Discovering Evolution: III. Darwin and Wallace.

“It was evident that such facts [species’ distributions in time and space] as these, as well as many others, could only be explained on the supposition that species gradually become modified; and the subject haunted me.” – Darwin (1905), Autobiography. [Emphasis added. South American Glyptodonts from Scott', W. B. A History of Land Mammals in the Western Hemisphere]
Readings.


His Majesty's Sloop *Chanticleer*.

- The importance of islands and archipelagoes: **Recall**

1. The **hints** (“mystery of mysteries”, *etc.*) that Darwin inserted into Chapter 17 (“Galapagos Archipelago”) and elsewhere in the 2nd edition of his *Journal of Researches* published in 1845.

2. His remarks regarding inter-island variability among mockingbirds undermining “the **stability of species**” (Figures 3.1 and 3.2) in his *Ornithological Notes* (Sept-Oct, 1835)

3. Which **may or may not** evidence a conversion to transmutation prior to the return to England (Sulloway, 1985; Kohn *et al.*, 2002).

4. But surely influenced his later thinking.
Now consider the observations of William Webster – ship’s surgeon, HM sloop Chanticleer (1829-1830)¹

“...It has always struck me that naturalists have been somewhat at variance with the geologists. They [naturalists] have found ... peculiar species of plants, &c. ... [on] remote islands ... thought to be of a later origin than the continents themselves; while species have been limited to the first periods of creation. For example; if St. Helena is of subsequent formation to the great continents, then its possessing a distinct and new species of plant, or animated being ... must either be a conclusive proof that a successive creation of species goes forward, or that the naturalists are wrong in their definition or discrimination of species ....” [quoted by Herbert (1974). Emphasis added]

Figure 3.3. St. Helena and Ascension Islands in the South Atlantic.

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1. Historical determinism?

“The existence of such a paragraph in a work such as Webster’s *Narrative* ... suggests that the occupation of voyaging naturalists was conducive to reflection on the origin of species.” [Herbert (1974, p. 252)]

2. Interestingly, Webster shows up in Darwin’s notebooks (*Beagle Field Notes, Geological Diary, Red Notebook*) and in Chapter 16 of *The Journal of Researches*

   a. With reference to **geology** and **hydrophobia**.

   b. But **not** with regard to species and their origination.

3. In the event, Webster **rejected** mutability:

   “I have no confidence in the vagueness and blindness of geological speculation; But abide rather by the wisdom of the Apostle, who says, ‘through faith we understand that the worlds were framed by the word of God, and the things which are seen were not made of things which appear.’”

   • Which brings us to another traveler, a naturalist, in fact, **less disinclined** to reject “the wisdom of the Apostle.”
Type and Antitype: Alfred Wallace’s Sarawak Law Paper (W55).

- Alfred Russel Wallace.

  1. Born to a **middle class** family that later fell on hard times.

  2. **Supported himself** by specimen collecting in South America\(^2\) with Bates\(^3\) and later, on his own, in Malaysia.

  3. Kept **duplicate sets of collections**: one for research; the other for sale.

  4. **Inspired** by reading *Vestiges*:

    “In a letter to Bates dated November 9th, 1847, he [Wallace] concludes by asking, ‘Have you read *Vestiges of the Natural History of Creation*, or is it out of your line?’ and in the next (dated December 28th), in reply to one from his friend, he continues, ‘I have a rather more favourable opinion of the 'Vestiges' than you appear to have. I do not consider it a hasty generalisation, but rather an *ingenious*

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\(^2\) The South American expedition ended in disaster when the ship on which Wallace was returning to England caught fire. Wallace survived, but most of his notes and specimens were lost – see, for example, Brackman (1980), Brooks (1984).

\(^3\) Henry Walter Bates (1825-1892), naturalist and explorer, best known today for the phenomenon now known as Batesian mimicry.
hypothesis strongly supported by some striking facts and analogies, but which remains to be proved by more facts and the additional light which more research may throw upon the problem.”

“Again, writing at about the same time, he adds: ‘I begin to feel rather dissatisfied with a mere local collection; little is to be learnt by it. I should like to take some one family to study thoroughly, principally with a view to the theory of the origin of species. By that means I am strongly of opinion that some definite results might be arrived at.” [Letters to Bates excerpted by Marchant (1916, 91-92. Emphasis added.]

5. Eight years later, in 1855, he published his preliminary conclusions.

a. Effectively made the case for DwM without actually saying that species descended the one from the other.

b. Made no mention of mechanism.

6. At the time, the “Sarawak Law paper”, as it is now called, was widely ignored – see correspondence with Darwin below.

7. Nonetheless, as also discussed below, it set in motion a chain of events that culminated in the writing and publication of The Origin.
“On the law which has regulated the introduction of new species” (Wallace, 1855).

“Every species has come into existence coincident both in space and time with a pre-existing closely allied species.”

1. Argues (recall Lecture I) the Law

“not merely explains, but necessitates what exists. Granted the law … many of the most important facts in Nature could not have been otherwise, but are almost as necessary deductions from it, as are the elliptic orbits of the planets from the law of gravitation.” [p. 190. Emphasis added]

2. Induces the Law from patterns of species distribution and affinity in time and space.

3. Looks not for species being created (recall Lyell’s argument) but for facts that could be explained thereby:

a. Taxonomic Affinity. The degree to which species are allied reflects from “the order in which … [they] came into existence, each one having had for its immediate antitype a closely allied species existing at the time of its origin.”

b. Tree of Life. “… species being so numerous and the modifications of form … so varied”, the pattern of relatedness is … as intricate as the twigs of a gnarled oak …”
Figure 3.4. Wallace’s “gnarled oak” as presently imagined for amniote phylogeny here represented as a branching tree. The tree is rooted in basal tetrapods, i.e., amphibians, that lack the amniotic membranes of reptiles, birds and mammals. Slices are characters or character changes that unite descendent groups. Thus birds are united by the loss of teeth but not by feathers, a character shared with related non-avian dinosaurs. As with all phylogenies, relationships evolve with time and systematist proclivity, an example being the position of turtles, alternately derived from the branch above that leading to mammals and below that leading to birds and dinosaurs.
c. **Difficulties in Classification.** Determining a “true, natural system of classification” is complicated by the fact that “we have only fragments of this vast system, the stem and main branches being represented by extinct species …”

d. **Endemism on Islands.** Age plus isolation on islands implies endemism with species in question “most nearly allied” to those of the nearest continent – e.g., Galapagos Islands and St. Helena. Conversely, islands of recent origin do not have endemics – e.g., Britain.

e. **Distributions in Space.**

i. On opposite sides of barriers of long standing, e.g., ancient mountain ranges, one observes replacement of genera by allied genera. Within genera, allied species occur in geographic proximity – e.g., Darwin’s rheas.

ii. **Higher Groups.** Endemic families, etc., require greater isolation, e.g., New and Old World warblers.

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Figure 3.5. Geographic replacement of genera per Wallace (1855)
f. Distributions in Time.

i. Geology suggests continuing extinction of old species and origination of new ones.

ii. Long-term balance between origination and extinction, with the former predominating in periods of geological quiescence and the latter in periods of geological activity offers a simpler explanation of variations in diversity than “obscure and hypothetical notions such as polarity.” [See “A Curious Motivation” below]

iii. Imperfection of the fossil record may account for existence of contemporary forms that appear “isolated” – i.e., closest relatives are extinct and their fossil remains undiscovered.

g. Rudimentary Organs. Either anticipatory (the “antitypal sketch of a wing ... in the scaly flapper of the penguin”) – or vestigial. Both inexplicable in terms of Design.

“To every thoughtful naturalist, the question must arise, What are these for? What have they to do with the great laws of creation?” [Emphasis added]
4. Two possible interpretations of Wallace’s Law:

   a. Existing species, by **virtue of proximity**, induce the **creation of** but **do not give rise to** new species.

   b. New species are the **modified posterity of old ones**.

5. **Regarding the Galápagos**\(^4\): Either

   “the same original emigration peopled the whole of the islands with the same species from which differently modified prototypes were created”

   or

   “the islands were successively peopled from each other, but that new species have been created in each on the plan of the pre-existing ones.”\(^5\) [Emphasis added]

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\(^4\) Wallace was familiar with Darwin’s observations, the latter’s *Journal of Researches* having been published in 1839 and in revised form, in 1845.

\(^5\) *Modulo* successive creation of the islands, Wallace’s second scenario is accepted by contemporary investigators, *e.g.*, Grant and Grant (2002).
6. Writing in 2000, paleobiologist Bernard Michaux⁶ opined that 

“... it is difficult to believe that Wallace had not worked it all out at least three years earlier than generally admitted. Wallace's use of language to conceal his evolutionary leanings is instructive. ... he refers to what are clearly common ancestors as ‘antitypes.' He even refers to ‘common antitypes' at one point! Wallace also manages to discuss the difference between analogy and homology without using the word homology at all, instead using ‘affinity.'” [Emphasis added]

7. Yes and no. By 1855, Wallace had assembled evidence supporting (DwM). But the mechanism eluded him: 

“Ever since I read the ‘Vestiges’ I had been convinced that development took place by means of the ordinary process of reproduction; but though this was widely admitted, no one had set forth the various kinds of evidence that rendered it almost a certainty. I endeavored to do this in an article written at Sarawak in February, 1855, which was published in the following September in the ‘Annals of Natural History.’ Relying mainly on the well-known facts of geographical distribution and geological succession, I deduced from them the law, or generalization, that, ‘Every species has come into existence co-incident both in Space and Time with a Preexisting closely allied Species’; and I showed how many peculiarities in the affinities, the

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⁶ Comment at http://people.wku.edu/charles.smith/wallace/S020.htm at i.e., following Smith’s transcription of Wallace (1855).
succession, and the distribution, of the forms of life, were explained by this hypothesis, and that no important facts contradicted it.”[7]

“Even then, however, I had no conception of how or why each new form had come into existence … ; and though the subject was continually being pondered over, no light came to me till three years later (February, 1858) under somewhat peculiar circumstance.” [Wallace (1898) p. 139]

8. Unable to provide a mechanism, Wallace apparently 
chose to muddy the waters.

- Wallace’s Law the logical endpoint of evolving views RE origination of species.

1. Linnaeus: One time, one place.  

2. Lyell: Multiple times, multiple centers of origin.

3. Wallace: Innumerable times, innumerable places.

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[7] Recall (Lecture I, Ruse, 1975) the hallmarks of a good theory; consilience, in particular.

[8] Modulo Linnaeus’ late in life admission that some species were “products of nature”, i.e., their origin, possibly by hybridization, traced to times more recent than the Creation. See, for example, Bowler (2003, Chapter 3).
• A Curious Motivation.

1. W55 was written in response to Edward Forbes (1815-1854) “theory of “polarity”:

“it was the promulgation of Forbes’s theory …” which led me to write and publish, for I was annoyed to see such an ideal absurdity put forth, when such a simple hypothesis will explain all the facts.” [Letter of 4 January, 1858 to Bates]

2. Forbes’ regarded species as **divine ideas** and posited high rates of their creation early and late in the earth’s history (Figure 3.6).

3. Ironically, Forbes’ time of minimum production more or less coincides with the **Permian-Triassic boundary**, now known to mark the end-Permian **mother of all mass extinctions**.

![Figure 3.7](image)
Friend and Correspondent.

• 1855-1857.

1. **Darwin** at Down House studying **pigeons**.


   
   a. 1st entry a summary of Wallace’s paper.

   b. Regarding the preeminence of secondary laws:

   “It may be asked why sh.d omnipotence tie itself down by restrictions – the answer is first that it does so – 2.dly Man is enabled therefore to study & understand the mechanism of the org.c & inorganic worlds. This may be a very small part of the reasons of fixed laws but one’s enough.” [28 November]

   c. Five and a half months later, having been apprised of Darwin’s views earlier that day, Lyell wrote that

   “… Mr. Wallace[‘s] introduction of species most allied to those immediately preceding in Time … seems explained by the Natural Selection Theory.” [16 April. 1856]
Figure 3.8. 19th Century engraving of Down House, Darwin’s residence from 1842 til his death forty years later. Down house is located in the village of Down in southeast England. Now designated an historical structure, the building can be viewed by the public. Engraving details at [http://catalogue.wellcomelibrary.org/record=b1555400/](http://catalogue.wellcomelibrary.org/record=b1555400/).
Figure 3.9a. **Top.** Five varieties of pigeon shown in 1851. In the foreground left to right: Jacobin, Carrier, Pouter, Almond Tumbler, Yellow Mottle. **Bottom.** Cartoon published in *Punch* magazine the same year. From Seccord (1981).
Figure 3.9b. Domestic pigeon phylogeny as inferred by Darwin who took up pigeon fancying from 1855-1858. Darwin believed that all the domestic varieties were descended from the wild rock dove, *Columba livia*. Reproduced by Secord (1981) from *The Variation of Plants and Animals under Domestication*, vol.1.

Figure 3.9c. The rock dove, from which Darwin believed all breeds of domestic pigeon, to be descended. Image from *Audubon Guide to North American Birds* – [http://www.audubon.org/field-guide/bird/rock-pigeon](http://www.audubon.org/field-guide/bird/rock-pigeon).
Lyell wasn’t Darwin’s only correspondent who appreciated the implications of Wallace’s paper. From India, Darwin received a letter from Edward Blyth.⁹

“What think you of Wallace’s paper in the Ann. M. N. H. [Annals and Magazine of Natural History]? Good! Upon the whole! But how about such forms as the Giraffe, which has typical representatives in the Siwálik tertiary deposits¹⁰? Or the true Elk (=Moose)? Can we suppose a lost series of gradations connecting these genera with the Deer type, & ramifying off to them paulatim [gradually]? Wallace has, I think, put the matter well; and according to his theory, the various domestic races of animals have been fairly developed into species.

“… What do you think of the paper in question? Has it at all unsettled your ideas regarding the persistence of species,—not perhaps so much from novelty of argument, as by the lucid collation of facts & phenomena.” [8 December, 1855. DCP-1776]

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⁹ Edward Blyth (1810-1873) was an English naturalist who spent most of his professional life in India where he served as curator of the museum of the Royal Asiatic Society of Bengal from 1841 to 1862. He was especially interested in the origin of domestic breeds concerning which and other natural history matters he corresponded with Darwin.

¹⁰ See Lecture II, RE CD’s correspondence with Hugh Falconer and Siwalik Hills formation.
e. Two weeks after the discussion of 16 April RE the selection theory, Lyell advises Darwin to publish.

“I wish you would publish some small fragment of your data, pigeons if you please & so out with the theory & let it take date & be cited & understood.” [Letter of 1-2 May, 1856, DCP-1862]

4. Darwin vacillates.


b. But five days later, he writes his cousin, William Darwin Fox, that he is hard at work on a sketch, even while complaining that “my work will be horridly imperfect.” [DCP-1895]

c. But by fall, the sketch abandoned; Darwin now working on a much larger work, his so-called “Big Species Book”\textsuperscript{11}, itself to be abandoned in 1858.

5. By this time, Darwin was corresponding with Wallace who had written him about species on 10/10/56.\textsuperscript{12}

\textsuperscript{11} The first two chapters became *Variation of Animals and Plants under Domestication* (1868). The remainder was finally published a hundred and twenty years later as *Natural Selection* (Stauffer, 1975).

\textsuperscript{12} Wallace’s letter has never been found [footnote to DCP #2086].
a. Darwin expressed **agreement** with Wallace’s conclusions. “I can plainly see,” Darwin wrote,

“that we have thought much alike & to a certain extent have come to similar conclusions. In regard to the Paper in Annals, I agree to the truth of almost every word of your paper; & I daresay that you will agree with me that it is very rare to find oneself agreeing pretty closely with any theoretical paper; for it is lamentable how each man draws his own different conclusions from the very same fact.—

b. Then advised the “new kid on the block” to **back off**.

“This summer will make the 20th year (!) since I opened my first-note-book, on the question how & in what way do species & varieties differ from each other.— I am now preparing my work for publication, but I find the subject so very large, that though I have written many chapters, I do not suppose I shall go to press for two years.” [Letter of 1 May, 1857, DCP-2086]

c. Reiterated his claim to priority in December:

“Though agreeing with you on your conclusion(s) in that paper, I believe I go much further than you; but it is too long a subject to enter on my speculative notions.— …

“You ask whether I shall discuss ‘man’;—I think I shall avoid whole subject, as so surrounded with prejudices, though I fully
admit that it is the highest & most interesting problem for the naturalist.— My work, on which I have now been at work more or less for 20 years, will not fix or settle anything; but I hope it will aid by giving a large collection of facts with one definite end: I get on very slowly, partly from ill-health, partly from being a very slow worker.— I have got about half written; but I do not suppose I shall publish under a couple of years. I have now been three whole months on one chapter on Hybridism!” [Letter of 22 December, 1857 DCP-2192]

6. And it worked!

a. The following year, Wallace would independently hit upon natural selection as the driver of differentiation. But —

b. Rather than submitting his manuscript announcing the discovery to a journal such as the Annals, Wallace sent it to Darwin – effectively seeking the latter’s permission to publish.

c. And knowing full well that publication might thereby be forestalled – see letter to Bates below.

• 1858 –

1. Wallace planning his book. To longtime friend, Henry Bates, he wrote
"To persons who have not thought much on the subject I fear my paper on the Succession of Species will not appear so clear as it does to you. That paper is, of course, merely the announcement of the theory, not its development. *I have prepared the plan and written portions* of a work embracing the whole subject, and have endeavoured to prove in detail what I have as yet only indicated. … *I have been much gratified by a letter from Darwin, in which he says that he agrees with almost every word of my paper.* He is now preparing his great work on Species and Varieties, for which he has been collecting materials twenty years. *He may save me the trouble of writing more on my hypothesis, by proving that there is no difference in nature between the origin of species and of varieties; or he may give me trouble by arriving at another conclusion; but, at all events, his facts will be given for me to work upon.* Your collections and my own will furnish most valuable material to illustrate and prove the universal applicability of the hypothesis. *The connection between the succession of affinities and the geographical distribution of a group, worked out species by species, has never yet been shown as we shall be able to show it.*" [Letter of 4 January [Wallace (1905, v. 1, p. 358). Emphasis added]

2. Meanwhile, **Darwin** at Down writing his Big Species Book.

3. And **Wallace** in Malaysia pondering species and varieties “The generally adopted opinion,” he wrote (Wallace, 1858)
“is that species are absolute independent creations, which during their whole existence never vary from one to another, while varieties are not independent creations, but ... have been produced by ordinary generation from a parent species. There does, therefore (if this definition is true), exist ... an absolute and essential difference in the nature of these two things that we are warranted in looking for some ... [qualitative] character to distinguish them [other] than one of mere degree, which is necessarily undefinable. If there is no ... [such] character, that fact is one of the strongest arguments against the independent creation of species, for why should a special act of creation be required to call into existence an organism differing only in degree from another which has been produced by existing laws?” [p. 5888 Emphasis added].

4. **Wallace** twigs to natural selection and, *contra* his “Law paper”, explicitly argues for DwM.

a. **NS solves** species-varieties problem – *i.e.*, NS a *vera* causa that **transforms varieties into species** and **accounts for their discreteness**.

b. Wallace writes up his ideas and forwards the manuscript to his “friend and correspondent,” Mr. Darwin.

c. Asks Darwin to communicate it to Lyell for publication if he thinks it worthy.

“It was while waiting at Ternate …, that the idea [natural selection] … occurred to me. … My paper written at Sarawak rendered it certain to my mind that the change had taken place by natural succession and descent … But the exact process of the change and the causes which led to it were absolutely unknown … . The great difficulty was to understand how, if one species was gradually changed into another, there continued to be so many quite distinct species, so many which differed from their nearest allies by slight yet perfectly definite and constant characters. … The problem then was, not only how and why do species change, but how and why do they change into new and well-defined species … and why do all the intermediate grades die out … and leave only clearly defined and well-marked species, genera, and higher groups of animals.

“At the time in question I was suffering from a sharp attack of intermittent fever [malaria] …. One day something brought to my recollection Malthuss‘ [sic] Principles of Population,’ which I had read about twelve years before. I thought of his clear exposition of ‘the positive checks to increase’ … It then occurred to me that these causes or their equivalents are continually acting in the case of animals also; … Vaguely thinking over the enormous and constant destruction which this implied, it occurred to me to ask the question, Why do some die and some live? And the answer was clearly, that on the whole the best fitted live. … Then it suddenly flashed upon me that this self-acting process would necessarily improve the race, because in every generation the inferior would inevitably be killed off and the superior would remain … [!]t
followed that *all the changes necessary for the adaptation* of the species to the changing conditions would be brought about … and in the very process of this modification the unmodified would die out, and thus the *definite characters* and the *clear isolation* of each new species would be explained. The more I thought over it the more I became convinced that I had at length found the long-sought-for law of nature that solved the problem of the origin of species. For the next hour I thought over the deficiencies in the theories of Lamarck and of the author of the "Vestiges," and I saw that my new theory supplemented these views and obviated every important difficulty. I waited anxiously for the termination of my fit so that I might at once make notes for a paper on the subject. *The same evening I did this pretty fully, and on the two succeeding evenings wrote it out carefully in order to send it to Darwin by the next post,* which would leave in a day or two.

*I wrote a letter to him in which I said that I hoped the idea would be as new to him as it was to me, and that it would supply the missing factor to explain the origin of species.* I asked him if he thought it sufficiently important to show it to Sir Charles Lyell, who had thought so highly of my former paper. [Wallace (1905, vol. 1, pp. 360-363. Emphasis in original]
5. Darwin was **horrified**. To Lyell, he wrote

“Your words have come true with a vengeance. ... if Wallace had my MS. Sketch written out in 1842, he could not have made a better short abstract! ... I hope you will approve of Wallace’s sketch that I may tell him what you say.” [18 June, 1858, DCP-2285]

6. But a week later, and mindful of his impending loss of priority, Darwin struck a different note\(^\text{13}\)

I should not have sent off your letter without further reflection, for I am at present quite upset ... . There is nothing in Wallace’s sketch, which is not written out much fuller in my sketch, copied out in 1844, and read by Hooker, some dozen years ago. About a year ago I sent a short sketch to Asa Gray, so that I could most truly say and prove that I take [[“stole” lined out in original]] **nothing from Wallace**. I should be extremely glad now [[double underlined in original]] to publish a general sketch of my views.” [25 June. Emphasis added. Transcribed by J. L. Brooks (1984, pp. 263-264).]

7. Hooker and Lyell then moved to **preserve Darwin’s priority**.

\(^{13}\) For comparison of the original and published versions of Darwin’s letter, see Brooks (1984), whose notations are indicated by double square brackets [[ ]].
8. **Upshot** was the Darwin-Wallace “paper” (DW58) communicated by Lyell, Hooker & Bennett consisting of 3 parts:

a. “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.”

b. “Abstract of a private letter\(^{14}\) addressed to Professor Asa Gray, in October 1857, by Mr. Darwin.” [actually 9/5/57; DCP-2136]

c. “Essay by Mr. Wallace … ‘On the Tendency of Varieties to depart indefinitely from the Original Type.’”

9. Both the **ordering** of the materials and the **communicating letter** designed to support Darwin’s priority:

   “An Essay by Mr. Wallace … 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 if 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

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\(^{14}\) Not surprisingly, the following was omitted: “You will, perhaps, think it paltry in me, when I ask you not to mention my doctrine; the reason is, if anyone, like the Author of the Vestiges, were to hear of them, he might easily work them in, & then I sh’d have to quote from a work perhaps despised by naturalists & this would greatly injure any chance of my views being received by those alone whose opinion I value.”
soon as possible. Of this step we highly approved, provided Mr. Dar-
win did not withhold from the public, as he was strongly inclined to
do (in favour of Mr. Wallace), the memoir which he had himself writ-
ten on the same subject …

“… in adopting our present course … we have explained to him
[Darwin] that we are not solely considering the relative claims to
priority … , but the interests of science generally; for we feel it to be
desirable that views founded on a wide deduction from 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 lead-
ing results of his labours, as well as those of his able correspond-
ent, should together be laid before the public.

Charles Lyell, Jos D. Hooker,
J. J. Bennett, Esq.” [Emphasis added]

10. These materials read at the Society's June meeting and
published in Vol. 3 of its Proceedings. Thereafter,

a. Wallace – unaware of the “joint” publication until after
the fact – remained in the East Indies until 1862.

b. Darwin went back to writing in earnest and produced
On the Origin of Species by means of Natural Selection,
or the Preservation of Favoured Races in the Struggle
for Life – published on 24 November, 1859.
• Delivering the Mail.

1. The traditional (e.g., Eiseley, 1961) chronology has Darwin

   a. Receiving Wallace’s manuscript in June and promptly dispatching a letter to Lyell urging that it be published: “Your words have come true with a vengeance. …“

   b. Subsequently indicating that he would “be extremely glad now to publish a general sketch of my views in about a dozen pages or so.” [Letter to Lyell of 25 June].

2. This view was challenged by John Brooks (1984) who claimed that

   a. Darwin received Wallace’s letter in May, i.e., a month earlier than is generally believed.

   b. Sat on Wallace’s manuscript while making changes to *Natural Selection*, said changes made possible by reading Wallace’s manuscript and then re-reading the 1855 Law paper.

• The Book that Never Was.

1. Wallace intended a book in which he would

“disprove all Lyell’s arguments [15], first at the commencement of my last chapter.” [Costa, 2013, 131]

2. Forestalled by CD and the events of 1858.

3. Would have expanded upon previously published papers and his contribution to DW58.

4. By tilting against Lyell, Wallace would likely have provoked a more violent response than Darwin because

a. Darwin lauded & was lauded by British elite naturalists.

b. Wallace was not a member of that club.

5. What Gould and Lewontin (1979) called Wallace’s pan-selectionism might have provoked a more brutal form of eugenics (Lecture I) than what actually developed.

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15 In his notebooks (Costa, 2013, pp. 128-131), Wallace argued that, contra Lyell’s Principle of Preoccupancy, resident species can adapt before being exterminated by immigrants, provided the rate of environmental change is sufficiently slow. Implicit in this argument is the requirement that changed conditions occur over a wide (better yet, a wide and remote) area, thereby impeding the influx of pre-adapted immigrants – think oceanic islands.

<table>
<thead>
<tr>
<th>Date</th>
<th>Charles Darwin</th>
<th>Alfred Russel Wallace</th>
<th>Charles Lyell</th>
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<tbody>
<tr>
<td><strong>1855</strong></td>
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<tr>
<td>1-Jan</td>
<td>Studying pigeons</td>
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<td>5-May</td>
<td>Every proposition requires such an array of facts</td>
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<td>6-Jun</td>
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<td>Opens 1st &quot;Species&quot; NB</td>
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<tr>
<td><strong>1856</strong></td>
<td></td>
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<tr>
<td>16-Apr</td>
<td>Talks with CL RE natural selection</td>
<td>Talks with CD RE natural selection</td>
<td></td>
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<tr>
<td>16-Apr</td>
<td></td>
<td>W55 explained by the selection theory</td>
<td></td>
</tr>
<tr>
<td>1-May</td>
<td>Letter from CL: Pigeons if you please</td>
<td>Letter to CD: Pigeons if you please</td>
<td></td>
</tr>
<tr>
<td>1-Sep</td>
<td>Working on Big Species Book</td>
<td></td>
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<tr>
<td>10-Oct</td>
<td>Letter from ARW now lost</td>
<td>Letter to CD now lost</td>
<td></td>
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<tr>
<td><strong>1857</strong></td>
<td></td>
<td></td>
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<tr>
<td>22-Sep</td>
<td>Letter to ARW: Two very good men …</td>
<td>Letter from CD: Two very good men …</td>
<td></td>
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<tr>
<td>Dec</td>
<td></td>
<td>W57 (Aru Islands)</td>
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<tr>
<td><strong>1858</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>4-Jan</td>
<td>Planning book on evolution</td>
<td></td>
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<tr>
<td>15-Jan</td>
<td></td>
<td>W58 published</td>
<td></td>
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<tr>
<td>15-Jun</td>
<td>CD receives Wallace's selection Ms.</td>
<td>Wallace's Selection Ms. received by CD</td>
<td></td>
</tr>
<tr>
<td>18-Jun</td>
<td>Letter to CL: Your words ring true</td>
<td></td>
<td>Letter from CD: Your words ring true</td>
</tr>
<tr>
<td>25-Jun</td>
<td>Letter to CL: I take nothing from Wallace</td>
<td></td>
<td>Letter from CD: I take nothing from Wallace</td>
</tr>
<tr>
<td>25-Jun</td>
<td>Letter to CL: Glad to publish a sketch</td>
<td>Letter from CD: Glad to publish a sketch</td>
<td></td>
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<tr>
<td>30-Jun</td>
<td></td>
<td>DW58 communicated to Linnaean Society</td>
<td></td>
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<tr>
<td>6-Aug</td>
<td>DW58 read to Linnaean Society</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20-Aug</td>
<td>DW 58 published</td>
<td></td>
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<tr>
<td><strong>1859</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>14-Nov</td>
<td><em>Origin</em> published</td>
<td>In Dutch East Indies</td>
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</tr>
</tbody>
</table>
Reaction to DW58 was muted.

1. Thomas Bell (1859), Linnaean Society President, infamously observed:

“The year … has not, indeed, been marked by any of those striking discoveries which at once revolutionize … the department of science on which they bear; A Bacon or a Newton … 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.”

2. Regarding which, England (1997) argued that the lack of reaction to DW58 (vis-à-vis that occasioned by *The Origin*), reflected the attendees’ failure to grasp its more radical implications. “Their reactions”, England wrote

“must be understood in light of … what they regarded as its zoological context: the question of the difference between varieties and species …[upon which the] work of Thomas Vernon Wollaston [16] had focused … attention …” [p. 268]

---

[16] Thomas Vernon Wollaston (1822-1878) was an English entomologist best known for his study of beetles. His belief that species could vary, but always within fixed limits, and thereby spawn varieties was essentially a restatement of the position advocated by Lyell (1832, v2).
3. **In fact**, conservative naturalists, Thomas Boyd and Arthur Hussey, **did grasp** the implications, and they dismissed them as **speculative** (England, 1997):

a. Boyd:

“Does he [Wallace] mean that by the tendency to vary we ... may trace back all organic life ... to some unknown root in the far-off geologic ages ...? ... If the tendency to vary were a law of indefinite variation, it might carry out this idea; but, being ... simply a tendency, it seems to me that painting such an ideal picture ... is like Science sitting down at the feet of Imagination.” [Boyd, 1859, p. 6359].

b. Hussey.

**Grandiloquently:** “Of the papers upon this subject which have appeared in the 'Zoologist' [17] those of Mr. Darwin seem to extend the operation of his theory into a period resembling geological epochs, which carries us at once into the region of conjecture,—a ‘barren ground,’ upon the boundless wastes of which I have no inclination to wander.” [Hussey, 1859, p. 6474].

---

17 England (1997) tells us that “the editor of the Zoologist ... was sufficiently impressed by the [Darwin-Wallace] papers to reprint them in his journal, a typically descriptive, staid publication. The comments of Thomas Boyd and Arthur Hussey followed ... in 1859.”
More Simply: “I will declare my opinion, that, in the wild state, after a very few generations at the utmost, any accidental variation … will be merged in a return to that original condition in which the creature was from the first adapted to the situation in which it was placed.” Hussey, 1859, p. 6475. Emphasis added.

4. Parson-ornithologist Henry Tristram (1859), to the contrary, did not appear to grasp said implications and endorsed the selection theory as a plausible explanation for color variation (selection for crypsis) in North African birds.

![European and North African Larks](image-url)

**Figure 3.10.** European (left) and North African (right) larks. Following DW58, Henry Tristram attributed the color differences to selection for crypsis.

5. But upon later realizing the broader implications, i.e., universal common descent, became an outspoken critic.
Publication of *The Origin*.

- Published the following November.

1. **An abstract of Natural Selection** – no references!

2. The first edition (1250 copies) **sold out** the 1st day.

3. 1/3 went to Mudie’s lending library, a number to Darwin himself, who sent copies to friends and colleagues.

- Darwin spent the next 20 years completing (and expanding) the rest of what was to have been part of his “Big Species Book” piecemeal.

1. This included “pangenesis,” his “provisional” theory of heredity, and a discussion of human evolution, – both subjects omitted from *The Origin*, the latter most glaringly.

2. Today, he receives the bulk of the credit for having “discovered evolution.”

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**Figure 3.11.** Book plate from Mudie’s library. For discussion of the library’s impact on Victorian publishing, see G. P. Landow, *Mudie’s Select Library and the Form of Victorian Fiction*.
Wallace remained in the Dutch East Indies until 1862.

1. Published *The Malay Archipelago* in 1869.

2. References natural & sexual selection five times in over a thousand pages.\(^{18}\)

3. “Father” of biogeography. Famous for **Wallace’s Line** (Figure 3.10). See Wallace (1857), p. 479 especially.

4. Published *Darwinism* in 1889, 7 years after CD’s death.

5. Thereafter, the leading defender of evolution generally, of Darwin especially, e.g., Wallace (1896a).

6. Rejected sexual selection and argued for a guiding hand of supernatural intelligence.

---

\(^{18}\) References are as follows: Vol I. Protective coloration of leaf butterflies (p. 207); instincts in relation to structure (p. 419). Vol. II. Large jaws and fighting between male Coleoptera (p. 277); male plumage and female choice in Birds of Paradise (pp. 398-399); Papuan racial characteristics (p. 455).
Figure 3.13. Protective coloration in the leaf butterfly was one of five instances in which Wallace referenced selection in *The Malay Archipelago*. Top. Seen from above. Bottom. Seen from below with wings folded.
Wallace’s Contribution to DW58.

- The thesis that all species trace to the Creation widely believed to be supported by the tendency of domestic creations to revert when released into the wild, which

  “instability is considered to be a distinctive peculiarity of all varieties … and to constitute a provision for preserving unchanged the originally created distinct species.” [p. 53]

1. But this presumption

  “rests entirely on the assumption, [that] varieties occurring in a state of nature are … analogous … with those of domestic animals …. [p. 54]

2. Which equivalence Wallace rejects.

3. Instead he proposes

  “a general principle … which will cause many varieties to survive the parent species, and to give rise to successive variations departing further and further from the original type, and which … produces, in domesticated animals, the tendency of varieties to return to the parent form.” [p. 54. Emphasis added]
• Wallace’s thesis in detail.

1. **Abundance in Nature.**
   Long-term, populations at **equilibrium**. Availability of resources, not reproductive rate, determines population size. *E.g.*, passenger pigeon – two eggs / clutch.

2. **Principle of Malthus.** “The numbers that die annually must be immense; … those that die … the weakest.” [p. 56].

3. **Ubiquity of Selection.** “Most … variations from the typical form of a species must have some definite effect … on the habits or capacities of the individuals. … [and] the powers of prolonging existence. … All varieties will therefore fall into two classes – those which … would never reach the population of the parent species, and those which would in time obtain and keep a numerical superiority.” [57-58]

4. **Replacement of Individuals, Varieties & Species.** “Now, let some alteration of physical conditions occur in the district … tending to render existence more difficult to the species in question; it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organized variety would suffer first, and, were [the] pressure severe, must soon become extinct. The
same causes continuing in action, the parent species would next suffer … , and with a recurrence of similar unfavourable conditions might also become extinct. The superior variety would then alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species … ” [p. 58]

5. Continuing Divergence from the Original Type. “The variety would now have replaced the species, of which it would be a more perfectly developed and more highly organized form. … Such a variety could not return to the original form; for that form is an inferior one, and could never compete with it for existence. … But this new, improved, and populous race might itself … give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must, by the same general law, in their turn become predominant. Here, then, we have progress and continued divergence deduced from the general laws which regulate the existence of animals in a state of nature, and from the undisputed fact that varieties do frequently occur.” [58-59]

6. Selection Not Frustrated by Chance. “Now the scale on which nature works is so vast … that any cause, however slight … must in the end produce its full legitimate results.” [p. 59]

Figure 3.15. Successive tosses of an honest coin. As \( n \to \infty \), the proportion, \( p \), of heads \( \to \frac{1}{2} \), which is the a priori expectation.
7. **Domestic Varieties Cannot Survive in the Wild.** Our quickly fattening pigs [*etc.*] … could never have come into existence in a state of nature, because the very first step towards such inferior forms would have led to the rapid extinction of the race … Domestic varieties, when turned wild, must return to something near the type of the original wild stock, or become altogether extinct.” [p. 60]

8. **Acquired Characters Not Inherited.** “Neither did the giraffe acquire its long neck by desiring to reach the … more lofty shrubs, and constantly stretching its neck …, but because any varieties … with a longer neck … secured a fresh range of pasture … [unavailable to] their shorter-necked companions, and on the first scarcity of food were … enabled to outlive them.” [p. 61]

9. **Trade-offs.** “We have also here [a] … cause … for that balance so often observed in nature, — a deficiency in one set of organs always being compensated by an increased development of some others ….” [p. 62], *i.e.*, varieties deficient in multiple ways would be outcompeted.
Wallace anticipates contemporary ecological theory:

1. Equilibrium density, not reproductive rate, determines the outcome of competition (Gause, 1934; MacArthur, 1962; MacArthur and Levins, 1967).

   “All varieties will therefore fall into two classes—those which under the same conditions would never reach the population of the parent species, and those which would in time obtain and keep a numerical superiority.” [p. 58]

2. Invasibility a fitness criterion.

   “The variety would now have replaced the species, of which it would be a more perfectly developed and more highly organized form. It would be in all respects better adapted … Such a variety could not return to the original form; for that form is an inferior one, and could never compete with it for existence.” [p. 58]


4. Winnowing within population diversity consequent to periods of environmental stress (Grant and Grant, 2002).

5. Contra Bulmer (2005), Wallace’s argument RE good vs. bad years does work – provided different genotypes have different ecological requirements.
Figure 3.17. Competition in good times (left) and bad (right) for varieties (genotypes) with partially non-overlapping niches. Shown here are zero growth isoclines, $\dot{X} = 0$ and $\dot{Y} = 0$, i.e., the combined densities, $(X, Y)$, for which $dX/dt = 0$ and $dY/dt = 0$ respectively. Points at which the isoclines intersect are equilibria. When resources are plentiful, the isoclines intersect at a point (•) corresponding to positive densities of both, in which case and the two types coexist. When resources are scarce, the isoclines intersect in the 4\textsuperscript{th} quadrant (equilibrial numbers of $Y$ negative), and $X$ drives $Y$ to extinction. Wallace’s argument works if one assumes that his superior and inferior varieties have different ecological requirements. If, on the other hand, the two varieties have identical requirements, the isoclines are parallel, and the probability of coexistence essentially zero.
Darwin also recognized that inferior and superior varieties can coexist. From his 1857 letter (DCP-LETT-2136) excerpted in DW58, we read

“I cannot doubt that during millions of generations individuals of a species will be occasionally born with some slight variation, profitable to some part of their economy. Such individuals will have a better chance of surviving, and of propagating their new and slightly different structure; and the modification may be slowly increased by the accumulative action of natural selection to any profitable extent. The variety thus formed will either coexist with, or, more commonly, will exterminate its parent form.” [Darwin and Wallace 1858, 52]

1. Which is relevant to disputes among historians as to the degree to which the two naturalists’ theories really were the same.

Darwin’s Contributions to DW58.

• From the 1844 Essay.

1. **Excess Biotic Potential.** Even slow breeding species, such as man, would quickly outstrip their food supply were there no checks.

2. **Changing Conditions Induce Variability.** “… changes of external conditions would, from their acting on the reproductive system, probably cause the organization of those beings … most affected to become, as under domestication, plastic.”

3. **Struggle for Existence.** “All nature is at war” [quoting De Candolle (Swiss botanist)]. … Can it be doubted, from the struggle each individual has to obtain subsistence, that any minute variation … adapting that individual better to the new conditions, would tell upon its vigour and health? … it would have a better chance of surviving; and those of its offspring which inherited the variation, be it ever so slight, would also have a better chance.”

4. **Natural Selection.** “Yearly more are bred than can survive; the smallest grain in the balance, in the long run, must tell on which death shall fall, and which shall survive. Let this work of selection on the one hand, and death on the other, go on for a thousand generations, who will pretend to affirm that it would produce no effect …?”
5. **Sexual Selection.** “... there is a second agency at work in most unisexual animals, ... namely, the struggle of the males for the females. These struggles are generally decided by the law of battle, but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship ... The most vigorous and healthy males, implying perfect adaptation\[19\] must generally gain the victory in their contests.”

- From the 9/5/1857 letter (DCP-2136), to Asa Gray.

1. **Artificial Selection.** “It is wonderful what the principle of selection by man, that is the picking out of individuals with any desired quality, and breeding from them, and again picking out, can do.”

2. **Darwin’s Demon.** “Now suppose there were a being who did not judge by mere external appearances, but who could study the whole internal organization, who was never capricious, and should go on selecting for one object during millions of generations; who will say what he might not effect? In nature we have some slight variation occasionally in all parts; ... and ... geology shows us what changes have taken place .... We have almost unlimited time; ... millions on millions of generations.”

3. **Natural Selection.** “Only a few of those annually born can live to propagate their kind. What a trifling difference must often determine which shall survive, and which perish!”

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\[19\] Rediscovered by Brown and Brown (1984) – their “truth in advertising” hypothesis.”
4. **Environmental Change Induces Variation.** “Now take the case of a country undergoing some change. This will tend to cause some of its inhabitants to vary slightly …”

5. **Principle of Divergence (PoD) and Affinity.** “… the varying offspring of each species will try … to seize on as many and as diverse places in the economy of nature as possible. Each … will … thus exterminate its less well-fitted parent. This I believe to be the origin of the classification and affinities of organic beings …; for organic beings always seem to branch and sub-branch like the limbs of a tree …, the flourishing … twigs destroying the less vigorous—the dead and lost branches rudely representing extinct genera and families.”

**Figure 3.18.** The only illustration in the 1st edition of *The Origin* depicts dichotomous branching.
Elucidation of the PoD a topic of continuing interest.

1. According to his autobiography (Barlow, 1958), Darwin didn’t twig to PoD until after writing the 1844 essay.

“… at that time I overlooked one problem of great importance; and it is astonishing to me ... how I could have overlooked it and its solution. This problem is the tendency in organic beings descended from the same stock to diverge in character as they become modified. That they have diverged greatly is obvious from the manner in which species of all kinds can be classed under genera, genera under families, ... and so forth; and I can remember the very spot in the road, whilst in my carriage, when to my joy the solution occurred to me ... “ [p. 120]

2. But the idea, as opposed to the name, appears to date to the 1844 essay [F. Darwin, 1909, xxiii-xxiv, 208-210 (Origin of genera and families); Richards, 2012].

3. Still CD felt PoD critical: along w. NS, the “key-stone of my book”; motivated inclusion of Gray letter in DW58.

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20 Letter to Hooker of 8 June, 1858 (DCP-2282).

21 Letter to Gray of 5 June, 1857 (DCP-2136).

a. Realization consequent to barnacle work that

i. Variation in nature more common than he had previously imagined (Browne, 1980, 58-59).

ii. Distinctions between allied species often blurred (Stott, 2003, 242) – shades of Lamarck.

b. Abandonment of isolation, so far as it applied to divergence, in favor of ecological specialization.

c. Assumption that differences in habits, mating preferences, etc., prevent “swamping” of new variations, thereby allowing for sympatric speciation.

d. Decreasing emphasis on the physical environment as a selective force and increasing emphasis on

i. Biotic interactions, e.g., competition causing niche expansion within and divergence between populations.

ii. Complex ecological interactions that can beget un-anticipated consequences.
5. From *The Origin*: Example of complex biotic interactions.

“I have found that the visits of bees, if not indispensable, are at least highly beneficial to the fertilisation of our clovers; but humble-bees \(^{[22]}\) alone visit the common red clover (*Trifolium pratense*), as other bees cannot reach the nectar. Hence I have very little doubt, that if ... humble-bees became extinct ... red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends ... on the number of field-mice, which destroy their ... nests; and Mr. H. Newman ... believes that ‘more than two thirds of them are thus destroyed all over England.’ Now the number of mice is largely dependent ... on the number of cats; and Mr. Newman says, ‘Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.’ Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district! [CD, 1859, 73-74]

\(^{[22]}\) *i.e.*, “bumblebees”
Figure 3.20. Top. Darwin’s example of complex ecological interactions. By their negative effect on field mice, which in turn destroy bumblebee nests, village cats promote (dashed blue line) the pollination and hence the abundance of red clover. Bottom. Self-satisfied (recently fed?) feline animal.
6. Darwin’s changing views on **sympatric vs. allopatric** speciation.

   a. Didn’t sit well with Ernst Mayr (1992) who would famously **champion** allopatric speciation a century later.

   b. Ignored Lyell’s **Principal of Preoccupancy** (PoP – see Lecture II).

7. It is undoubtedly true that PoP limits **in situ** adaptation.

   a. What **Lyell missed**, and what **Darwin now deemphasized**, was isolation as a **speciation facilitator**.

   b. Too bad! **Adaptive radiations** on **oceanic islands** and **after mass extinctions** critical counter examples.
Evolution According to Darwin.

Figure 3.21. “Darwin’s theory of evolution reduced to boxes and arrows. Note that the Conditions of Life can induce both random and adaptive variation, both of which are acted upon by selection. Compared to Lamarck’s theory, there are the following differences: Deleted – inherent tendency to progress; Retained – Inheritance of acquired characters; Added – natural and sexual selection. Compare with the corresponding diagrams in Lectures1 and 2.
• **Variation** (assumed heritable) plus **selection** (differential survival / reproduction) the major, but not the sole, evolutionary mechanism (Figure 3.21).

• Darwin recognized three principal sources of variability:

  1. Use and disuse.

  2. Conditions of life.

  3. Inherent.

• Over the years, Darwin **blew hot and cold** as to their relative importance.

  1. To Asa Gray (5 September, 1857; DCP-2136):

     "This [environmental change] will tend to cause some of its inhabitants to vary slightly – not but that I believe most beings vary at all times enough for selection to act on them." [Emphasis added]

  2. To Wallace (1 May, 1857; DCP-2086):

     "I most entirely agree with you on the little effects of "climatal [sic] conditions," which one sees referred to ad nauseam in all books: I suppose some very little effect must be attributed to such influences, but I fully believe that they are very slight."
3. But later, Darwin placed greater emphasis on use and disuse and direct environmental induction.

   a. Recall (Lecture I) his correspondence (1868) with J. J. Weir on inherited injuries.

   b. More explicitly, his Letter to Nature (1880):

      “I believe that no one has brought forward so many observations on the effects of the use and disuse … as I have done in my ‘Variation of Animals and Plants under Domestication’…”

4. Nor was Darwin’s interest restricted to his later years.

   a. In a questionnaire distributed to breeders in 1839, he requested examples of offspring having “inherited peculiarity of body form” from “parents trained to some particular way of life” (Darwin, 1839b, p.6)

   b. Likewise, his “provisional hypothesis of pangenesis” (Darwin, 1868, v2)

      i. Postulated a mechanism by which acquired characters could be inherited.

      ii. Predates (Olby, 1963, 251) the attacks later mounted by Fleeming Jenkin and Lord Kelvin (See Lecture IV).
• **Indirect vs. Direct Action of the Conditions of Life.**

1. **Indirect action:**

   a. Environmental factors, *changes* in an organism’s circumstances in particular, affect the *germ* so as to *promote variability* much in the way that we now understand mutagens affect DNA.

   b. Hence rearing animals under new circumstances, *e.g.*, under domestication, *promotes* variability.

   “With respect to what I have called the indirect action of changed conditions, namely, through the reproductive system of being affected, we may infer that variability is thus induced, partly from the fact of this system being extremely sensitive to any change in the conditions, and partly from the similarity ... between the variability which follows from the crossing of distinct species, and that which may be observed with plants and animals when reared under new or unnatural conditions.” [5th edition of *The Origin* (1869, 9-10)]

2. **Direct action** (environmental factors acting on the *soma* and inducing *adaptive* variations) received increasing emphasis in response to mounting criticism of variation and selection as sufficient evolutionary mechanisms (Lecture IV).

“[Darwin’s] books ... devote much more attention to variation than to natural selection, for he knew that no satisfactory theory of ... evolutionary change could be constructed until the causes of variation ... had been elucidated.” [Gould, 1993]

\textit{i.e.}, without heritable variation, \textbf{selection impotent}.

- Darwin also distinguished between what he called “single” and “individual” variations or differences.

1. \textbf{Single differences} referred to infrequent, qualitative variations, such as polydactyly.

2. \textbf{Individual differences} referred to variation in \textbf{metric characters} such as length and weight, \textit{i.e.}, the usual variability one observes in a group of conspecifics.

3. The distinction would later become important (F. Darwin, 1887, v3, 107-108) eight years after \textit{The Origin’s} publication. See Lecture IV.
• **Evolutionary Progress.** From the 6\textsuperscript{th} and final edition of *The Origin* (Darwin, 1876, pp. 98-99):

1. “If we take as the standard of high organisation the amount of differentiation and specialisation of the several organs …, natural selection clearly leads towards this standard: for all physiologists admit that the specialisation [*sic*] of organs … is an advantage to each being; … .”

2. “But it may be objected that if all organic beings thus tend to rise in the scale, how is it that throughout the world a multitude of the lowest forms still exist …? Why have not the more highly developed forms everywhere supplanted and exterminated the lower? Lamarck, who believed in an innate and inevitable tendency towards perfection in all organic beings, seems to have felt this difficulty so strongly, that he was led to suppose that new and simple forms are continually being produced by spontaneous generation. *Science has not as yet proved the truth of this belief* … On our theory the continued existence of lowly organisms offers no difficulty; for natural selection … does not necessarily include progressive development – it only takes advantage of such variations as arise and are beneficial to each creature under its complex relations of life.” [Emphasis added]

3. In other words, **evolution leads to progress except when it doesn’t.** (Sigh!)
Darwin vs. Wallace: Similarities.

- “Darwin’s Facts” (Lecture I) were Wallace’s facts.
  
  1. Patterns of species distribution in time and space.
  
  2. Observed patterns of affinity (tree of life).
  
  3. Vestigial organs.
  
  4. *Etc*.

- Accounted for by DwM.

- **Natural selection**, the principal mechanism by which species become adapted to their circumstances.

- Extinction of ancestral varieties / species by descendent varieties / species \(\Rightarrow \text{gaps in affinity} \) (Darwin’s “Principle of Divergence”).

**Figure 3.23.** Proposed “dual origin” theory of living Mammalia unites marsupials and eutherians. Anatomical isolation of egg laying species (monotremes) is consequent to extinction of intermediate forms (circled). From *Science*. 3 January, 2001.
Darwin vs. Wallace: Differences.

- **Individual vs. Group Selection.**


   “Wallace may have realized that the struggle for existence among individuals actually produced the permanent varieties (the essence of Darwin's theory), but he described natural selection *only* in terms of a struggle among the varieties themselves.” [Bowler (1974), p. 17. Emphasis added]

2. Likewise, Gould, Ruse and others dismiss Wallace’s view as **group selectionist** (Fagan, 2007, 628).

3. But this conflicts with Wallace’s belief that

   a. Competition is experienced by individuals and that those eliminated are less fit than those that survive.

   “…The numbers that die annually must be immense; and as the individual existence of each animal depends upon itself, those that die must be the weakest—the very young, the aged, and the diseased,— while those that prolong their existence can only be the most perfect in health and vigour—those who are best able to
obtain food regularly, and avoid their numerous enemies. It is …
‘a struggle for existence,’ in which the weakest and least perfectly
organized must always succumb.”

b. Likewise, his belief that the giraffe’s long neck the
result of competition for food between individuals.

c. Between group competi-
tion analogous to compe-
tition between individuals

"what takes place among the
individuals of a species must
also occur among the several
allied species of a group,—viz.
that those which are best
adapted to obtain a regular
supply of food, and to defend
themselves against the at-
tacks of their enemies and the vicissitudes of the seasons, must
necessarily obtain and preserve a superiority in population…
[DW58, 56-57; Emphasis added]

4. Moreover, it was Wallace who took the greater interest in
intraspecific variation when confronting nature in the field
(Fagan, 2007).
Variability.

1. In contrast to Darwin’s complicated partitioning of variability and its sources, Wallace believed that the kinds and causes were multiple and irrelevant.

2. Writing to a critic, Wallace (1905, II, 85) observed that

“'Spontaneous variability' is a ... universal fact in the organic world ... and is probably a fundamental fact, due to the impossibility of any two organisms ever having been subjected to exactly identical conditions, and the extreme complexity both of organisms and their environment. This normal variability wants no other explanation. Its absence is inconceivable, because it would imply that diversity of conditions produced identity of result. The wishes or actions of individuals may be one of the causes of variability, but only one out of myriads. Now to say that such an [sic] universal fact as this cannot be taken as a basis of reasoning because the exact causes of it are unknown in each case [sic], is utterly illogical. The causes of gravitation, of electricity, of heat, of all the forces of nature are unknown. Can we not, then, reason on them, and explain other phenomena by them, without having the words 'unknown causes' substituted, and thus making nonsense?”
Domestication.

1. Darwin viewed products of domestication as analogous to species produced in nature – in which regard he had been reading Herschel who believed that

“the most convincing evidence that something is a *vera causa* ... is when we can argue analogically from something else which we know already to be a *vera causa*. ... We have in artificial selection, a force *directly perceived and caused by us*; hence, analogically, given the struggle and given wild variation, it cannot be denied that there is a natural force of selection making different organisms, just as man makes different organisms. [Ruse, 1975, pp. 175-176]

2. Wallace viewed domesticated races as monstrosities that cannot survive absent man’s care.

“Domestic varieties, when turned wild, *must* return to something near the type of the original wild stock, or become altogether extinct.” [DW58, 60]

“It has always been considered a weakness in Darwin's work that he based his theory, primarily, on ... variation in domesticated animals and ... plants. I have endeavoured to secure a firm foundation for the theory in the variations of organisms in a state of nature;” [Wallace, 1889, vi]
• Evolutionary mechanisms.

1. Darwin viewed selection as one of several causes of evolutionary change – e.g., The Origin’s famous concluding paragraph.

“These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the external conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.” [Darwin, 1859, 490-491]

2. Wallace rejected all other material forces while at the same time advocating the necessity of immaterial forces in the case of man and certain other instances – see below.
• Sexual selection.

1. Darwin (1871) emphasized importance of **male-male competition** and **female choice** in human evolution.

   “... greater size, strength, courage ... of man ... were acquired during primeval times, and have subsequently been augmented, chiefly through the contests of rival males for the possession of the females. ... our male ape-like progenitors acquired their beards as an ornament to charm or excite the opposite sex ... The females apparently were first denuded of hair in like manner as a sexual ornament; but they transmitted this character almost equally to both sexes ...” [1871, v2, pp. 382-383]

2. Wallace emphasized


   b. Lack of female opportunity to choose in monogamous species with 1:1 sex ratio.

      “... there is no evidence ... that the number of healthy and competent males that fail to find mates bears any large proportion to those that do find them. ...” [Wallace, 1892, p. 750]

   c. Females’ typically less gaudy coloration reflects greater for concealment.
• Insufficiency of Secondary Laws

1. Wallace: Secondary laws cannot account for a variety of phenomena that can only be understood by positing the existence of an "organizing mind." Said phenomena include

a. Human characters that could not have been selected for because
   i. Primitive man had no need for them, e.g., intelligence; manual dexterity [Wallace, 1870, 356]
   ii. Or would have been selected against, e.g., hairlessness (Wallace, 1870, 356).

b. Non-human anatomical and developmental complexity, e.g., feathers; insect metamorphosis, which he believed could not have evolved absent a guiding hand (Wallace, 1914, 286-304).

Figure 3.25. The Engis Neanderthal calvarium was discovered in 1829. The existence of large-brained fossil hominins was a puzzle for 19th century evolutionists, a difficulty not resolved until the discovery of australopiths in South Africa.
Figure 3.26. Contemporary view of feather evolution. Only feathers of modern birds make for efficient flight.
2. Darwin:

a. Animal and human instincts / intelligence form a continuum — e.g., regarding human sympathy:

“Many animals, however, certainly sympathise [sic] with each other's distress or danger. This is the case even with birds; Capt. Stansbury found ... an old and completely blind pelican, which was very fat, and must have been long and well fed by his companions. Mr. Blyth ... saw Indian crows feeding two or three of their companions which were blind; and I have heard of an analogous case with the domestic cock. We may, if we choose, call these actions instinctive; but such cases are much too rare for the development of any special instinct. I have myself seen a dog, who never passed a great friend of his, a cat which lay sick in a basket, without giving her a few licks with his tongue, the surest sign of kind feeling in a dog.” [Darwin, 1871, I, 77]

b. Likewise, the human conscience.

“I agree with Agassiz that dogs possess something very like a conscience. They certainly possess some power of self-command, and this does not appear to be wholly the result of fear. As Braubach [German psychologist (Secord, 2009)] remarks, a dog will refrain from stealing food in the absence of his master.” [Ibid, p. 78]

c. Note: Continuity doesn’t counter lack of utility.
3. **In sum: Wallace.**

a. **An Intelligent Designer:** who believed that

“some higher intelligence may have directed the process by which the human race was developed ...”  
[Wallace, 1870, pp. 359-360]

b. **Continuing improvement of man’s “mental and moral nature” being evolution’s intended object, relieves mankind of**

“the crushing mental burden ... [of supposing] ... that all the slow growths of our race struggling towards a higher life ... all the struggles for freedom, all the efforts towards justice ... shall leave not a wrack behind.”  
[Wallace, 1879, 476-477]

c. **All of which may give added meaning to his referencing Vestiges as an “ingenious hypothesis”, i.e., Chambers’ “Law of Development”, whereby life’s history is one of continuing progress.**
In sum: Darwin.

a. A materialist.

“The old argument from design in Nature, as given by Paley, which formerly seemed to me so conclusive, fails, now that the law of natural selection has been discovered. We can no longer argue that, for instance, the beautiful hinge of a bivalve shell must have been made by an intelligent being, like the hinge of a door by man. There seems to be no more design in the variability of organic beings, and in the action of natural selection, than in the course which the wind blows. [F. Darwin, 1887, v1, p. 133]

b. To whom Wallace’s spiritualism an anathema.

“If you had not told me [23] I sh’d have thought that they had been added by some one [sic] else. As you expected I differ grievously from you, & I am very sorry for it. I can see no necessity for calling in an additional & proximate cause in regard to Man.” [CD to ARW, 14 April, 1869; DCP-6706]

• An Interesting Project: Evaluate Wallace’s scientific arguments for the existence of a controlling, non-material mind in light of current understanding.

23 The reference is to a letter from ARW to CD dated 24 March, 1869.
• Age and Predilection.

1. Darwin (1809-1882): Older; an “Oxbridge” gent; independently wealthy.

2. Wallace (1823-1913): Younger; self-educated; supported himself via the sale of exotic specimens.

3. Divergent reactions to *Vestiges* consistent with their differing ages, stations, *etc*. Additionally,

   a. Darwin had a **proprietary interest** in dising *Vestiges*, **and did so** in correspondence (Schwartz, 1990) as well as in the Historical Sketch.\(^{24}\)

   b. Wallace, to the contrary, was inspired by *Vestiges*. Didn’t begin seriously thinking about species til 1847.

4. Different political views: **Whig**\(^{25}\) vs. **Utopian Socialist**.

\(^{24}\) Schwartz further notes that Darwin also had a personal bone to pick with Chambers whom he strongly suspected to be the anonymous author.

\(^{25}\) Whiggism was more or less analogous to today’s libertarianism and supported by non-Anglican protestants, abolitionists and the emerging middle classes. Darwin’s father, Robert, a closet atheist, staunch liberal and extremely successful investor (J. Browne, 1995. *Charles Darwin: Voyaging*. Ch. 1), was representative. On the political spectrum, Whigs were between conservative Tory (God, King and Country) aristocrats and the street radicals who urged outright revolution (Lecture V).
5. Desmond and Moore (2009) emphasize Darwin’s opposition to slavery. But compare Wallace and Darwin on savage and civilized man:

a. **Wallace on Injustice / Exploitation of the Poor.**

“Our vast manufacturing system, our gigantic commerce, our crowded towns and cities, support and continually renew a mass of human misery and crime absolutely greater than has ever existed before. They create and maintain in life-long labour an ever-increasing army, whose lot is the more hard to bear, by contrast with the pleasures, the comforts, and the luxury which they see everywhere around them, but which they can never hope to enjoy; and who, in this respect, are worse off than the savage in the midst of his tribe.

“This is not a result to boast of, or to be satisfied with; and, until there is a more general recognition of this failure of our civilization--resulting mainly from our neglect to train and develop more thoroughly the sympathetic feelings and moral faculties of our nature, and to allow them a larger share of influence in our legislation, our commerce, and our whole social organization--we shall never, as regards the whole community, attain to any real or important superiority over the better class of savages.” [The Malay Archipelago, Vol. II, pp. 462-463]

“With savages, the weak in body or mind are soon eliminated; and those that survive commonly exhibit a vigorous state of health. We civilised [sic] men, on the other hand, do our utmost to check the process of elimination; we build asylums for the imbecile, the maimed, and the sick; we institute poor-laws,[26] and our medical men exert their utmost skill to save the life of every one to the last moment. There is reason to believe that vaccination has preserved thousands, who from a weak constitution would formerly have succumbed to smallpox. Thus the weak members of civilised societies propagate their kind. No one who has attended to the breeding of domestic animals will doubt that this must be highly injurious to the race of man. … [E]xcepting in the case of man himself, hardly any one is so ignorant as to allow his worst animals to breed …” [1871, Vol. 1; p. 168]

[26] The Poor Law Amendment Act was passed by Parliament in 1834 and accelerated the already ongoing replacement of alms for the indigent by the rigors of the workhouse. That Darwin, writing in 1868, could point approvingly to such an institution speaks volumes, it might be argued, of his upper class, squire’s perspective. One cannot help but wonder if he did not approve workhouse mortality rates, which were higher than the norm, even making allowance for the admission of sickly individuals (Davenport, unpubl.). Also worth noting is that the ranks of the poor were swelled by soldiers, many of whom were disabled, returning from the Napoleonic Wars and by so-called Corn Laws that inflated the price of grain. See Lecture V.
c. Darwin accepted the “scientific” argument for eugenics but rejected the practice on moral grounds:

“The aid which we feel impelled to give to the helpless is mainly an incidental result of the instinct of sympathy, which was originally acquired as part of the social instincts, but subsequently rendered ... more tender and more widely diffused. Nor could we check our sympathy ... without deterioration in the noblest part of our nature. Hence we must bear without complaining the undoubtedly bad effects of the weak surviving and propagating their kind;” [Ibid, pp.168-169]

d. Wallace’s (1890) alternative was

i. Creation of an egalitarian society: “... when we have cleansed the Augean stable of our existing social organization ... the future of the race will be ensured ...” [pp. 330-33].

ii. Delayed reproduction: Marriage (and the production of children) to be delayed until age of 30 or older.

iii. Female choice: Educated women would reject idle, selfish men as fathers of their children, the quality of which would thereby be improved – which seems to be contradicted by his argument against sexual selection
• Differences Aside.

1. As Wallace (1889) later observed,

“Darwin wrote for a generation which had not accepted evolution … . He did his work so well that ‘descent with modification’ is now universally accepted as the order of nature in the organic world; and the rising generation of naturalists can hardly realise [sic] the novelty of this idea, or that their fathers considered it a scientific heresy to be condemned rather than seriously discussed.” [p. v]

2. But it was not just Darwin.

3. Rather, it was accumulating evidence for the reality of phylogenic lineages and transitional forms.

   a. Horses with five toes; and

   b. Birds with teeth.

Figure 3.28. Hesperornis. A flightless toothed Cretaceous bird as reconstructed by O. C. Marsh in his 1880 monograph.
4. As Darwin acknowledged to O. C Marsh,

“Your work on these old birds and on the many fossil animals of North America, has afforded the best support to the theory of Evolution, which has appeared within the last twenty years.” [F, Darwin, 1887, 3, 241-242. Letter of 31 August, 1880]

5. Still while DwM became the conventional wisdom, the mechanism by which old species are modified into new ones remained controversial.

a. Thus, Huxley (1896) would later write

“… the fact of evolution is to my mind sufficiently evidenced by palæontology; and I remain of the opinion … that until selective breeding is definitely proved to give rise to varieties infertile with one another, the logical foundation of the theory of natural selection is incomplete. [pp. v-vi]

b. Or as Wallace (1898) put it,

“What was a ‘great heresy’ to Sir John Herschel in 1845, and ‘the mystery of mysteries’ … is now the common knowledge of every clever schoolboy … The only thing discussed now is … whether or not the causes alleged by Darwin are themselves sufficient to explain evolution of species, or require to be supplemented by other causes …” [p. 142]
# Darwin-Wallace Timeline: Post-Origin.

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<th>Date</th>
<th>Darwin</th>
<th>Wallace</th>
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<tr>
<td>1859</td>
<td>Publishes <em>Origin</em>; Sells out 1st day.</td>
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<tr>
<td>Next 20 years</td>
<td>Completes and expands <em>Natural Selection</em> piecemeal.</td>
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<td>Spring 1862</td>
<td>Returns to England</td>
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<td>1868</td>
<td>Publishes <em>Animals and Plants under Domestication</em>. Includes “Provisional Hypothesis of Pangenesis”</td>
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<td>1863</td>
<td></td>
<td>Publishes <em>The Geological Evidences of the Antiquity of Man</em></td>
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<td>1869</td>
<td>Publishes <em>Malay Archipelago</em></td>
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<td>1870</td>
<td>Publishes <em>Contributions to the Theory of Natural Selection.</em></td>
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<td>1871</td>
<td>Publishes <em>Descent of Man, and Selection in Relation to Sex</em></td>
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<td>1872</td>
<td>Publishes <em>Expression of the Emotions in Man and Animals.</em></td>
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<td>1875</td>
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<td>1882</td>
<td>Dies</td>
<td>Becomes leading defender of evolution, CD in particular.</td>
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<tr>
<td>1889</td>
<td>Publishes <em>Darwinism</em></td>
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<td>1923</td>
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