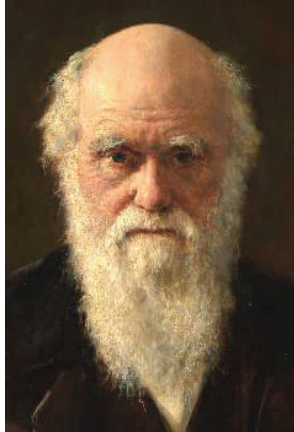


The Driving Forces of Evolution: From Darwin to the modern age

Thursday 3rd and Friday 4th July 2008



Programme and Abstracts



In the early 1930s the synthesis of Darwinian natural selection, mutation and Mendelian genetics gave rise to the paradigm of “modern Darwinism”, also known as “neo-Darwinism”. This has contributed greatly to our understanding of evolutionary change. But increasing knowledge of other forces, such as symbiogenesis (including our growing understanding of the role of virus-host interactions), hybridogenesis, horizontal gene transfer in prokaryotes, epigenetics, and events specific to evolutionary development, all variously coupled to natural selection, have widened our horizons to a diversity of evolutionary possibilities.

In celebration of the 150th anniversary of the presentation of Darwin’s theory of evolution to the Linnean Society of London, in July 1858, we have brought together experts from these key arenas to present a more comprehensive explanation of how, in Darwin’s own words, ‘endless forms most beautiful and most wonderful have been, and are being, evolved’.

Programme

Day 1, 3rd July

09.00 Arrival and registration

09.30 Welcome and introduction by **David Cutler**, president of the Linnean Society of London

Session 1: Chair, **Hugh Dickinson**

09.35 **Lynn Margulis** - *Origin of Eukaryotes in the Proterozoic Eon: Symbiogenesis in the Sulfuretum*

10.20 **Jan Sapp** - *Evolution Reconsidered: On the Origin of Kingdoms*

11.05 Coffee

11.30 **Eva Jablonka** and **Marion J. Lamb** - *The Role of Epigenetic Variation in Adaptive Evolution*

12.15 **Hugh Dickinson** and **Robert Grant-Downton** - *Epigenetics in Plant Evolution*

13.00 Lunch

Session 2: Chair, **Loren Rieseberg**

14.00 **Loren Rieseberg** - *The Role of Hybridisation in Plant Evolution*

14.45 **Barbara Mable** - *Hybridisation in Animals: Why Should Only Plants Have Flexible Reproductive Systems*

15.30 Tea

16.00 **Mauricio Linares** - *Homoploid Hybrid Evolution in Heliconius butterflies*

16.45 Summary and close

The meeting will be followed by a reception in the Library and an optional dinner.

Abstracts

Day 1, 3rd July

Origin of eukaryotes in the Proterozoic Eon: symbiogenesis in the sulfuretum Lynn Margulis

We present a plausible evolutionary scenario: members of at least two bacterial higher taxa (prokaryotes) merged in the origin of the first nucleated organisms to form eukaryotes (e.g., protocists, animals, fungi, plants). Symbiogenesis generated the earliest protocists under sulfurous conditions as the concentration of atmospheric oxygen increased. Eukaryosis, the origin of nucleated cells, occurred by the middle Proterozoic Eon, prior to the deposition in sediments of well-preserved microfossils such as *Vandalosphaeridium* (Vidal, 1998) or the spiny spheres in the Doushantou cherts of China (Knoll, 2003). The defining seme of

eukaryosis, the membrane-bounded nucleus as a component of the karyomastigont, evolved as *Thermoplasma*-like archaeobacteria and *Perfiel'va-Spirochaeta*-like eubacteria symbiogenetically formed the earliest amitochondriates: LECA, the last eukaryotic common ancestor of all nucleated organisms. Extant descendants of such amitochondriate cells (Archaeoprotista such as *Mastigamoeba*, *Mixotricha*, *Pelomyxa* or *Trichomonas*) thrive in organic-rich anoxic habitats where they are amenable to study.

Evolution reconsidered: on the origin of kingdoms

Jan Sapp

The study of microbial phylogeny and evolution, over the past three decades, represents an interdisciplinary synthesis divergent in both methods and concepts from the classical evolutionary synthesis of the 1930s and 1940s. The deployment of macromolecular sequencing to microbial classification has provided a deep evolutionary taxonomy hitherto deemed impossible. Microbial phylogenetics has greatly transformed the landscape of evolutionary biology, not only in revitalizing the field in the pursuit of life's history over billions of years, but it has also transcended the structure of thought that has shaped evolutionary theory since the time of Darwin. A trio of primary phylogenetic lineages, along with the recognition of symbiosis and lateral gene transfer as fundamental processes of evolutionary innovation, are core principles of microbial evolutionary biology today. Their scope and significance remain contentious among evolutionists.

The role of epigenetic variation in adaptive evolution

Eva Jablonka and Marion J Lamb

Most of the problems about the nature and origin of heritable variations were thought to have been solved when genetics became part of the Evolutionary Synthesis of the 1930s and 1940s. In that Synthesis it was assumed that heritable variation depends on random gene mutations with small effects. The inheritance of developmental variations was deemed to be impossible, and was explicitly excluded from the Synthesis. Development was thought to have no direct effect on heredity, and therefore no direct effect on evolution.

We believe that the rise of epigenetics during the 1990s has necessitated significant changes in the gene-centred view that dominated 20th-century evolutionary thinking about variation. Epigenetics influences evolutionary theory in two ways: first, it shifts the focus from single genes to phenotypes and

developmental networks; second, it demonstrates that heritable phenotypic variations may be independent of DNA variations, and that the origin of such variations may be developmental.

In our talk we will explore the concepts of epigenetics and epigenetic inheritance from a historical point of view, and outline some of the epigenetic routes through which variations can be transmitted from generation to generation. Our main focus will be on cellular epigenetic inheritance, which is ubiquitous, but we will also consider how animals transmit variations through behaviour. We maintain that all types of non-DNA variation have been important in adaptive evolution, and we will use domestication to illustrate the interplay between genetics and epigenetics in epigenetically driven evolution.

Although an epigenetic approach to evolutionary problems – an approach that emphasizes phenotypes and plasticity rather than genes and gene shuffling – is not incompatible with the Evolutionary Synthesis, the inheritance of epigenetic variations is a direct challenge to it. The old Synthesis and most 20th century theorizing denied a role for Lamarckian processes in evolution, but epigenetic inheritance means that Lamarckian processes are significant, and under certain conditions can lead to targeted and saltational changes. We therefore believe that the Synthesis no longer provides an adequate theoretical framework for evolutionary biology, and that epigenetic inheritance has to be an important component of the new, 21st-century, evolutionary synthesis.

Epigenetics in Plant Evolution

Hugh Dickinson and Robert Grant-Downton

In plants, transgenerational inheritance of epigenetic information is a genuine, if not well-studied, phenomenon. Inheritance of epigenetic information can be seen in situations such as endosperm imprinting, paramutation and meiotically stable epialleles. Additionally, disturbed epigenetic states in interspecific and interploidy hybrids, some of which may be heritable, have been revealed by several recent studies. However, apart from DNA methylation, little is known about what kinds of epigenetic marks and epigenetic information are heritable in plants. The implications for stable or even metastable epigenetic variation in plant genomes generating phenotypic variation and related phenomena such as hybrid vigour and phenotypic plasticity remain to be fully appreciated. As a consequence, the potential importance of transmission of epigenetic information on the evolution and adaptation of plant populations is probably underrated. Technological advances in high-throughput 'epigenomic' technology are likely to reveal their influence and alter our view of plant evolutionary biology.

The role of hybridization in plant evolution

Loren Rieseberg

Hybridization can have a diversity of possible outcomes. Outcomes that lead to increased biodiversity include the development of extreme or novel adaptations and the origin of introgressive races or hybrid species. In addition, it has been suggested that hybrid zones may serve as focal points of biodiversity and represent centers of abundance for normally rare species. Alternatively, hybridization may reduce biodiversity when species are assimilated by congeners or weakened by outbreeding depression, in which mean fitness and population size decline due to gamete wastage in the formation of unfit hybrid individuals. Consequences of hybridization with less direct effects on species diversity include reinforcement of preexisting reproductive barriers, the introgression of adaptive or neutral traits across hybrid zones, and the maintenance of stable hybrid zones.

I will first review theoretical studies that predict the likely frequencies of these different outcomes and then compare expectations with what we know from empirical investigations. I will then highlight studies of wild sunflowers that illustrate how hybridization can lead to the release of cryptic phenotypic variation and thereby facilitate adaptation and speciation. Lastly, I will describe a new method for identifying ancient hybrids through analyses of a single genome, as well as several surprising discoveries resulting from the application of this approach to a wide range of plant and animal species.

Hybridization in animals: why should only plants have flexible reproductive systems?

Barbara K. Mable

The appeal of the biological species concept is that it provides a simple and testable criterion by which to classify individuals into species. Although there are a number of variants to the original definition, the basic idea is that reproductive isolation is the critical defining feature of a species. Under the strictest version of this view, viable hybrids between species should thus be a conceptual impossibility. Although this basic type of concept was also prevalent in the time of Charles Darwin, he was fascinated by hybridization (although he was concerned more with relative fertility of different types of crosses than he was with what they might say about species definitions). His experimental data on crosses in plants and domestic animals convinced him that inability to cross is often completely unrelated to “systematic affinity”. Nevertheless, he was perplexed that whereas hybridization could create individuals that were

superior to their parental types, this was often rendered an evolutionary dead end by sterility of even very vigorous hybrid individuals. He was thus left with an overall negative view of the role of hybrids in speciation and evolution.

The birth of Mendelian genetics opened the opportunity to re-evaluate the consequences and benefits of hybridization. Botanists have long accepted that plants have extraordinary flexibility in their reproductive systems and that hybridization, while inconvenient for defining independent lineages, is an important creative evolutionary force. Animals have not been given as much credit for reproductive flexibility and animal biologists have been more reluctant to deviate from the “hybrids as mongrels” view. However, this is not a realistic view in the post-genomic era. It is already apparent that dramatic genomic changes such as whole genome duplication are much more frequent in animal evolution than previously considered and the tools now exist to document the extent of historical hybridization events as well. Already techniques such as genomic in situ hybridization are revealing that previous rules about genetic compatibility are too rigid to explain observed patterns and that epigenetic changes can no longer be relegated to the realm of interesting anomalies. The purpose of this talk is to set a historical context for views on hybridization in animals as compared to plants and to review modern evidence for the role of hybridization in animal evolution.

Homoploid hybrid evolution in *Heliconius* butterflies

Mauricio Linares

Speciation is generally seen as resulting from the splitting of a single lineage. An alternative is hybrid speciation, considered to be extremely rare, in which two distinct lineages contribute genes to a daughter species. Here we shall compare three cases in which hybridization may have contributed to speciation and wing colour pattern diversification from the eastern Andes of Colombia: *Heliconius heurippa*, *Heliconius tristero* and *Heliconius* sp. nov. We shall present evidence from several sources: geographic distribution, adult and larval morphology, molecular markers, and genetic and behavioural experiments. Although the role of homoploid hybrid speciation has been profoundly studied in the case of *H. heurippa* from Villavicencio, it is quite likely that hybridization, with the closely related *H. melpomene*, has also provided major colour pattern genes for wing pattern divergence in all three taxa. It is especially puzzling how *Heliconius tristero* and *Heliconius* sp. nov may have evolved close Müllerian mimicry with *H. melpomene* in Mocoa and Florencia, respectively, given that wing colour pattern appears to be very important for mate recognition in these butterflies.

Programme

Day 2, 4th July

09.30 Arrival and welcome

Session 1: Chair, Luis Villarreal

09.35 **Frank Ryan** - *Viruses as Symbionts*

10.20 **Luis Villarreal** - *The role of Virus in Host Evolution: Haystack Models From a Viral Perspective*

11.05 Coffee

11.30 **Marilyn Roossinck** - *RNA Viruses in Symbiosis and Symbiogenesis*

12.15 **Erik Larsson** - *Evolutionary Aspects of Human Endogenous Retroviruses (HERVs), Based On Their "Activities" in Human Tissues*

13.00 Lunch

Session 2: Chair, Frank Ryan

14.00 **Michael Syvanen** - *Gene Transfers During the Metazoan Radiation*

14.45 **Donald Williamson** - *Larval transfer and the Cambrian Explosion*

15.30 Tea

16.00 **Lynn Riddiford** and **James Truman** - *Molecular and Endocrine Perspectives on the Evolution of Metamorphosis in Insects*

16.45 Summary and close

Abstracts

Day 2, 4th July

Viruses as symbionts

Frank P Ryan

Until recently biologists have not considered viruses as potential symbionts. In large part this has resulted from a series of misunderstandings about viral complexity, behaviour and evolution. The consequences have been detrimental to evolutionary biology, with a wide diversity of symbiogenetic evolution ignored or misinterpreted. I propose to address these misunderstandings and thus formally define the role of viruses in symbiosis.

Over the last decade or so, we have become increasingly aware that viruses play a subtle and complex role that can have a profound influence on the evolution of

their hosts – indeed we now believe this has been a key factor in the evolution of most if not all of life. All viruses are parasites, in the sense that they cannot survive, or reproduce, without the involuntary assistance of their hosts, but all such parasitic relationships come within the wider definition of symbiosis. Indeed, viral symbiosis extends much further than parasitism. One factor viruses can bring to a symbiotic partnership is aggression, so it is not altogether surprising that certain viruses play an important role in “aggressive symbiosis”. This is a feature of plague viruses, such as smallpox and HIV-1, as in the myxomatosis that almost exterminated rabbits in Australia, and it changes the host species genotype through “plague culling”, which can lead to coevolution of virus and host. But perhaps the most important contribution of viruses to symbiogenesis is at the genetic, and indeed, whole genomic level, for example the endogenous retroviruses that have invaded genomes as early as the marine invertebrates, giving rise to a novel virus-host holobiont.

In probing how viral symbiosis, and more particularly virus-host holobiontic evolution, works, we need to examine the application of natural selection to such partnerships as a whole. The arena of viral-host symbiogenesis is conceptually new and offers major potential for future research. I shall offer some suggestions that might interest future generations of evolutionary biologists.

Role of virus in host evolution: haystack models from a viral perspective

Luis P. Villarreal

Virus evolution involves a form of group interaction (quasispecies) in which overall viral fitness (survival) is determined by the interaction and dynamics of individual genomes. This is a form of social selection. Persistence of virus in specific host can also be mediated by such interactions when defective genomes regulate infectious virus. Such states are prevalent in nature. However, viral persistence can also be considered an epigenetic host state that can affect host specific group survival by killing those that are not colonized. The concept of group selection was rejected following the 1966 book by G. Williams. Maynard Smith (1964) presented a model of cooperative group behaviors in populations (i.e. altruism), in which he used a ‘haystack’ model that were initially colonized by individual mated females to estimate frequencies of ‘altruistic’ genes. Historically, however, a role for virus (persistence) in group behavior or selection has not been considered.

However, biologists who maintain real colonies of mice are well aware of the crucial importance of viruses. Previously, I have asserted that the colonization

and persistence of genetic parasites can involve ‘addiction’ strategies in which survival of persistently infected groups (defined by transmission potential) is forced by the potential of the same parasite to kill uncolonized host groups. All wild population of *Mus musculus* are known to be persistently infected with various viruses (both genomic and epigenomic). Here I examine a haystack model of group selection from the perspective of persistent virus and argue that group selection is the expected outcome of such viral persistence. Other possible examples of such a relationship will also be presented.

RNA viruses in symbiosis and symbiogenesis

Marilyn Roossinck

Viruses are most often thought of as antagonistic (pathogenic) symbionts, but that is only one lifestyle alternative. This bias is predominantly due to a lack of knowledge about non-pathogenic viruses that have gone almost completely unstudied. However, viruses can be mutualistic symbionts of their hosts, and can play critical roles in adaptation of their hosts to ecological niches. For example, in geothermal soils a virus, a fungus and a plant are all involved in an obligate mutualistic symbiosis that allows them to survive an adverse environment. In plants several RNA viruses display a conditional mutualism under extreme conditions such as drought or cold. In addition, symbiosis is seen in mixed infections, where some viruses can interact and affect the evolution of other viruses in the same host.

These interactions can lead to symbiogenesis, or the generation of new species by the combining of two symbiotic entities. Symbiogenesis has been a predominant driving force in the evolution of plant viruses, as evidenced by phylogenetic analyses. Phylogenetic studies also imply that many plant viruses have acquired genes from their hosts, another form of symbiogenesis that has been important in their evolution. These studies are helping us understand how symbiogenesis works and its role in the deep evolution of RNA viruses and virus-host interactions.

Evolutionary aspects of human endogenous retroviruses (HERVs), based on their “activities” in human tissues

Erik Larsson, Fredrik Ponten and Jonas Blomberg

During evolution several exogenous retroviruses have been introduced into our genome by infections, resulting in a considerable amount of HERV “genetic load”. Depending on definitions, as much as 8% of our genome consists of

HERV sequences. These sequences are all inactivated at different degrees and at different levels by mutations, deletions, epigenetic silencing or recombination. HERV sequences were introduced into our genomes roughly between 100 and 5 million years ago. After primary infection and before fixation into the human genome (endogenization process), retroviral genome copy numbers often increased by proliferation, reinfection and retrotransposition. In contrast to other species, there is no known complete HERV-genome with the ability to encode a fully replication competent retrovirus. However, recently introduced HERVs, such as HERV-K, tend to have less mutations and a subset of these could probably transpose and interact with other genes.

Through successful sequencing of several different genomes it is now possible to obtain information regarding “unique” HERV integrations in humans, as also the chimpanzee genome is identified. Interestingly, several HERVs retain open reading frames (ORFs), strongly indicative of a function.

Putative functions of HERVs in human tissues include a) shaping the genome, b) controlling human genes by providing alternative promoters (usually single LTRs) and c) “hijacking” viral structural proteins and using them for important normal functions. In reproductive tissues such functions could be exemplified by the integration of the syncytin gene from HERV-W, others are in the immune system, brain development and as a host defence against hazardous exogenous retroviruses by receptor blockage. There is a growing body of evidence that an insufficient control of HERV activity is involved in initiation of certain human diseases, such as autoimmunity and cancer. In my talk, I shall give a general background on HERV-genomes, regarding classification, phylogeny and expression, with a focus on recently obtained data on protein expression in human normal and diseased tissues, as determined by using an antibody based proteomics strategy (according to HYPERLINK <http://www.proteinatlas.org>). I shall try to integrate the data in an evolutionary context.

Gene transfers during the Metazoan Radiation

Michael Syvanen

The Cambrian radiation has puzzled biologists for the past 150 years and Darwin was quite aware that his theory had difficulty explaining the suddenness with which all of the metazoan phyla appeared in the fossil record. Recent comparative sequence analysis as well as paleontological studies of Ediacaran fossils supports the idea that diversification of some of the phyla may

have already begun about 40 MY before the Cambrian. These results suggest that the emergence of the metazoan phyla might not have been as sudden as previously assumed. However an earlier diversification would underscore another longstanding puzzle concerning the Cambrian radiation, which is the widespread occurrence of parallel evolution. Molecular evolutionary studies have for the most part supported taxonomic relationships based on comparative anatomy and embryology, but have not as yet shed light on the puzzles posed by the fossil record. When I first started thinking about the evolutionary implications of horizontal gene transfer, it seemed quite natural to suggest that gene transfer between phyla could explain the phenomena of both the speed and observed parallelisms of the Cambrian radiation (see paper 1 at <http://www.yvm.net/vme/hgt/>). If this explanation were correct, then there should be evidence for such transfers in genomic sequences.

The complete genomic sequences of species from five metazoan phyla are currently available. In this talk, the results of whole genome comparisons will be presented. There are about 3000 genes with sufficient information content to enable construction of 3000 gene trees. By analyzing four taxa at a time, each of these trees can be defined by certain metrics that permit the computation of averages with characteristic variances. In addition, these data are amenable to molecular clock calculations. For most of the phyla, a picture emerges that is consistent with the traditional expectations of metazoan evolution, though the diversification appears to be somewhat earlier than would be predicted from paleontological evidence. However, there is one major taxonomic group whose genome sequence places it significantly outside of the phylum to which it had been traditionally assigned. In addition, the variance about the average which places it outside of its assigned phyla is much greater than the variances seen with the other taxa. This latter result is most easily explained by postulating that this taxonomic group contains genes from two different phyla that fused either by a multiple gene transfers or possibly a trans phyla hybridization event.

Larval transfer and the Cambrian explosion

Donald Williamson

Most biologists have followed Darwin in assuming that adult animals and their larvae evolved from the same genetic stock (the 'same-stock' theory), and much of 'evo-devo' is based on this assumption. I, however, believe that the basic forms of larvae originated as adults in other taxa and were transferred by hybridization (the 'larval transfer' theory). Larvae, therefore, were later additions to life-histories, and they tell us nothing of how the adults evolved.

The development of many animals is difficult or impossible to explain in terms of the same-stock theory, but it is consistent with larval transfer. The metamorphosis of hydrozoans, echinoderms and bryozoans illustrates this point.

Hybrid transfer has affected not only larvae but also components of animals, such as lophophores. Cambrian and Ordovician animals had no true larvae, and there were no true larvae until after the establishment of classes in the respective phyla. In the evolution of animals, component transfer preceded larval transfer and holds the key to the Cambrian explosion. This rapid appearance of a wide range of complex animals could not have resulted from Darwinian gradualism, but I suggest that many hybridizations between simple animals produced chimeras of increasing complexity relatively quickly. The results included the ancestors of modern phyla and other combinations that did not survive. Phyla and classes arose suddenly, by transfer, not by Darwinian 'descent with modification'.

Molecular and endocrine perspectives on the evolution of metamorphosis in insects

James W. Truman and Lynn M. Riddiford

The evolution of complete metamorphosis in insects with its distinct larval and adult stages has been one of the major successes in the evolution of life history strategies. With metamorphosis, the goal of embryonic development shifted from the ancestral pattern of making a miniature version of the adult body form to making the novel, larval body plan with its unique morphological and physiological adaptations for feeding. The production of the adult body plan was then deferred to the end of larval growth, through the introduction of a new pupal stage. We have proposed that a key factor in the evolution of the larval stage has been a heterochronic advance in the time of appearance of the insect developmental hormone, juvenile hormone (JH), during embryonic development.

The precocious appearance of JH during embryogenesis has the dual actions of suspending embryonic patterning processes and evoking premature differentiation. Our subsequent tests of this idea focused on exploring the actions of JH and its main target gene, the *broad* transcription factor. We will discuss the larval role of JH in suppressing embryonic patterning centers during larval growth which defers the resumption of embryonic patterning to the last larval stage, in preparation for metamorphosis. Also, we will discuss how the

role of *broad* has changed through evolution from an ancestral function of facilitating anisomorphic growth in the nymphal stages of basal insects, to specifying the unique characteristics of the pupal stage in the more derived, holometabolous insects.

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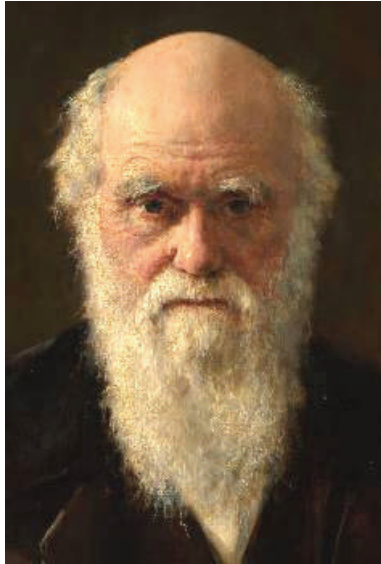
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