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# Antenna



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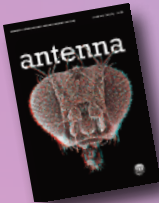
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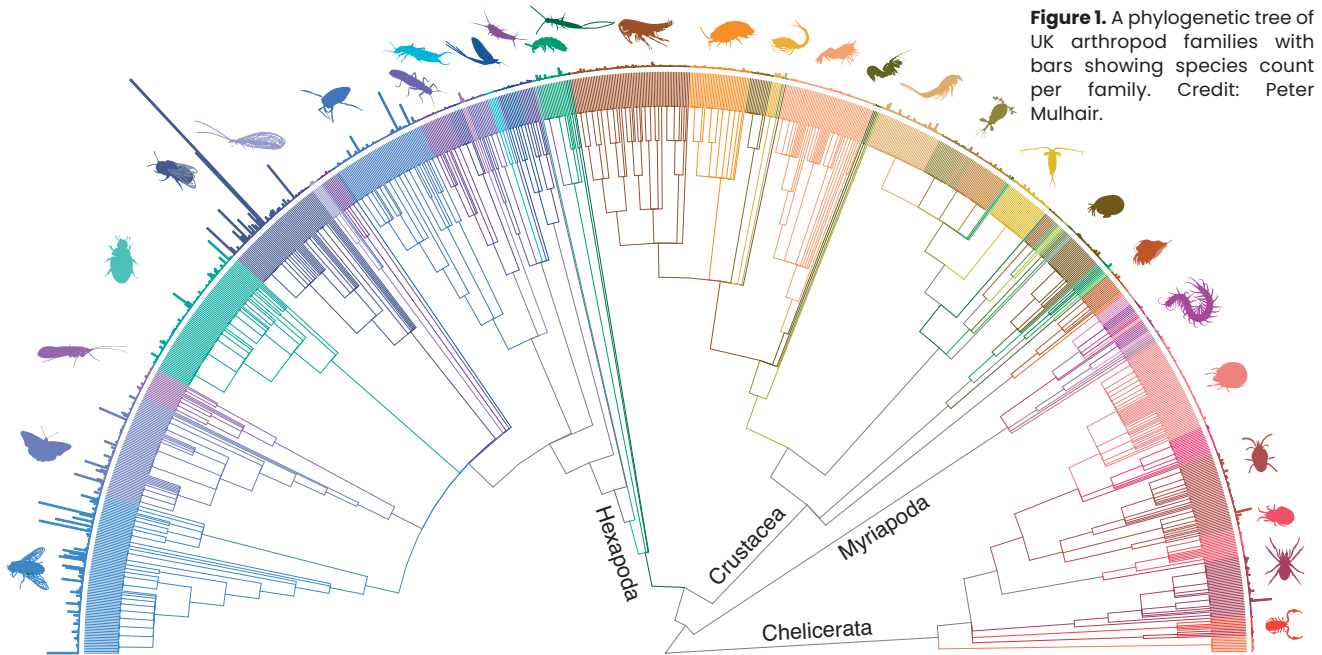
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**Cover Picture:** Twin-lobed Deerfly (*Chrysops relictus*).

Photo: Marc Brouwer; Specially Commended, 2022 Photography Competition (over-18s category).

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**Figure 1.** A phylogenetic tree of UK arthropod families with bars showing species count per family. Credit: Peter Mulhair.

# The Darwin Tree of Life Project: sequencing everything!

Back at the turn of the millennium, a significant milestone was reached in our understanding of biology with the announcement of a first draft of the human genome. This remarkable achievement had taken over a decade and cost somewhere in the region of \$4 billion. Sequencing our genome has revolutionised biomedical science and provided the foundation for many genomics projects, such as the 100,000 Genomes Project (Turnbull *et al.*, 2018). Now it's the turn of every other species.

Commencing in 2020, the Darwin Tree of Life (DToL) Project is an ambitious, groundbreaking project with the aim of sequencing the genomes of every species of eukaryotic organism in Britain and Ireland (Darwin Tree of Life Project Consortium, 2022). It sits within the aspirational Earth BioGenome Project, aiming to sequence every eukaryote on the planet (Lewin *et al.*, 2018). DToL is the first funded effort to attempt to sequence the complete flora and fauna of an entire region. The core of the funding for the project comes from the Wellcome Trust, with additional support from a discretionary award and in-kind funds from partner institutions. One of the reasons why this project is so exciting is because it

is truly trailblazing. Advances in sequencing technologies and exponential decreases in associated costs mean that this is the first time ever that a project of this scale is even feasible.

Naturally, such a gargantuan task requires a huge collaborative effort, which indeed the project has, with involvement from a multitude of organisations with expertise in biodiversity, sequencing, data management and more. The nine core partners are the Wellcome Sanger Institute, Natural History Museum, Royal Botanic Gardens Kew, Royal Botanic Garden Edinburgh, University of Oxford, University of Cambridge, University of Edinburgh, Marine Biological Association and Earlham Institute. The majority of the sequencing itself is undertaken at the Sanger Institute, with the biodiversity focused partners taking on the role of 'Genome Acquisition Laboratories' (GALs), finding, identifying, collecting and preserving samples of all the species. Wytham Woods at the University of Oxford is one such GAL. Based in the university's famous research and education woodland, the Oxford team is aiming to sequence the full genome of every species that occurs within the site, establishing

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it as the world's first 'genomic observatory'.

As well as the production of an unprecedented number of genomes, the project has a set of guiding principles that can be summarised by four 'Cs': Complete, Calibre, Comprehensive and Collaborative. 'Complete' refers to the target of all genomes produced being fully finished, with almost every nucleotide mapped, chromosomally complete and including all nucleic and extranucleic DNA. 'Calibre' describes the quality of genomes being produced. Next-generation sequencing methods, such as long-read sequencing, are being used to produce some of the most accurate genomes ever. For example, the first wave of Lepidopteran genomes produced had N50 values (a way of measuring the lengths of sequence fragments to infer the accuracy of genomes produced) that were in some cases an order of magnitude greater than any produced previously for the group. 'Comprehensive' relates to the coverage of taxa being sequenced, with an aim to eventually sequence every animal, plant and fungus in Britain and Ireland and initially prioritise a breadth of species across the eukaryote phylogeny. Finally, 'Collaborative' conveys how the project is fundamentally open to all. This includes both participation in, and benefitting from, the project. Large numbers of people

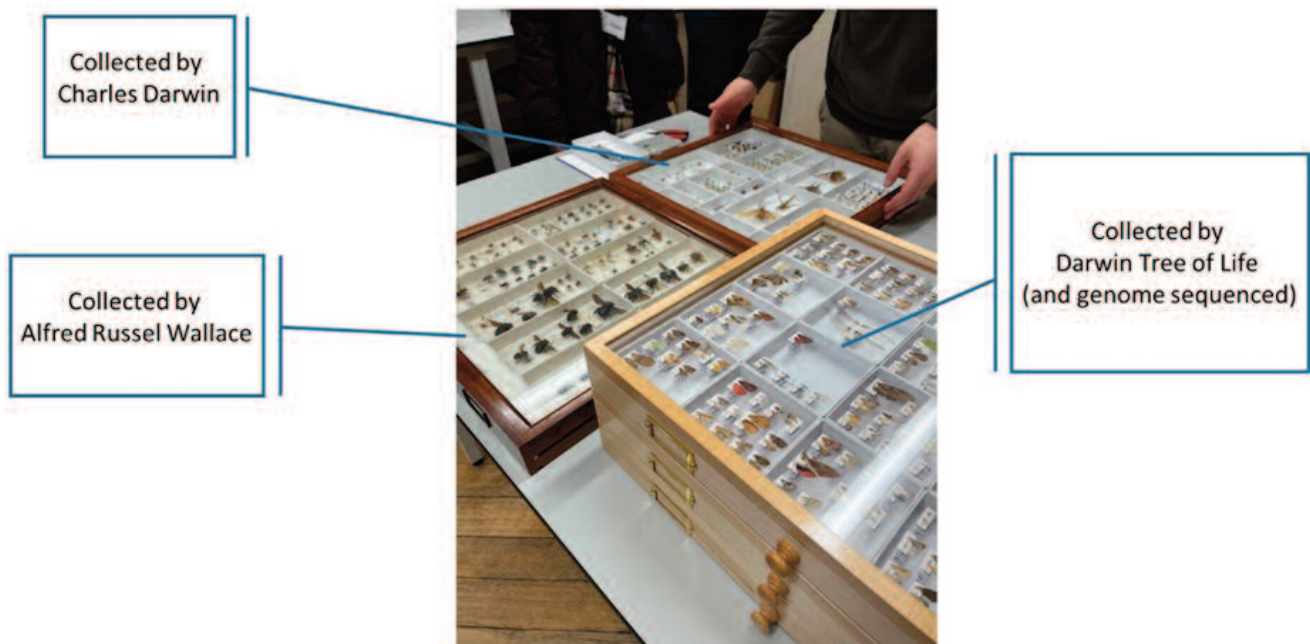
and organisations have, and continue to, contribute to the scheme by suggesting species, assisting with sample acquisition and contributing specimens. All data are also open and freely accessible by anyone, anywhere, even when incomplete. This means that genomes have already begun to contribute to research and conservation efforts around the world, often in unexpected ways!

The question of exactly how many species are included in the overall aim is rather difficult to answer. The UK Species Inventory currently lists more than 70,000 species, although many of these are rare vagrants, introductions restricted to buildings/greenhouses or no longer resident. The project, therefore, applies a remit of including only those species that occur in Britain and Ireland with a self-sustaining, outdoors population (Crowley *et al.*, 2023). This still leaves tens of thousands of species, with some 40% being terrestrial arthropods, especially insects (Fig. 1). The work at the Wytham Woods GAL has focussed on terrestrial arthropods, collecting more than 2,000 species from the site during the first 5 years of the project.

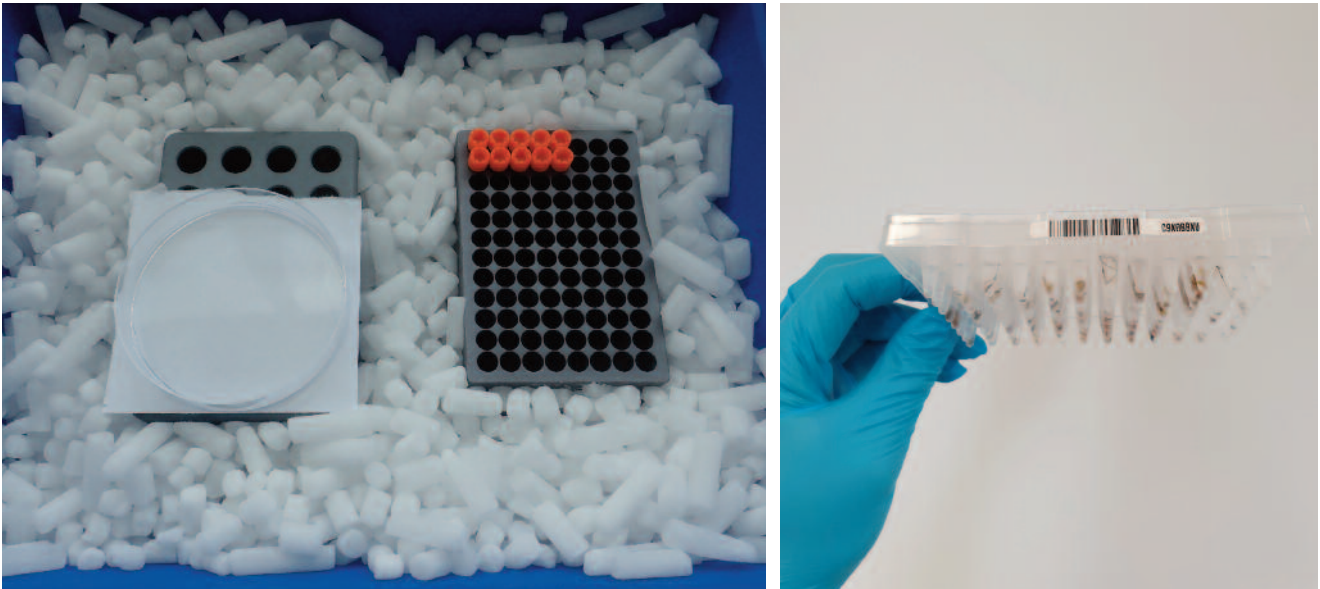
Whilst the ultimate aim is to sequence everything, it is necessary to start somewhere, and we therefore employed a prioritisation process to select species that should be targeted

first. It was important that the first genomes delivered were as useful as possible, so species were prioritised based on a hierarchy of criteria (Crowley *et al.*, 2023). Breadth and depth of sampling maximises the potential for comparative genomic analysis, whilst genomes of specific species are useful for investigations and applied research into those species. Breadth of sampling was achieved by aiming to sequence species from as many different taxonomic families as possible. Depth was delivered by focussing on certain groups for 'deep dives', sequencing as many species as possible from the group. The hierarchy for selecting family representatives and deep dive taxa started with those species/groups that were most important, iconic and/or interesting. For example, hoverflies were selected as a deep dive group as they are economically, ecologically and evolutionarily important and there is an existing research interest, with multiple groups already researching Syrphidae genomics. The following steps in the hierarchy are selection of taxa based on availability, representativeness and relative ease of sequencing.

But what is genome sequencing and how does it work? When we say "genome sequencing", we are talking about creating a reference genome. A reference genome is a complete record of the DNA sequence of a representative



**Figure 2.** The macro-Lepidoptera wings genomic voucher specimens in the Oxford University Museum of Natural History, next to collections from Charles Darwin and Alfred Russel Wallace. Credit: Peter Holland.



**Figure 3. Left:** The cryogenic preservation system used by several GALs, bathing specimens in pellets of dry ice to flash-freeze them at  $-80^{\circ}\text{C}$ . **Right:** A 96-well plate with legs dissected from specimens for DNA barcoding. Credit: Liam Crowley.

individual of a species. Therefore, where possible it is useful to keep some form of voucher specimen from the individual sequenced to act as a ‘genomic type’ specimen. For example, a set of wings (usually the right-hand set) has been kept from all the macro-Lepidoptera sequenced from the Wytham Woods GAL, which are now kept in the Oxford University Museum of Natural History (Fig. 2).

DTol is using long-read sequencing technology to produce high-quality genomes. Much like how a jigsaw with a few large pieces is much easier to assemble correctly than one with many small pieces, the same is true for assembling sequences of DNA into a genome. This is especially true given the highly repetitive nature of genomes, whereby repeats of sequences can be missed by sequencing smaller reads.

One of the implications of long-read sequencing is the requirement it has on how samples are collected and preserved. DNA is a remarkably unstable molecule, constantly breaking from the wear and tear of everyday life in a cellular environment. Normally, this is not an issue as cells contain repair machinery that continuously repairs DNA (remarkably accurately almost all of the time!). However, once an organism dies this machinery ceases to work, meaning that within minutes DNA begins to break down into shorter segments that are not usable in long-read sequencing. The result

of this is that in order to collect high molecular weight DNA for genome sequencing, we need to instantaneously preserve it in long fragments. This is achieved by flash-freezing live or recently live samples at  $-80^{\circ}\text{C}$  (or colder) using dry ice (or liquid Nitrogen) (Fig. 3). The consequence of this is that once frozen, samples must be maintained at this temperature in a continuous ‘cold-chain’ until DNA can be extracted and sequenced.

Perhaps a more significant constraint resulting from the requirement of flash freezing live specimens is that this makes species identification by traditional morphological methods challenging. Ideally, identifications need to be made on live specimens that can then be flash-frozen, which for the majority of the British list is extremely difficult. Fortunately, we have developed a few ways to deal with this issue. Firstly, we began with species that could reliably be identified in the field, e.g., many macro-moths. For many taxa where this is not possible, temporary knockdowns using either  $\text{CO}_2$  or low temperatures to incapacitate specimens for a short period of time to allow ID using a stereomicroscope have been very successful. Other groups have been identified by removing key pieces of morphology as the specimen freezes and identifying this later. This is typically male genitalia but can include various diagnostic features that can be easily dissected.

Every specimen that is submitted for genome sequencing also undergoes DNA barcoding (Twyford *et al.*, 2024) (Fig. 3). This is undertaken for two reasons: 1) as an insurance against error – the DNA barcode region of the resulting genome can be checked against the original barcode to ensure that no mix-ups have occurred; 2) as a confirmation of ID – the barcode can be checked against barcode reference libraries to determine if the specimen matches against the putative taxon.

Once a genome is completed for a species, a ‘genome note’ micro publication is written and released in the journal Wellcome Open Research (e.g., Crowley *et al.*, 2022; Hawkes *et al.*, 2023). This serves as an announcement of the successful completion and release of the genome as well as containing information on the natural history of the species and details of the sequencing process and features of the genome.

To date, the project has collected over 9,000 species, started sequencing over 6,000 and finished over 2,000 genomes (Fig. 4). Globally, 50% of all high-quality genomes sequenced come from this project. Furthermore, a ‘genome engine’ of methods and processes has been developed, that is now being used by various genome sequencing initiatives around the world such as the Aquatic Symbiosis Project, European Reference Genome Atlas, Project Psyche and AEGIS that are collectively sequencing



**Figure 4.** Fieldwork collecting specimens of insects for genome sequencing at Wytham Woods. Credit: Liam Crowley and Luke Lythgoe.



**Figure 5. Left:** One of the two adult female Large Blue butterflies (*Phengaris arion*) collected and preserved for genome sequencing. **Right:** An adult Large Blue butterfly in situ at Daneway Banks nature reserve. Credit: Liam Crowley.

around 12,000 species.

The arrival of the quantity and quality of genomes produced by DTOL is revolutionising bioscience, both in terms of discovery science and enabling science. Reference genomes are quickly becoming an essential component of the 21<sup>st</sup> century biology toolkit, facilitating myriad methods of investigation from evolution to physiology, from ecology to behaviour. Examples include resolving difficult phylogenies where existing markers are insufficient, examining genome structure such as karyotypes and studying the evolution of genes and gene families (e.g., Mulhair *et al.*, 2023a, b).

One of the most powerful applications of whole genomes is in the field of comparative genomics. High-quality genomes from different species can be compared and differences examined. For example, recent work by the University of Oxford DTOL team looked at rates of evolution and gene duplication across Lepidoptera. One intriguing case of gene duplication involved the Lipocalin gene superfamily. A subgroup, the bilin-binding proteins (BBP), are present in all

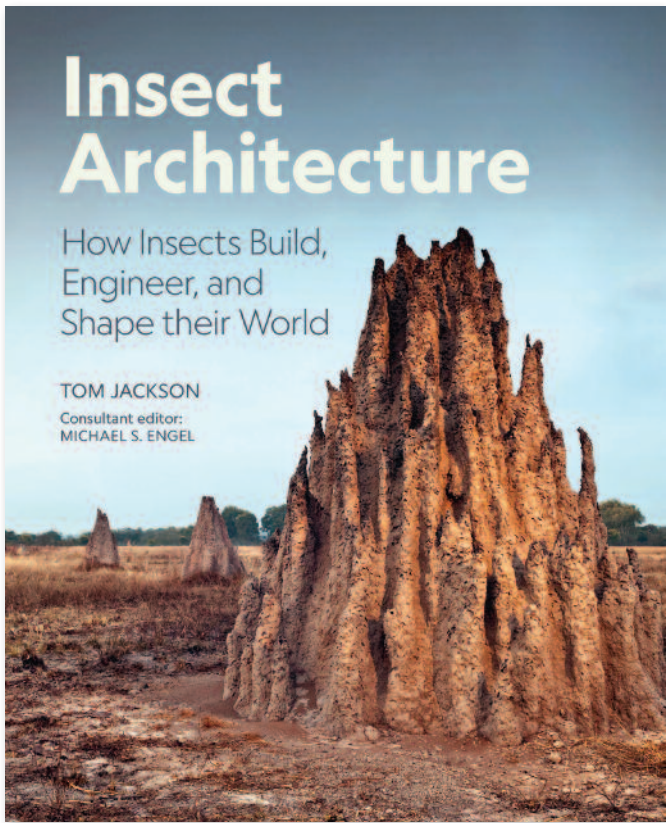
Lepidoptera and are involved in binding the pigments responsible for blue colouration. Interestingly, this subgroup underwent extensive duplication within the Lycaenidae family, which contains 'the blues', with as many as 24 copies in some species! The large and consistent duplication of BBP in Lycaenidae may be linked to the blue colouration of many species, providing a potential answer to the question 'how did the blues become blue?'. Another area where full genomes are incredibly useful is in conservation population genetics. The Large Blue butterfly (*Phengaris arion*) is the current focus of conservation efforts in Britain following the successful reintroduction in Somerset and Gloucestershire. As populations of this species grow and spread, it is important that we understand their genetic make-up, for example to determine if interventions are required to safeguard genetic diversity. A reference genome is a vital pre-requisite for identifying suitable marker regions to enable targeted sequencing of multiple individuals. Two adult females were collected from Daneway Banks in 2022 (under licence), and the resulting

genome released in 2024 (Meredith *et al.*, 2024) to facilitate this important work (Fig. 5).

Whilst the first phase of the DTOL project has come to a close, sequencing continues, with thousands of additional genomes expected to be produced over the coming years. This data avalanche will unlock many different opportunities for genome-enabled research as well as practical applications, revolutionising biodiversity science.

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