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The session that did not shake the world (the Linnean Society, 1st July 1858)

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On July 3 and 4, 2008, the Linnean Society of London (Fig. 1) commemorated with a meeting the presentation of the joint papers outlining evolutionary theory authored by Darwin and Wallace (1st July 1858). One hundred fifty years after that meeting—probably the most famous of all held at the Linnean Society since its foundation in 1788—and the following publication of *On the Origin of Species by Means of the Natural Selection, or The Preservation of Favoured Races in the Struggle for Life* (London: John Murray, 24th November 1859), the concept of evolution has itself "evolved". Not that the foundations established by Darwin are no longer valid; rather, the body of knowledge currently available—the product of enormous technological developments—has made it possible to study living organisms at a level inconceivable during Darwin's time. New insights and new ideas on evolution have arisen from fields of biology that either were in their infancy in Darwin's time or have emerged since then. Together, biochemistry, molecular genetics, population genetics, microbiology, ecology, genomics, proteomics, and a better understanding of cell ultrastructure and evolutionary phenomena have consolidated Darwin's "dangerous idea".

Fig. 1. The arms of the Linnean Society of London.

In celebration of both the 150th anniversary of the presentation of Darwin–Wallace papers and the publication of *On the Origin of Species*, the Linnean Society organized the aforementioned meeting to discuss "The driving forces of evolution: from Darwin to the modern age", with the participation of experts from several related fields, including symbiogenesis, virus-host interactions, hybridogenesis, horizontal gene transfer, and epigenetics. These are among the many scientific areas that have provided new insights into evolution, thus expanding our recognition of the seemingly countless manifestations of natural selection and consequently biodiversity [5]. The meeting was organized by David Cutler, current president of the Linnean Society, and of the Royal Botanical Gardens, at Kew, and by Frank Ryan, Honorary Research Fellow at the University of Sheffield, and author of the well-known books *Darwin's blind spot* and *Tuberculosis: the greatest story never told*.

The introductory lecture was given by Lynn Margulis, from the University of Massachusetts, Amherst, who talked on the origin of eukaryotes in the Proterozoic Eon and the influence of sulfur metabolism [3]. What, in the late 1960s, seemed to be the dream of the brilliant young researcher she was then, is now the widely accepted hypothesis that explains eukaryotic evolution as the merging of several eco-

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physiological abilities of prokaryotic cells [4]. Jan Sapp, from York University, Toronto, discussed how the landscape of evolutionary biology has changed over the last few decades in light of microbial evolutionary biology, which has introduced new concepts, such as the above-mentioned symbiogenesis as well as lateral gene transfer. Eva Jablonka, from Tel Aviv University, Marion Lamb, from the University of London, and Hugh Dickinson, and Robert Grant-Downton, both from the University of Oxford, addressed the many different roles of epigenetic variation in adaptive evolution. The term epigenetics was coined by Conrad Waddington, in 1947, and refers to a branch of biology that studies the causal interactions between genes and their products, those that shape the phenotypes of living beings. However, it was not until the 1990s that use of the term became widespread among biologists, although by that time its definition was no longer as Waddington's. Nowadays, epigenetics refers to changes in gene function that can be inherited through mitosis and/or meiosis but do not involve changes in DNA sequences. Jablonka and Lamb focused their presentation on cellular epigenetic inheritance from a historical point of view, while Dickinson and Grant-Downton talked about trans-generational inheritance of epigenetic information as a genuine phenomenon in plants, albeit one that is not yet completely understood.

Loren Rieseberg, from Indiana University, and Barbara Mable, from the University of Glasgow, discussed the role of hybridization in plant and animal evolution. Rieseberg explained that one of the consequences of hybridization is to increase or reduce biodiversity in plants. Mable set the historical context for our view of hybridization in animals versus that in plants, and reviewed modern evidence for the role of hybridization in animal evolution. The last lecture of the day was given by Mauricio Linares, from the University of Los Andes, Colombia, who presented a phenomenon of alternative speciation in insects, the case of *Heliconius* butterflies. This genus did not result from the splitting of a single lineage but from the merging of two distinct lineages, each of which contributed genes to a new species.

The second day's lectures started with those of Frank Ryan and Luis Villarreal, from the University of California, Irvine, who provided new insights into the role of viruses in host evolution. Ryan talked of viruses as potential symbionts ("aggressive symbionts") and the major role they may play in evolution. Villarreal discussed different roles of viruses in nature, beyond the usual assumption that viruses are "killers". Instead, viruses promote the interactions and dynamics of individual genomes in a kind of social selection that reflects the outcome of viral persistence in specific hosts and in nature. The topic of symbiogenesis came up again in the contribution of Marilyn Roossinck, from the Samuel Roberts Noble Foundation, Ardmore, Oklahoma. In her view, viruses are mutualistic symbionts of their hosts and as such can play crucial roles in host adaptation to ecological niches. Erik Larsson, from the University of Uppsala, pointed out the genetic load that the human genome has acquired from infections with exogenous retroviruses. According to recent data, as much as 8% of the human genome consists of human endogenous retroviruses.

The meeting concluded on the afternoon of the second day with three final lectures. Michael Syvanen, from the University of California, Davis, and Donald Williamson, Emeritus Reader at the University of Liverpool, took their audience back through the history of life to the Cambrian explosion, marked by the sudden evolution of the metazoan phyla. This event has been difficult to explain within the framework of Darwinian theories. Syvanen presented the results of whole-genome comparisons carried out in species from five metazoan phyla. These data, which have allowed molecular clock calculations, suggest that diversification of some of the phyla might have started earlier than traditionally believed. Williamson presented another approach to the study of the Cambrian explosion. Contrary to the traditional assumption that adult animals and their larvae evolved from the same genetic stock, he proposed that the basic form of larvae originated as adults in other taxa and were transferred by hybridization, becoming later additions to life-histories. Finally, James Truman and Lynn Riddiford, both from the Howad Hughes Medical Institute, discussed the role of the insect developmental hormone (i.e., juvenile hormone, JH) in the evolution of insect metamorphosis. They suggested that a heterochronic advance in the time of appearance of JH might have been a key factor in the success of insect evolution.

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It is well-known that Charles Robert Darwin (Shrewsbury, Shropshire, 12 February 1809–Down, Kent, 19 April 1882) had been preparing drafts of chapters for *On the Origin of Species* at least since the mid-1840s, but the letter he received on 18 June 1858, from Alfred Russel Wallace (1823–1913), forced him and his mentors, Sir Charles Lyell and Joseph Hooker, to accelerate the writing and publication of the book. Wallace's letter, written in February 1858, enclosed a short essay, *On the Tendency of Varieties to depart indefinitely from the Original Type*, in which Wallace put forward essentially the same hypothesis on the origin of species that Darwin had sketched as early as 1842 and, with the advice of Lyell, had started to expand upon in 1856. At the end of June, Darwin hesitantly consented to leave the matter in the hands of Hooker and Lyell, permitting them to simultaneously com-

municate his own and Wallace's papers to the Linnean Society [1]. Darwin, already a famous naturalist permanently living in England, was a member of that prestigious Society; Wallace, at the time an obscure naturalist errant in the Malay Archipielago, was not. But, once again, Death played a role in shaping history.

Robert Brown (1773–1858), president of the Linnean Society between 1849 and 1853, had died on June 10. To recognize the loss incurred by the death of the great Scottish botanist, the meeting of June 17, which would have been the last of the 1857–1858 session, was adjourned after formal business; thus, no papers were read. But, as Brown was a member of the Council at the time of his death, a substitute had to be elected within three months. Accordingly, the Council decided to prolong the session of 1857–1858 by an additional meeting on Thursday, July 1. At this meeting, the papers whose presentation had been postponed on June 17 were to be read. To avoid further delay in communicating the research of Darwin and Wallace, Hooker and Lyell were determined to present the papers at the extra meeting of the session, although neither Darwin nor Wallace was able to attend (Wallace was far away in the Moluccas; Darwin was ill and grief-stricken by the death of one of his sons). Hooker and Lyell wrote a joint letter to the secretary, John Joseph Bennett, accompanying an enclosure with Darwin–Wallace papers. It was sent out on June 30, just one day before the meeting. This was too late for the Members to read the scientific papers prior to the meeting, in case they wanted to do so. The letter said [http://www.linnean.org/index.php?id=380]:

My Dear Sir,

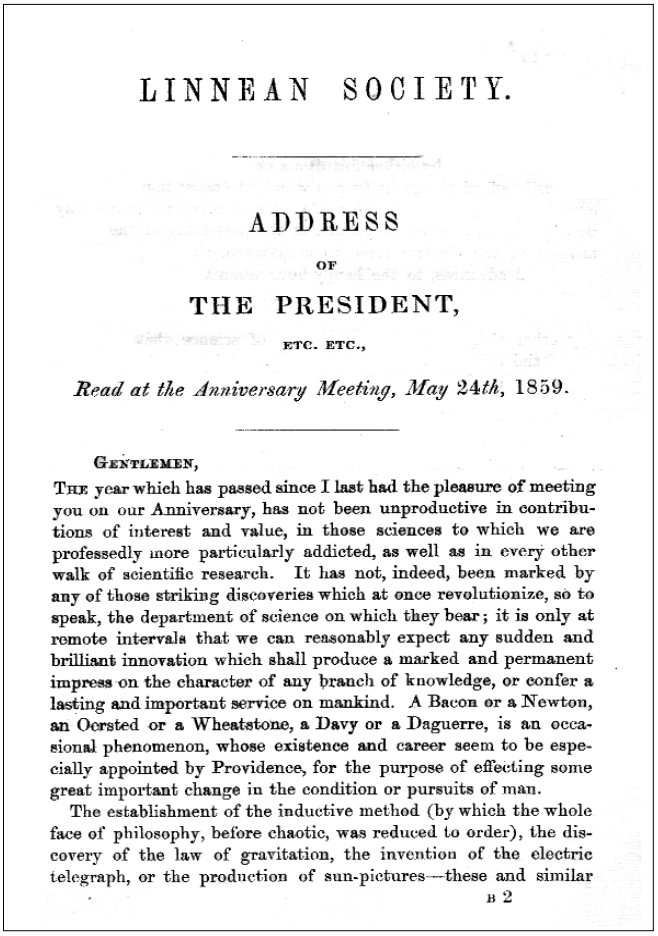
The accompanying papers, which we have the honour of communicating to the Linnean Society, and which all relate to the same subject, viz. the Laws which affect the Production of Varieties, Races, and Species, contain the results of the investigations of two indefatigable naturalists, Mr. Charles Darwin and Mr. Alfred Wallace.

These gentlemen having, independently and unknown to one another, conceived the very same very ingenious theory to account for the appearance and perpetuation of varieties and of specific forms on our planet, may both fairly claim the merit of being original thinkers in this important line of inquiry; but neither of them having published his views, though Mr. Darwin has for many years past been repeatedly urged by us to do so, and both authors having now unreservedly placed their papers in our hands, we think it would best promote the interests of science that a selection from them should be laid before the Linnean Society.

Taken in the order of their dates, they consist of:

I. Extracts from a MS. work on Species*, by Mr. Darwin, which was sketched in 1839, and copied in 1844, when the copy was read by Dr. Hooker, and its contents afterwards communicated to Sir Charles Lyell. The first Part is devoted to "The Variation of Organic Beings under Domestication and in their Natural State", and the second chapter of that Part, from which we propose to read to the Society the extracts referred to, is headed, "On the Variation of Organic Beings in a state of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and true Species".

* This MS. work was never intended for publication, and therefore was not written with care.—C.D. 1858.



LINNEAN SOCIETY.

ADDRESS

OF

THE PRESIDENT,

ETC. ETC.,

Read at the Anniversary Meeting, May 24th, 1859.

GENTLEMEN,

THE year which has passed since I last had the pleasure of meeting you on our Anniversary, has not been unproductive in contributions of interest and value, in those sciences to which we are professedly more particularly addicted, as well as in every other walk of scientific research. It has not, indeed, been marked by any of those striking discoveries which at once revolutionize, so to speak, the department of science on which they bear; it is only at remote intervals that we can reasonably expect any sudden and brilliant innovation which shall produce a marked and permanent impress on the character of any branch of knowledge, or confer a lasting and important service on mankind. A Bacon or a Newton, an Oersted or a Wheatstone, a Davy or a Daguerre, is an occasional phenomenon, whose existence and career seem to be especially appointed by Providence, for the purpose of effecting some great important change in the condition or pursuits of man.

The establishment of the inductive method (by which the whole face of philosophy, before chaotic, was reduced to order), the discovery of the law of gravitation, the invention of the electric telegraph, or the production of sun-pictures—these and similar

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Fig. 2. First page's facsimile of the address of Thomas Bell (president of the Linnean Society of London from 1853 until 1861) read at the annual meeting held between the meeting of July 1st, 1858 and the publication of *On the Origin of Species*, on November 24th, 1859.

II.An abstract of a private letter addressed to Professor Asa Gray, of Boston, U.S., in October 1857, by Mr. Darwin, in which he repeats his views, and which shows that these remained unaltered from 1839 to 1857.

III. An Essay by Mr. Wallace, entitled "On the Tendency of Varieties to depart indefinitely from the Original Type". This was written at Ternate in February 1858, for the perusal of his friend and correspondent Mr. Darwin, and sent to him with the expressed wish that it should be forwarded to Sir Charles Lyell, if Mr. Darwin thought it sufficiently novel and interesting. So highly did Mr. Darwin appreciate the value of the views therein set forth, that he proposed in a letter to Sir Charles Lyell, to obtain Mr. Wallace's consent to allow the Essay to be published as soon as possible. Of this step we highly approved, provided Mr. Darwin did not withhold from the public, as he was strongly inclined to do (in favour of Mr. Wallace), the memoir which he had himself written on the same subject, and which as before stated, one of us had perused in 1844, and the contents of which we had both of us been privy to for many years. On representing this to Mr. Darwin, he gave us permission to make what use thought proper of his memoir, &c.: and in adopting our present course, of presenting to the Linnean Society, we have explained to him that we are not solely considering the relative claims to priority of himself and his friend, but the interests of science generally; for we feel it to be desirable that views founded on a wide deduction from the facts, and matured by years of reflection, should

constitute at once a goal from which others may start, and that, while the scientific world is waiting for the appearance of Mr. Darwin's complete work, some of the leading results of his labours, as well as those of his able correspondent, should together be laid before the public.

We have the honour to be yours very obediently,
Charles Lyell. Jos. D. Hooker.

Both the title and topic selected for Darwin's contribution (clearly dated many years before) and the inclusion of a letter written undoubtedly in advance of the reception of Wallace's short essay, strongly suggest the aim of Hooker and Lyell of emphasizing that Darwin was first in having the idea, and that his idea had been more elaborated than Wallace's.

In those days, the Members of the Linnean Society did not receive in advance either the agenda of the meetings or the titles of the papers to be read. But even if that had been the custom, there would have been no time to inform them about the Darwin–Wallace papers, which Hooker and Lyell sent to the secretary of the Society just the day before the scheduled meeting. It was therefore a surprise to most of the Members who attended it. Although fewer than 30 Fellows, and only one Associate and two visitors, are named in the Minutes, surely more people attended the meeting. In fact, the Minutes do not include the names of any of the officers, except that of the president, Thomas Bell [2].

The meeting had two parts, one "bureaucratic" and another "scientific". The first one dealt with the formal business of recording gifts to the Library, electing George Bentham as a Councillor and nominating him as a vicepresident in place of Brown; finally, it was read a resolution recording the meeting's appreciation of Brown's great services. The second part consisted of the reading of several scientific contributions: The Darwin–Wallace papers came first, followed by five of the six papers that had not been read in the former meeting. All those papers were related to Botany, dealing with: the organization of *Phoronis hippocrepis*, observations on *Ammocaetus*, a new genus of *Cucurbitales*, a new genus named *Hanburia*, the *Nueva Quinologia* of Pavon and the vegetation of Angola. The sixth paper was to be presented by the just nominated vicepresident, George Bentham. But the hearing of the Darwin–Wallace papers so perturbated Bentham that he withdrew his paper, and it was not read at that meeting.

It may seem ironic that Bentham's paper was based on his work on the British flora, and supported Linné's position of the fixity of species. (Later on, Bentham was the president of the Linnean Society from 1861 until 1874, the second longest presidential tenure at the Linnean Society. Only the first president, Sir James Edward Smith, has held that position for longer—40 years!, from 1788 until 1828.) After the reading of the Darwin–Wallace papers, Bell did not call for remarks, and Bentham later indicated that Bell would not have allowed anyone to discuss the startling hypothesis so unexpectedly presented and thereby prolong an already long meeting [2].

President Bell had little or no idea that he was presiding over the start of a revolution in biology, the foundation of a theory that would change the intellectual framework of humankind. In his presidential address in May 1859, when reviewing the period from May 1838, he made the following remarks, which seem awkward nowadays: "The year which has passed [...] has not, indeed, been marked by any of those striking discoveries which at once revolutionize, so to speak, the department of science on which they bear; it is only at remote intervals that we can reasonably expect any sudden and brilliant innovation which shall produce a marked and permanent impress on the character of any branch of knowledge, or confer a lasting and important service on mankind. A Bacon or a Newton, an Oersted or a Wheatstone, a Davy or a Daguerre, is an occasional phenomenon, whose existence and career seem to be specially appointed by Providence, for the purpose of effecting some great important change in the conditions or pursuits of man" (Fig. 2).

The improvised gathering at the Linnean Society, without the presence of either Darwin or Wallace, attended only by a few Members, most of them "classical" botanists or zoologists, who must have get mortally tired or bored by the Darwin–Wallace papers, did not seem to convey the idea that a new theory was emerging, that it was the birthday of a new era in biology. Nevertheless, from then on, other people have had their feelings deeply stirred and have realized the far-reaching significance of that question. In fact, the publication of Darwin's revolutionary book only seventeen months afterwards was a sudden success, and the whole edition was sold the same day of its release. People were eagerly waiting for the book, and soon many different disciplines or thinkers (from biology to economy, from historians to anarchists) were "impregnated" by Darwin's dangerous idea. But this would be another story.

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