some species by better monitoring, surveillance and management. She



*Episyrphus balteatus* (Marmalade hoverfly).  
Photo: Sam Rogerson



Four-arm olfactometer

Photo: Gareth Thomas

collected larvae in conifers in Wales to link beetle species with tree characteristics and conditions such as stress level. Barcoding revealed the unexpected presence of larvae of the weevil *Kykliaacalles roboris* in Noble fir. In addition, she studied the *Ips typographus* invasive population and its origins, and she worked on population genetics of *Tomicus*

*piniperda* (Common pine shoot beetle), *Gnorimus nobilis* (Noble chafer) and *Lucanus cervus* (Stag beetle).

There has been much argument about the relationship between Acute oak decline (AOD) and *Agrilus biguttatus* (Two-spotted oak buprestid). Does the beetle have a role in disease spread or is its

association with the disease benign? Gareth Thomas (Rothamsted Research) is studying whether the beetle is attracted to volatile organic compounds (VOCs) produced by the three bacteria which cause AOD and whether disease status impacts VOC production. His aim is to optimise semiochemical-based lures for monitoring the beetle. Using air entrainment to collect volatiles, and GC-MS (gas chromatography coupled with mass spectrometry) to analyse them, 18 foliage volatiles were identified, four being indicative of diseased oak. Using a 4-arm olfactometer, Gareth found evidence that virgin beetles are attracted to disease-related foliage VOCs. Furthermore, coupled GC-electroantennography showed beetle antennae to respond to two bacterial volatiles, and in olfactometer experiments increased time was spent by gravid females in treatment arms containing bark and bacterial VOCs.

A four-year NERC-funded project (RestREco) aims to progress restoration of degraded ecosystems. Emily Waddell and Sam Rogerson (University of Stirling) are part of a team looking at the role of invertebrates in restoring resilient broadleaf woodland. Thirty sites in Scotland have been surveyed so far, 15 of which are former agricultural sites

*Rilaena triangularis* (Spring harvestman) Photo: Sam Rogerson



*Aphrophora alni* (Alder spittlebug).  
Photo: Sam Rogerson



and 15 former industrial sites, each set covering different stages of transition (10–50 years post establishment). In each woodland, five circular plots (20 m diameter) were surveyed for vascular plants (June to July) and invertebrates, soil microbes and bioacoustics signatures (June to September). Different measures of complexity will be calculated to investigate how complexity influences ecosystem functions, e.g., pollination services, predation rates and herbivory rates, and the resilience of these functions to perturbation.

Co-convenor Kirsty Godsman (Caledonian Conservation Ltd) reported her PhD studies, done whilst at Edge Hill University, on the value of plantation forests for spider conservation. Spiders play a crucial ecosystem role and are sensitive to small-scale changes in habitat structure. Kirsty wanted to know whether plantations support spiders of conservation interest and which

environmental parameters are important. Her work was done in Scots pine and Sitka spruce plantations at a range of developmental stages and in mature Oak plantations. Pitfall traps were used and hence only ground-active spiders were recorded. Thirty-five species of conservation interest were recorded, including some UK biodiversity action plan species. Location, age of trees, litter depth and vegetation cover were important in determining spider counts, but tree species had no direct effect.

With an ever-increasing number of devastating tree diseases, Fiona Plenderleith (James Hutton Institute) reported work on the consequences of disease and pre-emptive felling on functional and genetic connectivity for forest invertebrates. Ash is home to 953 species, including 239 invertebrates, in the UK. A stochastic individual-based model was used to look at impacts of Ash tree loss on insect species with different dispersal

traits. Removal of a randomly selected 10% of Ash trees away from forests resulted in a reduction in successful dispersal of up to 15%. The consequences of tree loss for woodland connectivity were influenced by species dispersal traits, but the consequences for gene flow may depend on the arrangement of trees within the landscape.

Rachel Cripps (RM Conservation) gave a fascinating presentation on the potential of detection dogs in forestry and other aspects of ecology and conservation. With up to 300 M scent receptors in their noses and an ability to cover large areas quickly, over difficult terrain whilst causing minimal disturbance, dogs can, for example, detect all life stages of *Anoplophora glabripennis* (Asian long-horned beetle) and have assisted with an eradication programme in Kent. Rachel gave other examples, and the possibilities for targeted screening of imported plants

and timber for pests and diseases and for monitoring the spread of invasive pests or the distribution of rare invertebrates are seemingly endless, as the dogs rarely bark up the wrong tree. For more information, see <https://www.ecologydetectiondogwg.org/ecology-detection-dogs>.

Newly-emerged *Hylobius abietis* (Large pine weevil; LPW) can completely destroy young trees, threatening 3.4 M ha in Europe and causing losses of £120 M in the UK alone. Luis Quinzo-Ortega (Liverpool John Moores University) is hoping to manage this pest by using locally-obtained entomopathogenic fungi (EPF) and nematodes (EPN). Adult beetles are attracted by volatiles to stumps, where they lay eggs, and the larval stage lasts one to three years

depending on temperature. Six commercially-available EPN can give good control, and recycle in the host, producing new infective nematodes. EPF do not provide as good control as EPN, but there is an additive effect when both are used. In order to find new, local candidate EPN and EPF, soil baited with *Galleria mellonella* (Wax moth) and *Tenebrio molitor* (Mealworm) larvae was sampled at depths of 0–10cm and 10–20 cm at eight Wildlife Trust sites. Sixty-one nematodes and 213 fungi were found. Thirteen candidate EPF are currently being screened. Luis plans to adopt a 'total kill' approach whereby, in addition to targeting larvae, adults will be lured with volatiles such as alpha-pinene to traps containing EPF. Mark-recapture experiments will

inform the development of an effective chemical-free method to control *H. abietis*.

To end the meeting, Allan Watt (UK-CEH) gave a moving tribute to Simon Leather who did much pioneering work on forest insects including *Rhopalosiphum padi* (bird cherry-oat aphid) and *Panolis flammea* (Pine beauty moth). A large part of *Antenna* 46(2) will be devoted to the work of Simon and his students.

Very many thanks to Anne and Kirsty for organising an excellent meeting, attended by 61 delegates, to all presenters and their co-authors, and to Fran (again) for managing the technical side. If you would like to join the mailing list for this SIG, please contact Anne at [anne.oxbrough@edgehill.ac.uk](mailto:anne.oxbrough@edgehill.ac.uk).

*Araneus quadratus* (Four-spotted Orb Weaver)  
Photo: Sam Rogerson



# Orthoptera Special Interest Group Meeting



A pair of released Large marsh grasshoppers *Stethophyma grossum* enjoying their freedom. Picture by Stuart Green

This was the 42<sup>nd</sup> Orthoptera SIG and the second online-only meeting. Hopefully, though, orthopterists will soon have the chance to meet in person, as Luc Willemse (Naturalis Biodiversity Centre, Leiden) announced the third European Congress on Orthoptera Conservation (ECOCIII). It will be held in Leiden, The Netherlands, on 1<sup>st</sup>–2<sup>nd</sup> April 2022. Information can be found at <https://www.grasshoppersofeurope.com/content/european-congress-orthoptera-conservation-ecociii-1-2-april-2022>.

Online Meeting 3rd November 2021

Convenor: Darron Cullen  
Report by Richard Harrington  
and Darron Cullen

Stuart Green (Citizen Zoo, UK) began the meeting with an update on the re-introduction of *Stethophyma grossum* (Large marsh grasshopper) to East Anglia. The basics of the project are reported in the account of last year's meeting (*Antenna* 45(1) 32–33). Over three years, a total of 3,237 home-reared grasshoppers have been released by volunteers at four Norfolk wetland sites. At the main site, surveys suggest a population is now established, with approximately 500 adults. Future introductions are planned, possibly including new sites in the Norfolk Broads, the Cambridgeshire Fens and Suffolk. To maintain genetic health, fifteen wild grasshoppers are collected each summer from the New Forest to join the captive-breeding population.

Hugh Rowell (University of Basel, Switzerland) introduced Nick Jago's *Grasshoppers of East and North East Africa*. Nick died in 2005 without having had the chance to prepare fully his vast knowledge and photographs for publication. Hugh was asked to do this and has been helped by several people. It has been a labour of love for ten years. There are now five volumes, each self-published. Hugh is seeking funding to get this extraordinary work published

in a more widely available form, and would appreciate thoughts from any members to this end.

The IUCN 'Red List of Threatened Species' is a vital tool for informing conservation strategy. Axel Hochkirch (Trier University, Germany) said that 1,479 orthopteran species are on the list. In Europe, 30% of orthopteran species are decreasing, 8% are stable, 3% increasing and 59% are unknown in this regard. A global Sampled Red List Index for Orthoptera is being produced with 115 contributors. Results for the first 200 species show 2% as 'critically endangered', 4% 'endangered', 18% 'vulnerable', 7% 'near-threatened' and 40% 'least concern'. Axel gave examples of the status of species from Gran Canaria. *Dericorys minutus* (Gran Canaria crested grasshopper) is critically endangered, mainly because of coastal habitat destruction for hotel building. It has, however, been rediscovered in the north and south-east of the island, the latter population not being under threat. *Evergoderes cabrera* (Gran Canaria bush-cricket) was rediscovered in 2018 in the same place as it was last known, and more localities have been found as a result of publicity. Wildfires appear to have wiped out important populations of

*Calliphona alluaudi* (Gran Canaria green bush-cricket). A conservation strategy is being devised for the highly threatened *Prionotropis rhodarnica* (Crau plain grasshopper) in southern France. It is difficult to find, but detection dogs have helped. It is at risk from predation by rooks. As its requirements, including carefully managed sheep grazing, have become better known, populations have risen from around 50 in 2015 to around 250 in 2019.

Mathematical modeller Emine Celiker (University of Lincoln, UK) is studying the hearing system of bush crickets. In *Copiphora gorgonensis* the ears are on the forelegs and acoustic tracheae are located inside the legs. Emine is interested in the role of the acoustic tracheal geometry and the function of the tympanal cavity. Sound pressure amplitude increases at the end of the acoustic tracheae. The mating call of this bush cricket is at 23kHz and the greatest pressure gain is in this region. Tympanal cavities were found to act as resonators and play an important role in survival as the pressure gain helps them to detect the high frequencies of bat predators. Other species have evolved similar structural geometries to detect different ranges because of different mating-call frequencies and different predators.

Chu-Cheng Lin (University of Cambridge, UK) spoke about his PhD work on the role of abdominal ganglia in controlling song patterns in crickets. He played recordings of four cricket species with diverse patterns of chirps, trills and intervals. By applying lesions to the abdominal nerve cord at various points and analysing songs before and after, he was able to determine that cutting between thoracic ganglion 3 and abdominal ganglion 3 (A3) resulted in no song. Cutting between A3 and A4 resulted in single pulses or broken song. The outcome of cutting between A4 and A5 depended on the song type. Cutting between A5 and A6 had no effect on the song. The conclusion was that the region between A3 and A4 acts as a pulse timer and the region between A4 and A6 as a chirp and trill structure timer.

There are five species of grasshopper on Jersey and Michelle Gray (Jersey Biodiversity Centre, UK) is interested in whether colour polymorphisms occur in *Oedipoda caerulea* (Blue-winged grasshopper) and, if so, how they relate to microclimate and substrate preferences. Fifty-five grasshoppers

were caught and photographed. Images were quantified and grouped using the 'R' package 'colordistance'. The grasshopper was found to prefer 50–70% groundcover and low vegetation. There are three colour groups: grey, red and black. Black morphs were found where temperature was lower and so the colour may be related to thermoregulation. Where there were multiple colour-morphs, the likelihood of predation was reduced. Increasing habitat connectivity, maintaining grazing and limiting natural succession should help in conservation efforts. Michelle hopes to establish a long-term monitoring system for Jersey's grasshoppers, alongside the well-established butterfly monitoring scheme.

In the past, the UK has funded much research on *Schistocerca gregaria* (Desert locust) because of the problems it caused in parts of the British Empire, notably Kenya, Tanzania and Uganda, as a result of the colonial policy of agricultural development. Sabine Clarke (University of York, UK) and Ed Baker (Natural History Museum, London) gave an overview of this research. In the early part of the 20<sup>th</sup>

Century, locust control was devolved to the colonies. This was a problem because flame throwers and arsenic were used, both being labour intensive and dangerous. In 1930, the Imperial Institute for Entomology, headed by Guy Marshall, brought Boris Uvarov over from the USSR. He reorganised its programme by demonstrating that the benefits of a nationally-organised locust-research and control programme would outweigh the costs and facilitate international cooperation. As a result of the Colonial Development and Welfare Act of 1940, the Anti-Locust Research Centre (ALRC) was established in 1945, combining the Desert Locust Survey and the Desert Locust Control Programme, and the control campaign became much more specialised and professional. Archives of the ALRC include locust report forms, narrative reports, survey reports, maps, control campaign reports, field notebooks, meteorological and hydrological data, photographs, films etc. These have the potential for feeding into current forecasts and historical research but are little used. Digitisation is a long-term goal.

*Schistocerca cancellata* nymphs marching © Stav Talal (from Mira Word)



Following Uvarov's death in 1971, the ALRC merged with other overseas development agencies to become the Centre for Overseas Pest Research. Subsequent mergers further reflected Britain's decreased coordination of locust monitoring and control, which passed to the Food and Agriculture Organization of the United Nations (FAO). The FAO continues to work with national and regional monitoring agencies across Africa, the Middle East and South Asia, and remains predominately focused on *Schistocerca gregaria* (Desert locust). The Global Locust Initiative (GLI), founded in 2018 at Arizona State University in Tempe, seeks to engage key actors in locust research and management to develop partnerships and solutions for locust management. GLI representatives Rick Overson and Mira Word introduced the GLI and outlined their current projects. The GLI Network includes agriculturalists, monitoring specialists, entomologists, social scientists and economists from around the world. Recent work has included a particular focus on connecting global stakeholders through online resources like HopperLink, an online community for



Ash Murray, Norfolk Wildlife Trust, releasing home-bred Large marsh grasshoppers at site 3.

Picture by Stuart Green

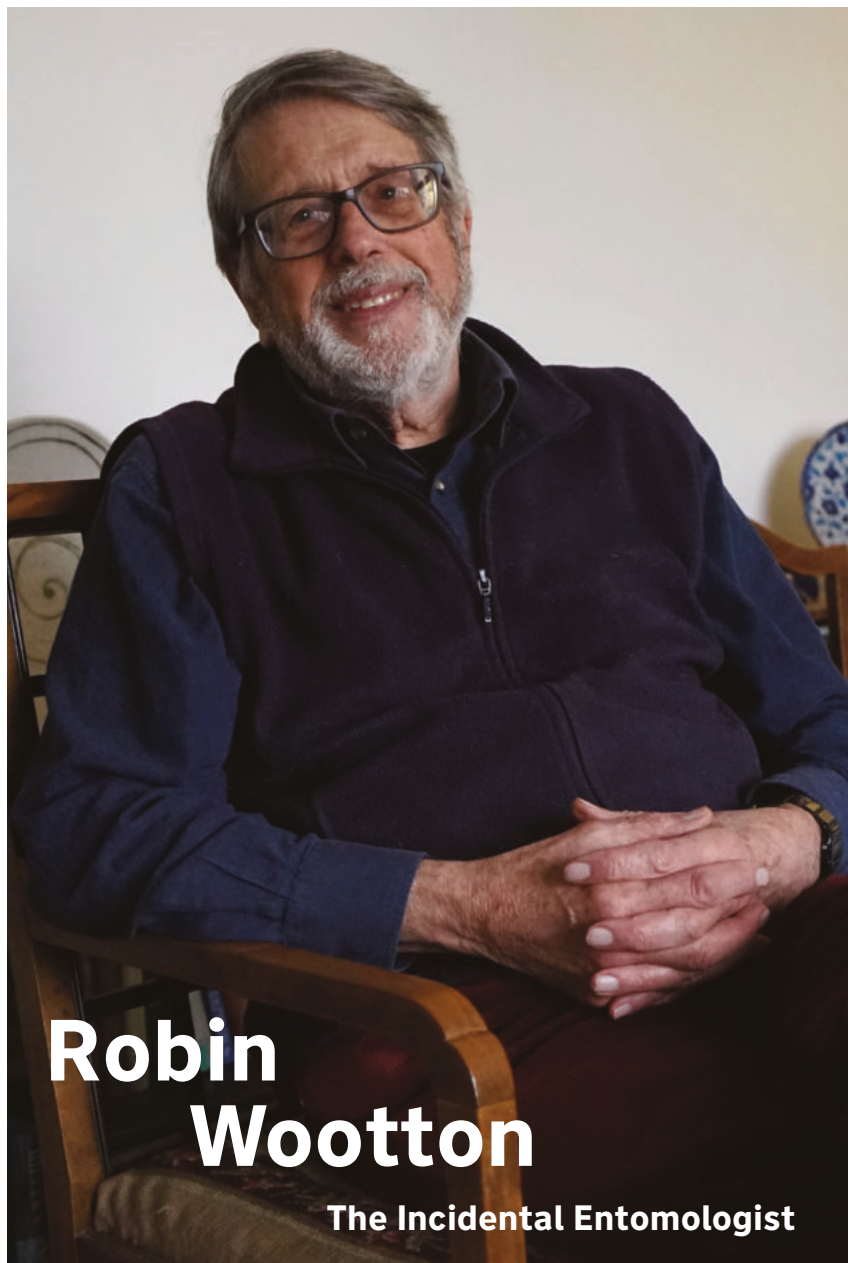


the GLI Network. The GLI Laboratory houses a number of locust species for basic research, including *S. gregaria*, *S. cancellata* (South American locust), *Oedaleus senegalensis* (Senegalese locust) and *Chortoicetes terminifera* (Australian plague locust). More details about the GLI's research can be found at <https://locust.asu.edu>.

The final talk came from Hojun Song (Texas A&M University, USA) who is one of the principal investigators on a major new locust research grant funded by the US National Science Foundation in 2020. The funding, which totals \$12.5 million over 5 years, creates a virtual research centre called the 'Behavioral Plasticity Research Institute' (BPRI), which brings together researchers from Texas A&M University, the GLI members at Arizona State University, Baylor College of Medicine, Washington University in St. Louis, University of California Davis, Southern Illinois University Edwardsville, and the United States Department of Agriculture. The BPRI will undertake the most ambitious and wide-ranging investigation of locust phase polyphenism in a generation, using cutting-edge techniques in molecular

biology, physiology and behavioural analysis. Hojun's group has already sequenced genomes for several species, which is a significant achievement given the notorious size and complexity of orthopteran genomes. These genomic data will enable an in-depth gene-expression study across multiple timepoints along the behavioural transition from solitary to swarming, and will enable a comparative approach between different locust species. More details about the BPRI can be found at <https://behavioralplasticity.org/>.

It was unfortunate that, once again, we were unable to meet in person and enjoy the usual displays of live specimens, and Judith Marshall's kind hospitality at the Natural History Museum. Nevertheless, we were pleased to start with over 90 in attendance online, more than half of whom joined us for 'breakout' chats following the talks. The online nature of the SIG also allowed us to hear from many overseas colleagues, and we hope that future SIGs will adopt a hybrid format to maintain the best of both worlds; a global overview of orthopterology, coupled with livestock and a glass of wine!



# Robin Wootton

The Incidental Entomologist

## HONORARY FELLOW INTERVIEW

My fondest memories of Robin are the wonderfully dynamic lectures on insect wing folding mechanisms that he delivered at Plymouth University; once to our students as part of the departmental lecture series and once to a group of artists at a conference on 'Insects and Art'. The giant cardboard structures would spring to life at the slightest flex of Robin's wrist, drawing sounds of incredulity from students and artists alike. Insect origami always wowed.

Robin was one of my first contacts with the society via the excellent day meetings that he held at Exeter University as secretary of the new South West Regional Committee. I remember one in the late 1990s on entomological outreach, a fringe concept at that time but extremely

well attended. It was shortly after this that Robin suggested that I organise meetings in Plymouth and we worked together to make this happen. In 2002 he retired and passed the baton of SW Regional Hon. Secretary to a slightly nervous entomologist from Plymouth with the encouraging words "good luck" and a simple hand shake.

Robin had been on my list of possible interviewees for some time but, as so often in life, his close proximity meant I could talk to him anytime so he was always next on my list. However, the pandemic and my conscience finally raised Robin to the top of the list so I arranged to visit him in his home in Exeter to reminisce over his six decades of investigations into various aspects of insect flight.

## Early life

"Birds were my introduction to the natural world. In Ealing, where I grew up, a friend encouraged me to join the RSPB's Junior Bird Recorders Club. When I was about 10 my godfather gave me 'Birds on the Wing', by John Barlee, which had wonderful photographs of seabirds flying around the coast of Ireland. I still have it. I was fascinated by the beauty of the gulls gliding over the White City stadium, which I watched from the train on the way to school. From that time, I was hooked on flight.

At this stage of my life, I had no expectations to become a biologist. Later, at St Paul's School, I took biology at A level with a vague idea of farming, but was soon converted to zoology by Sidney Pask, a superb, unorthodox biology teacher whose pupils included several who became outstanding scientists, now household names. He organised many trips for us, one of which was to what was then called Rothamsted Experimental Station. On these occasions a staff member would be buttonholed to talk to the visiting youngsters. For us, this was H.F. Barnes, an international expert on gall midges. He told us that entomologists and taxonomists would always be needed and I thought how wonderful it was to be needed!"

## University

"So, in my applications to various universities I put 'entomological taxonomist' as my intended career. This caused great amusement amongst the interview panel at UCL. I discovered later that the panel chair was the Reader in Taxonomy, and an entomologist. He was Richard Freeman, a rather austere scholarly figure who later published the definitive bibliographies of both Charles Darwin and Philip Henry Gosse. He would eventually supervise my PhD.

At UCL I took entomology as my special third-year subject: essentially a systematic tour of the groups, based on the now legendary *General Textbook of Entomology* by A.D. Imms; but this actually inspired me less than had my second-year courses in vertebrate palaeontology. I was particularly fascinated by the application of functional morphology to deduce the ways of life of extinct vertebrates from fossil evidence and, graduating with a first and deciding to do a PhD, I chose to work on insect palaeontology.

There were very few palaeontologists in the world at



Robin as a PhD student c.1959.

that time, but one, F.E. Zeuner, was now Professor of Environmental Archaeology at the Institute of Archaeology, immediately behind UCL. He recommended I work on a spectacular, butterfly-like family of Mesozoic bugs, the Palaeontinidae. Zeuner was not prepared to co-supervise me, and neither Richard nor anyone else in the UK knew much about pre-Tertiary fossils, so I was effectively on my own. There was almost no material in the UK and although I was able to borrow specimens from various European museums, I still needed to expand my topic to other Mesozoic bugs, establishing incidentally that Coleorrhyncha, represented today by the curious Peloridiidae, were the sister group of Heteroptera.

Finding an external examiner was a problem. Entomologists approached “knew nothing about fossils”, palaeontologists “knew nothing about insects”. My eventual examiner, Howard Hinton, devoted almost all the viva to a discourse on Hennigian systematics, the forerunner of cladistics, which he had recently introduced to British entomology. He passed me.”

## Exeter

“I was appointed as assistant lecturer, primarily to teach entomology, in the new, lovely University of Exeter – and

have been here ever since. But continuing in insect palaeontology was a problem. Of the very few active palaeontologists most were in Moscow, publishing exclusively in Russian, and it was clear I would need to learn the language, or visit Moscow, or both. Fortunately, there was a new exchange research programme between the Royal Society and the USSR Academy of Sciences, and I was lucky enough to get one of two annual exchange fellowships to work in Moscow, Leningrad and Central Asia. In the summer, my wife Pamela, who had been in the Diptera section at the NHM, with Harold Oldroyd, came out and joined us in time to go on an expedition collecting insect fossils in Kazakhstan, Kirghizia and Uzbekistan. I believe we were the very first westerners to be allowed on an Academy of Sciences expedition after the war. The sun was baking. No suntan lotion was offered; we have never since been so brown.

Working with the very welcoming Russians was a delight, and their material – mostly wings – was a revelation. At that time insect wings were treated almost exclusively as systematically-useful venation patterns, with no regard to the functional significance of their structure. Working with fossil bug wings, I became aware that they were much more complex than was

generally acknowledged. They had relief, which must have structural value. There were breaks in some veins, which must give local flexibility in flight and might perhaps have aerodynamic significance – but I knew no aerodynamics. On my return I published a few orthodox palaeontological papers, but what I really wanted was to understand what the wings were about. How did they work?

It was clear that to move forward I needed to know a lot more about insect flight. The impetus came when I was invited to contribute a paper on ‘flight and the fossil record’ to the RES symposium on insect flight in 1974. Torkel Weis-Fogh, a brilliant, charismatic Dane who was then *the* authority on insect flight, had just moved to a chair at Cambridge, and I nervously visited him. He listened in silence to my naive ideas about how to approach the problems of wing functioning, then asked: “and where would that get you?!” At lunch in his college he described a completely new aerodynamic mechanism he had discovered by high speed filming of the tiny chalcid *Encarsia formosa*, and he recommended that I get a high-speed cine camera to film insects in free flight, to find out what was happening to the wings, and why.

In the mid-1970s several technical developments coincided to make real progress possible. New high-speed cine cameras allowed the movements of the wings to be studied, and potentially quantified when motion analysis software became available, which provided an inroad into proper aerodynamic analysis. Weis-Fogh’s discovery in *Encarsia* was the first of many aerodynamic mechanisms, completely new to aerodynamicists, which give bursts of exceptionally high lift, allowing insects – including the much-quoted bumblebees – to fly. Another breakthrough was in high-speed still photography. In 1975 Stephen Dalton published *Borne on the Wind*, a superb book of photographs using a high-speed shutter and short duration flash that showed the instantaneous shapes of the wings of a wide range of freely-flying insects in far greater detail than had ever been possible before, and revealed a range of orderly deformations through the stroke cycle. These made clear, as I had suspected from the fossil bugs, that some wing components are adapted for support while others are adapted for controlled deformation in flight to optimise the forces generated. I

Robin on a field trip to Deer Park Farm 2009.



realised that wings are what engineers call 'smart' structures, much of their shape from moment to moment through the stroke being passively determined by their morphology. We could now begin to interpret wing morphology in functional terms, and new instruments, like scanning electron and differential phase contrast microscopy, made it possible to study them in new detail."

## Wings in flight

"I could now see the way forward. The Odonata were an obvious place to begin. I remembered watching dragonflies, demoiselles and coenagrionid damselflies while on student field courses. Three very different flight patterns and three very different wing morphologies – they must be related! We borrowed a high-speed camera and gained access to a scanning electron microscope, and David Newman carried out an

outstanding PhD study, filming the insects flying freely in enclosures in the lab – he was one of the first to do so – analysing the wing movements, studying their morphology in unprecedented detail, mechanically testing components of the wings and making physical models of internal mechanisms which he discovered. This pioneering work established the basic methodologies for all our later work, and Dave's use of paper and cardboard models has proved particularly useful in entertaining demonstrations of the operation of wings at talks and conferences ever since!

The complex aerodynamics involved were beyond us; but Weis-Fogh had recently taken on a brilliant American PhD student, Charlie Ellington, to investigate the aerodynamics of hovering insect flight. David and I went to Cambridge to talk to him. He was welcoming and communicative, but I at least hardly understood a word of what he was

explaining! In a very few years he was leading the world in insect aerodynamics and in due course gained a chair at Cambridge and an FRS. He became a good friend, and our careers ran in parallel from then on, with his group studying the airflow around the wings while we worked on the mechanics of the wings themselves. We only collaborated once, in fun experiments gliding lightweight balsa models to investigate the aerodynamics of the origin of insect flight, but we organised meetings and conferences together, including two at consecutive ICEs, and we exhibited together at the prestigious Royal Society soirees.

In my lab, in the years that followed, we studied the wings and flight of a range of groups: Heteroptera with Clive Betts, Diptera and Mecoptera with Roland Ennos, butterflies with Clive and with Sarah Bunker, and with Chris Smith, Rolf Herbert and two engineering colleagues in a multifaceted investigation of the fascinating hind wings of locusts. Revisiting my palaeontological roots, our work was casting new light on

Robin and parrot near Brisbane, ICE 2004.





adaptive trends in fossil wings, leading to papers on the origin of Diptera and on flight in Palaeozoic Palaeoptera.

For many years, while our work was treated with respect, it seemed to have little impact on either mainstream entomology or in the engineering world. This suddenly changed in the mid-1990s when the United States Department of Defense became interested in developing Micro Air Vehicles – tiny drones, primarily for surveillance in urban warfare. Those of us who worked in insect flight suddenly found ourselves courted for advice and potential collaboration. I was invited to contribute and co-organise a series of joint conferences with robotics engineers and artificial intelligence specialists, and, bizarrely, was visited several times in Exeter by researchers from the US Airforce Research Division! I was close to retirement and never became directly involved, but since then interest in the field of insect flight and wing engineering has rocketed, and I have been astonished – and become disgustingly smug – to find

though ResearchGate and Academia the extent to which our pioneering papers are cited – and possibly even read, especially by engineers.”

## Wing folding models

“Wings don’t just operate in flight, and we had a brief but fascinating digression when Fabian Haas came from Germany to spend a year working with me on hindwing folding mechanisms in beetles. As muscles stop at the wing base, the wonderfully complex folding and unfolding processes of beetle and earwig wings have to be remotely driven and controlled, and again the information for this has to be built into the wings’ morphology. We realised that these were largely achieved by variations in, and combinations of, two basic mechanisms in which four fold lines, three convex and one concave, or vice-versa, meet at a single point. These are familiar to designers of pop-up books and greeting cards, and we suddenly found ourselves in a

completely interdisciplinary world of folding-structure research, talking with artists, mathematicians, chemists, origami masters and even aerospace engineers concerned with opening complex solar panels, aerials etc. in zero gravity way beyond our atmosphere.”

At this point Robin brought out a box of folding models, some of which I remembered from his lectures but some I would not have believed if I had not seen them with my own eyes. A box of magical origami delights indeed. One of these was a very simple paper model that demonstrated how the fly thorax operates to flap the wings.

“I constructed this model shortly after I retired, to show how a flapping machine could be built on insect principles, and produced it at a conference of robotics engineers and insect flight researchers in a beautiful Bauhaus-designed villa overlooking Lago Maggiore. The flying robots on show were so complex, and so clearly expensive, that I feared mine, which was made from three index cards and two elastic bands, would be laughed out of the conference hall, but they loved it, and insisted that the details of how to build the model be included in my paper in the proceedings. Insects use a lovely principle, quite alien to engineers, which relies on the reversible buckling of thin plates. No drones have resulted from my model – yet. They would need linear actuators to replicate the action of the flight muscles. Engineers prefer rotary actuators – cogs, wheels and worms, and they hate buckling.”

## RES

“I joined the RES early in my career but was not particularly involved in the Society’s operation until the regional committees were set up. The first SW Regional Hon. Secretary was Keith Charnley at Bath University who asked me to join his team to organise local events. When he stepped down in 1990, I took over the role, and also began attending more meetings at Queen’s Gate. I was on Council for a while and then was asked to chair the Library Committee, attempting, with mixed success, to introduce temperature and humidity controls and a disaster emergency policy to the library. I stood down on retirement, more or less when the Society moved to The Mansion House.”

Post retirement, both Robin and Pamela are deeply involved with the



Robin, Prawle, 2013.

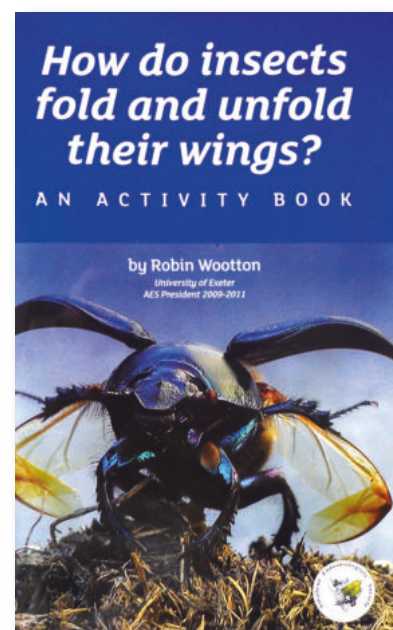


unique Devonshire Association for the Advancement of Science, Literature and the Arts, a venerable society founded in 1862. Its Entomology Section, one of six special interest groups, was launched in 1948 by, among others, A.D. Imms. It holds regular talks and field meetings and annually publishes Devon records of all the major orders. Robin has been chairman and secretary of the Section, chaired the Association for six years, and is currently its President.

Robin has always been a pioneer, a biologist who did much to promote functional morphology and biomechanics in entomology and who has revolutionised our understanding of wings – the structures that above all allowed insects to achieve their dominance and extraordinary diversity. Though perhaps not a mainstream entomologist, he has stepped into areas of insect science that were seen as unfashionable, even uninteresting, and made them vital new avenues of investigation. His

pioneering spirit has also seen him holding meetings on entomological outreach before it was widely recognised by the Society as important – and he also sat at the table at the Society's first ever insect-based dinner. Insect science has finally caught up with him and now recognises the cutting-edge nature of his work. Now 85 and long retired, he is as busy as he has ever been, publishing three papers during Covid: on dragonfly flight, on the geometry of wing deformations and, sadly, the Royal Society Biographical Memoir of Charlie Ellington, who died tragically young in July 2019. The fact that he is an entomologist may be almost incidental to his work, but his contribution to our understanding of wing mechanics cannot be overstated. I sincerely hope that I will continue to have the privilege of witnessing the magic of Robin's models over the years to come.

**Peter Smithers**



For those who would like to explore the alternative universe of folding models, Robin's book *How do insects fold and unfold their wings*, published by the AES, is recommended (available from the AES website [shop.amentsoc.org](http://shop.amentsoc.org)).

# Grant Reports

## Report on an L.J. Goodman Award for Insect Physiology and Behaviour

(also supported by the Arts Council Lottery Project Fund and the University of Central Lancashire)



Supported using public funding by  
**ARTS COUNCIL ENGLAND**



Red admiral, Purple emperor and Adonis blue, a part of the Urban Oasis performing butterfly collection by Neighbourhood Watch Stilts International.  
Image: Paul Miskin.

### Urban Oasis at the Lancashire Science Festival: Pollinating minds and spreading ideas like wild flowers

**Paul Miskin**

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'Urban Oasis' is a science, arts, games and community response to insect depletion, presented by Neighbourhood Watch Stilts International. The RES Goodman Award enabled us to present a supercharged version of Urban Oasis at the Lancashire Science Festival as part of our summer 2022 tour of the north. We aim to accelerate insect regeneration in cities through multidisciplinary, live events.

Humans seem to be hard-wired to experience fear or irritation with insects. Charismatic species like butterflies and bees, and even perceived villainous species like wasps, are great ice breakers at our events. Conveniently, they are also indicators of ecosystem health. Insect conservation opens a door into a mind-bending contemporary revolution in attitudes to nature.

The change of perspective on wasps is good start in developing a new view of nature, hopefully leading to a more flexible mindset. Professor Seirian Sumner, our wasp ambassador, was very popular with the children as a wasp partner in the 'dance of the insects'. At one unforgettable moment she had everyone shouting and chanting O- VI- POS- IT- OR. In our questionnaire, some children claimed to have learned that wasps are better than bees. Of course, Seirian didn't say that, but it wasn't a surprising conclusion given her infectious enthusiasm.

Often, we are not aware of ecosystem services before serious damage has already been done to their providers. Seirian has shown that the ecosystem services of wasps, as well as being underrated by most people, are also under-researched. Without wasps as pest controllers, our future without toxic agrichemicals becomes less certain.

Ordinary people are key to change because they have consumer choices, can influence politicians and change governments. In order to get beyond the often-dry terminology of science, we offer an emotional, imaginative, playful community action, free of gatekeeper vocabulary.

It often seems that children love insects but adults don't. Children are endlessly fascinated by our simulations and this draws the parents in. Art can be a microscope that shows the invisible, and we have discovered that it can also be a time machine for adults to rediscover their inner child.

For further insights, see the following URLs:  
Professor Seirian Sumner's 2 minute talk as a wasp:  
<https://youtu.be/0Haru-sPIUE>

A two-minute video introduction to Urban Oasis:  
<https://youtu.be/3W4D5vB-ETI>

A seven-minute video documentary on Urban Oasis at Lancashire Science Festival 22: <https://youtu.be/I9UI6v9w-0w>

A full presentation on Urban Oasis: <https://tinyurl.com/y7cukmh9>  
An atlas of the future press review: <https://tinyurl.com/bkcdusz4>

# Report on an L.J. Goodman Award for Insect Physiology and Behaviour



## Immense Insects Exhibition at Leeds Museum

### Ed Hall

Entomology collections in museums are often out of sight and out of mind. Some go decades without seeing the light of day, and most are rarely seen by the general public. But this rich biological diversity deserves to be in the limelight, and exhibiting this realm of fascinating creatures is a great way to engage the wider public in exploring a side of the natural world they don't often see up close.

I'm a photographer with an ecology research background, and I've been working on digitally preserving insect specimens for the last few years using high resolution imaging. This work went into creating an exhibition held at Leeds City Museum to showcase insect diversity, anatomy and colouration. It was printed on huge canvases three metres wide and the images were displayed next to the actual specimens. The Royal Entomological Society Goodman Award was key in helping to pitch the idea of an insect exhibition to the museum. By fully funding the printing of the huge insect canvases it really helped get the exhibition off the ground.

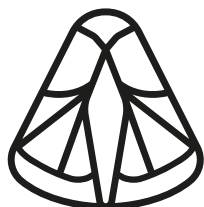
Modern photographic techniques that involve precise computer-controlled equipment, and sophisticated computer processing, allow photographers to create images of tiny specimens on a vast scale. Macro photography of this type requires individual specimens to be scanned by taking thousands of high-magnification images, which are then processed to create the final image. This ensures the full image is in focus, and is of high enough resolution to be printed on a large scale in full detail. Printing them at these sizes was key to my vision of the exhibition: to show visitors insects on a grand scale and give them a new perspective on an aspect of the natural world that they see every day.

I believe it's much more effective to build people's interest in the natural world by simply showing them something they've never seen before, and leaving the rest up to them. Giving people the chance to make their own emotional connections with the natural world is so important, and exhibitions are a great way to achieve this.

Holding the exhibition in an inner-city museum was also key to targeting an audience who might not be inherently connected to nature.

Spanning two months, the exhibition brought in thousands of visitors, most of whom were not insect enthusiasts. I spent some time speaking to visitors, and it was fascinating to hear how people found their own connections to the insects in ways I could never have predicted; from a seamstress who saw similarities between butterfly scales and textiles, to a 3D animator interested in how light reflects off insect wings and bodies, to a lady reminiscing about watching hawk moths in her mother's potting shed as a child. The feedback I received from people of all different backgrounds was great, and I hope the exhibition has had a lasting impact on the visitors who took the time to explore it.





# Royal Entomological Society Insect Identification Service 2021

Jim Hardie Hon. FRES <sup>1</sup>  
Andrew Whittington FRES <sup>2</sup>  
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The RES Insect identification service was busy again in 2021 (Fig. 1). There were 3,412 responses to queries, around 40% fewer than the previous two years but more than 2015–2018. Numbers continued to peak over the same period, June to August (Hardie *et al.*, 2021). Where reliable identification of rare insects and those outside their known distribution range is possible, enquirers are encouraged to report their observations to iRecord. Of course, many of the photographs received are not of good quality. Nevertheless, we are usually able to provide an identification (not necessarily down to species even with superb images) to the satisfaction of the enquirer.

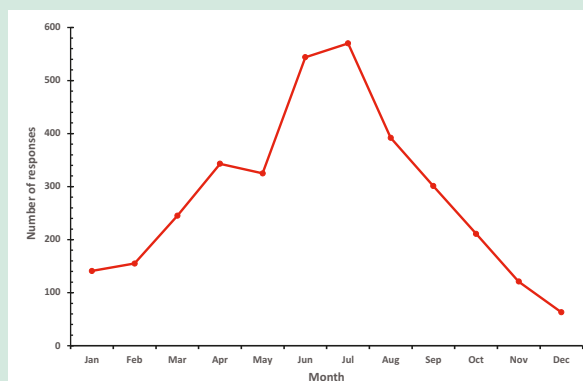


Fig. 1. Monthly responses to insect identification queries during 2021.



Fig. 2. *Graptopsaltria nigrofuscata*.  
Photo by Jess Greville

## ***Graptopsaltria nigrofuscata* (Large brown cicada) (55–60 mm)**

*Graptopsaltria nigrofuscata* (Cicadidae) is a native of East Asia but this one was found by Jess Greville and family on a rainy August day in South Wales (Fig. 2). It was alive on the tarmac drive but didn't survive long. That its appearance was due to long-haul tourism seems unlikely due to Covid-19 travel restrictions and seemingly no exotic plants had been purchased locally. The finding in August coincides with peak numbers reported by iNaturalist in Asia (2021). As far as we are aware, this species has not been recorded previously in the UK and how this one arrived remains a mystery.

## ***Paropsisterna selmani* (Tasmanian eucalyptus beetle) (8–9 mm)**

The chrysomelid *Paropsisterna selmani* was described as a new species in 2013 (Reid *et al.*, 2013) but was first reported from the UK a year earlier with a specimen seen in London. Both adults and larvae cause damage by feeding on leaves of a number of *Eucalyptus* species (Fanning *et al.*, 2013). This one (Fig. 3) was spotted by the Lothian family on a garden bench in Amersham in April and shows the characteristic ring/diamond-shaped pattern on the distal region of the elytra. Two other queries about this beetle were submitted this year with one from the Royal Botanic Gardens, Kew in London (see cover image) and the other from near Newry, Northern Ireland.



Fig. 3. *Paropsisterna selmani*.  
Photo by the Lothian family



Fig. 4. *Pareophora pruni* larva.

Photo by David Wareham

***Pareophora pruni* (sawfly larva)** (5–6 mm)

This rather fine sawfly larva, *Pareophora pruni* (Tenthredinidae), is feeding on blackthorn. It is the only species of this genus in UK and a rare find with just 11 records in the National Biodiversity Network (NBN) Atlas. The individual shown in Fig. 4 was spotted by David Wareham in June near Bournemouth.

***Lymexylon navale* (Ship-timber beetle)**

(7–13 mm)

*Lymexylon navale* is one of two species of ship-timber beetle, family Lymexylidae, found in the UK and is deemed nationally scarce. The larvae are wood-borers and it used to be a notorious pest of ships' timber as well as structural timbers in ports and buildings. These days *L. navale* is more usually associated with ancient woods in Britain south of Manchester although it is widespread in Europe and Asia. *Lymexylon navale* has a fondness for oak and may be found in imported timber.

In March, a concerned SD submitted an image of some insects he had found in his recently refurbished house near Godalming. He described them as long and thin, looking like seahorses as they flew with the body held almost vertically. They were only present in the room which had a new oak purlin installed to create a high ceiling space. These were adult *L. navale* of both sexes (Fig. 5) and a local pest-control company has now managed to control the beetles.

Fig. 5. A female *Lymexylon navale* with others.

Photo by SD

Fig. 6. Male *Machimus atricapillus*.

Photo by Keith Simpson

***Machimus atricapillus* (Kite-tailed robber fly)** (15–20 mm)

A male *Machimus atricapillus* (Asilidae) was photographed by Keith Simpson at Birnie Loch, Fife in August (Fig. 6). The distinctive reddish fore-femur and the ventral spur on the eighth sternite (arrow) are visible. Also on this sternite is a red phoretic mite hitching a ride. *Machimus atricapillus* is widespread in southern Britain with a few scattered records in Scotland but this may be a new record for Fife.

***Eristalis tenax* (Drone-fly)** (10–13 mm)

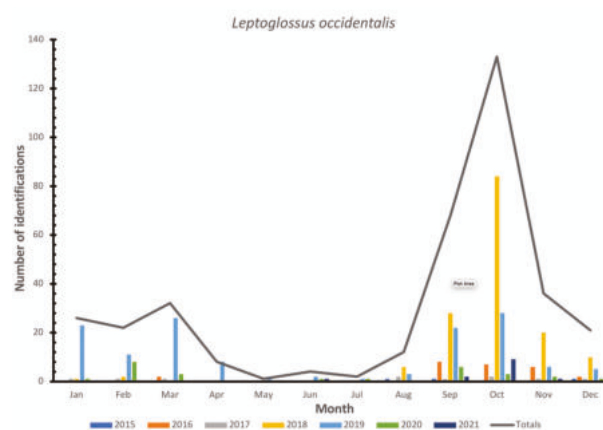
An interesting observation by Llywelyn Owen was recorded on November 17 at a disused slate quarry in Llangynog, Powys. Five drone-flies, *Eristalis tenax* (Syrphidae), had clustered in a dynamite borehole about 355 m above sea level (Fig. 7). This honey bee-mimicking drone-fly is a familiar species that can be seen throughout the year as mated adult females overwinter in buildings, under eaves of roofs, in crevices in trees and walls. They may venture out during winter in clement conditions. This observation is unique in two ways – firstly, communal clustering in a rather limited space (the borehole was roughly 2.5 cm in diameter) and secondly, the altitude is interesting as winter temperatures are low and in January average a low of 0°C and high of 5°C (weatherspark.com).

Fig. 7. *Eristalis tenax*.

Photo by Llywelyn Owen

**Seasonal pattern of queries for the identification of the *Leptoglossus occidentalis* (Western conifer seed bug)**Fig. 8. *Leptoglossus occidentalis*.

Photo by Martin Elsworth

Fig. 9. Identifications of the western conifer seed bug, *Leptoglossus occidentalis*, over the last 7 years.

*Leptoglossus occidentalis* (Coreidae) (Fig. 8) is native to North America. It was first reported in Europe (Italy) in 1999 and later in Dorset, UK in 2007 (Malumphy *et al.*, 2007). The NBN Atlas shows that it is now widespread in England and Wales with scattered reports in Scotland as far north as Shetland. Nymphs and adults feed on flowers and seeds of some 40 conifer species so can reduce seed viability and yields in nurseries. With a body length of 15–20 mm, leaf-like expansions on the rear tibiae and the white zig-zag pattern across the centre of the forewings, *L. occidentalis* is easily recognised, even in images with poor definition. The appearance and noisy flight of this species are impressive enough to catch people's eyes, ears and curiosity, so we get quite a few enquiries. Fig. 9 shows numbers of *L. occidentalis* images submitted to the Society's insect identification service over the past 7 years; numbers fluctuate year on year but they contribute between 0.3% (2015) and 4.9% (2018) to the overall number of responses to queries. This species overwinters as adults and the beginning of the autumn peak seems to coincide with the insects' need to locate suitable sites for hibernation, which can involve entering houses and outbuildings. The elevated numbers in winter/spring, compared with reduced sightings during April–September, may correspond with hibernation in or around houses and population dispersal in spring.

We thank all the Members and Fellows who have helped during the year and in particular Liam Crowley, Andy Salisbury and Helmut van Emden.

The service is appreciated and a response towards the end of the year identifying a lygaeid, ground bug found on a bed elicited the following message.

"Hi Jim. Wow! Thank you so much! I can't believe you responded so quickly, even on Christmas Eve! I was so worried because I have family coming to stay for Christmas and I was worried I might give them bed bugs as a very unwelcome Christmas present! So, your message was the best Christmas present I think I've ever had.

Many, many thanks and Merry Christmas. Rachel".

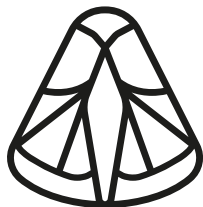
**References**

Fanning, P.D. *et al.* (2014) *Agricultural and Forest Entomology* **16**, 4553.  
Hardie, J. *et al.* (2021) *Antenna* **45**, 93–96.

iNaturalist (2021) <https://spain.inaturalist.org/taxa/325363-Graptopsaltria-nigrofusca> (accessed 21/12/2021).

Malumphy, C. *et al.* (2007). *HetNews* **10**, 2–3.

Reid, C.A.M. *et al.* (2013). *Zootaxa* **3681**, 395–404.



# Royal Entomological Society Schedule of New Fellows and Members

## As at 1st December 2021

### New Fellows

(1st announcement)

Dr Lucy Alford

### New Fellows

(2nd announcement and election)

Prof. Shashi Bhushan Vemuri

Dr Radhika Venkatesan

Dr Catherine Matilda (Tilly) Collins

Dr Vootla Shyam Kumar

### Upgrade to Fellowship

(2nd announcement and election)

Dr Ramasamy Srinivasan

### New Members admitted

Dr Julie Ewald

Mr Paul Ivor Bowman

Dr Kim John Ly

Dr Karen Kloth

Mr Patrick Hugh Beresford Vyvyan

Mr Nigel Semmence

### New Student Members admitted

Miss Sian Katherine Davies

Mr Christian Pulver

Mr Abadi Mashlawi

Mr Avishek Dolai

Miss Stephanie Glendinning

Mr David John Owen

Mr Emeka Emmanuel Ekejiuba

Miss Maria Isabel Silva Torres

Miss Maria Vila Pena

Mr Daniel Lim

Miss Tiffany Lok Tung Ki

Mr Oluwasegun John Jegede

Miss Geeta Devi

Mr Heiloi Yip

Miss Faye Brown

Mr Fidelis Kojo Awotwe

Mr William Jacob Pitt

Mr Alessandro Roman

Miss Aayushi Ashok Sharma

Miss Laura Marcela Martinez Chavez

Mr Serge Christian Bengue

Mr Benjamin Chanda

## As at 7th February 2022

### New Honorary Fellows

Prof. Jim Hardie

### New Fellows (1st announcement)

Dr Frances Hawkes

Dr Vivek Kemparaju

D.Sc Arthur Evans

Dr Francesco Martoni

### New Fellows

(2nd announcement and election)

Dr Lucy Alford

Prof. John William Oman Ballard (as at 1/12/21)

### Upgrade to Fellowship

(2nd announcement and election)

Dr Christoph Öhm-Kühnle (as at 1/12/21)

### New Members admitted

Mr Simon Ward

Mr Robert Spencer

Miss Kate Watkiss

Miss Kerry Barnard

Mr Ken Norman

Mr Keiron Derek Brown

Ms Mairi Carnegie

Mr Samuel Rogerson

Dr Martyn James Wood

Dr Subramanian Sevgan

Dr David Roy

Mr Terry Allen

### New Student Members admitted

Miss Rossina Parvanova

Mr Alexander Borg

Ms Jackline Martin

Miss Emily Jane Hickenbotham

Mr Robert Calvert

Ms Clare Boyes

Miss Lysa Hare

Miss Sophie De Becquevort

Miss Sophie Armstrong-Jordan

Mr Andrew Boardman

Ms Beartice Dale

Miss Qonaah Iilma

Miss Yuqian Huang

Mr Jack Walker

Mr Tiago Fernandes

Mr Archie Mathison

Mr Sen Aniruddha

Mr James Wallace

Mr Ben Hawthorne

### Re-Instatements to Fellowship

Dr Luke Tilley

### Re-Instatements to Membership

Ms Francisca Sconce

### Deaths (Fellows)

Mr Christopher Anselm O'Toole



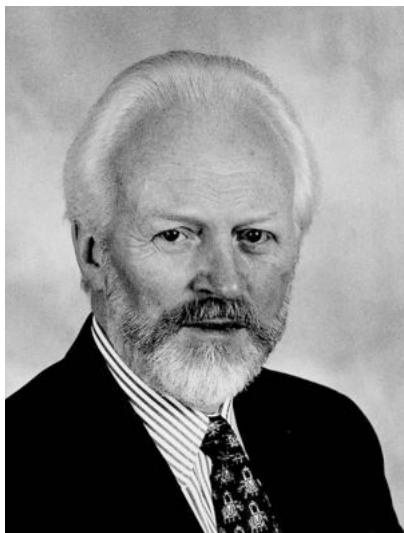


# Obituary

## Professor Walter M. Blaney

27th November 1935 – 22nd October 2020

Jenny Mordue (Luntz)



Walter (Wally) Blaney was Professor of Insect Physiology and Dean at Birkbeck College, University of London, until his retirement in December 1997. He was President of the Royal Entomological Society from June 1997 to June 1998 and was awarded Honorary Fellowship of the RES in 2020. Teaching and research were Wally's joint loves,

starting with his career as a schoolteacher after national service and moving on to research at Birkbeck College after graduating. His research on insect–plant relationships was at the forefront of exciting new areas. Wally was one of the principal movers in initiating the analysis of the complex neuronal signals from mouthpart chemoreceptors and gaining an understanding of how insect taste worked and how feeding decisions by insects are made.

Wally grew up in the countryside on a farm in southwest Scotland and loved biology, developing a knowledge of nature that owed nothing to discipline or order. Insects were a constant fascination and played a prominent role in his career. His teaching role started in a secondary school, teaching maths and English before joining the RAF in 1956 where he taught electronic theory of airborne radar to all ranks in Coastal Command for his two years of National Service. Thereafter followed a teacher-training diploma and the teaching of maths, science, biology and botany, whilst undertaking his own studies, culminating in a BSc in Biology at Birkbeck College in 1967, MSc in Zoology in 1969 and PhD in 1974. He was awarded the Thomas Henry Huxley Award for his PhD work in 1974 by the Duke of Edinburgh for contributions to Zoology. During his years in Birkbeck, Wally taught on the MSc Entomology course, MSc Physiology and BSc courses. His enormous commitment to his students is remembered as a relaxed style, a scrupulous attention to gaining full student participation and always being available for help, advice and discussion.

Wally's initial research was with Reg Chapman on food selection in locusts, involving the modality of taste. At that time the research area of insect–plant relationships was developing in depth and complexity. The mutual dependency of insects and plants for food and pollination coupled with the enormous diversity in plant chemicals and in host plant preferences by insects rendered the study of insect–plant relationships exciting, challenging and

essential for an understanding of crop protection and food security.

Wally worked on insect chemoreception and behaviour, from food selection in locusts to that of serious moth pests such as *Spodoptera* species and many others. He developed an in-depth knowledge of the role of the maxillary palps in gustation using morphological, behavioural and electrophysiological techniques to gain an understanding of diet selection. The polyphagous desert locust *Schistocerca gregaria* was shown to have a high discriminatory ability in plant selection compared with the oligophagous graminivorous African migratory locust, *Locusta migratoria migratoriodes*, due to differences in the presence of excitatory and deterrent/inhibitory receptors within the palp sensillae and the ability to learn from experience. Wally was able to use his wartime experience to build equipment that enabled him to record neural responses from the palp sensilla. The extremely high variability in gustatory receptor responses required detailed analysis of the shape and height of action potentials and led him to an understanding of the sensory coding of phagostimulants and deterrents in the diet selection of phytophagous insects.

Wally built up many key collaborations in his work. At Birkbeck he worked with Reg Chapman where a close collaboration and personal friendship developed which lasted until Reg died; also with Louis Schoonhoven, Wageningen University, who was working on similar studies with the cabbage white butterfly and with Monique Simmonds, Jodrell Laboratory Kew, where over many years they explored the role of antifeedant chemicals in host and non-host plants of several insect pest species. A detailed understanding of the role of plant secondary compounds in feeding deterrence, particularly azadirachtin from the neem tree, was built up in studies with Steve Ley looking at the antifeedant effect of deterrent molecules after the manipulation of key chemical groups.

Wally was on the editorial board of *Entomologia* and was co-editor of *Physiological Entomology*. He gave lectures all over the world, wrote a semi-popular book called *How Insects Live* which was widely used as a text for first year undergraduate students, made films and took part in BBC radio programmes. He was made Honorary Research Fellow at Kew in recognition of his work with Monique Simmonds. His significant contribution to the field was in providing knowledge on insect–plant relationships which, as Lipke & Fraenkel (1956) stated, 'constitutes the very heart of agricultural entomology'.

Wally is missed by his wife Jane and son David. His daughter Rachel predeceased him in 2015. He is remembered by members of the RES as an utterly charming and self-effacing man who was a delight to talk to.

Lipke, H. and Fraenkel, G. (1956) *Annual Review of Entomology* **1**, 17–44.





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# Antenna Reviews



We welcome and thank our new book review coordinator Richard ('Bugman') Jones. Very many thanks to Peter Smithers who has taken this on for countless years. If you wish to recommend a book for review, please contact: [antenna@royensoc.co.uk](mailto:antenna@royensoc.co.uk).

The following reviews have been added to the *Antenna* website:  
<https://www.royensoc.co.uk/publications/book-reviews/>



**Iconotypes: A Compendium of Butterflies & Moths  
or Jones's Icones Complete: An Enhanced Facsimile**

Introduced by Richard I. Vane-Wright.  
In partnership with Oxford University Museum of Natural History.  
Published by Thames & Hudson.  
ISBN 978-0-500-02432-4. £65.00.  
Reviewed by Richard Harrington.



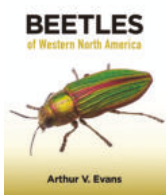
**The Man Who Shot Butterflies**

John Tennent.  
Published by Storm Entomological Publications.  
ISBN 978-0-954-20452-5. £89.00 (plus P&P).  
Reviewed by Richard Harrington.



**British Craneflies**

Alan E. Stubbs.  
Published by British Entomological and Natural History Society.  
ISBN 978-1-899-93509-3. £36.00.  
Reviewed by Richard Jones.



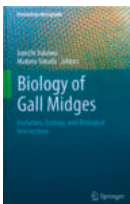
**Beetles of Western North America**

Arthur V. Evans.  
Published by Princeton University Press.  
ISBN 978-0-691-16428-1. £35.00.  
Reviewed by Richard Jones.



**Much Ado About Nothing: A Year Intoxicated by Britain's Rare and Remarkable Moths**

James Lowen.  
Published by Bloomsbury Wildlife.  
ISBN 978-1-472-96697-1. £18.99.  
Reviewed by Richard Jones.



**Biology of Gall Midges: Evolution, Ecology and Biological Interactions**

Edited by Junichi Yukawa & Makoto Tokuda.  
Published by Springer.  
ISBN 978-9-813-36533-9. eBook £95.50 / hardcover £119.99.  
Reviewed by Graham Stone.



# EVENTS

Details of the meetings programme can be viewed on the Society website ([www.royensoc.co.uk/events](http://www.royensoc.co.uk/events)) and include a registration form, which usually must be completed in advance.

Offers to convene meetings on an entomological topic are very welcome and can be discussed with the Chair of the Meetings Committee.

## April 2022

**Fri**  
**1** 1 April - 2 April  
**European Congress on Orthoptera Conservation (ECOC) III**

**Mon**  
**25** 25 April  
**EntoSci**

**Tue**  
**26** 26 April - 27 April  
**Insects as Food & Feed (IAFF) conference (hybrid)**

## May 2022

**Tue**  
**10** 10 May - 11 May  
**Aquatics Special Interest Group & Scottish Regional meeting**

## June 2022

**Mon**  
**20** 20 June - 26 June  
**Insect Week 2022**

## July 2022

**Sun**  
**17** 17 July - 22 July  
**XXVI International Congress of Entomology (ICE)**

## September 2022

**Tue**  
**6** 6 September - 8 September  
**Pollinators in Agriculture meeting in collaboration with the AAB & BES**

**Tue**  
**13** 13 September - 15 September  
**ENTO '22**

## November 2022

**Wed**  
**2** 6 November  
**Orthoptera Special Interest Group**

## October 2023

**Wed**  
**2** 16 October - 20 October 2023  
**XII European Congress of Entomology (ECE)**

**Full details on all RES meetings please visit**  
**[www.royensoc.co.uk/events](http://www.royensoc.co.uk/events)**

Tasmanian Eucalyptus beetle, *Paropsisterna selmani*, see front cover description.



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