Some of the great scientists, carefully ciphering the evidences furnished by geology, have arrived at the conviction that our world is prodigiously old, and they may be right but Lord Kelvin is not of their opinion. He takes the cautious, conservative view, in order to be on the safe side, and feels sure it is not so old as they think. As Lord Kelvin is the highest authority in science now living, I think we must yield to him and accept his views.” [Mark Twain quoted by Burchfield (1990)]
Lecture IV. The Demise of Darwinism.

I. A Paucity of Time.
   A. The Scylla and Charybdis between which Darwin found himself having to navigate by 1870 were paucities of
      1. Time;
      2. Heritable variation.

B. Denudation of the Weald.

   “I ... give one other case, the well-known ... denudation [erosion] of the Weald. ... [It] has been a mere trifle, in comparison with that which has removed masses of our Palaeozoic strata ... . Yet it is an admirable lesson to stand on the North Downs and to look at the distant South Downs; ... [O]ne can safely picture ... the great dome of rocks which must have covered up the Weald within ... since the latter part of the Chalk formation [lower Cretaceous]. The ... thickness of the several formations is on an average about 1100 feet ... . If, then, we knew the rate at which the sea commonly wears away a line of cliff of any given height, we could measure the time requisite to have denuded the Weald. ... [A]ssume that the sea would eat into cliffs ... at the rate of one inch in a century. ... At this rate, ... the denudation of the Weald must have required ... three hundred million years.” [*The Origin*, 1st Edition. Ch. 9].

Figure 1. Geology of south-eastern England. The High Weald is in lime green (9a); the Low Weald, darker green (9). Chalk Downs, pale green (6).
1. Darwin’s geological model no longer accepted.
2. Base of the Cretaceous about 105 Mya (million years ago). Darwin’s estimate about 3.5 times too long.

C. The Time Killer.
1. William Thomson (Lord Kelvin) argued that

“To suppose, as Lyell, ... an endless cycle, violates the principles of natural philosophy in exactly the same manner, and to the same degree, as to believe that a clock constructed with a self-winding movement may fulfil the expectations of its ingenious inventor by going for ever.” [t62]¹

¹ At least as early as 1852 (“On a Universal Tendency in Nature to the Dissipation of Mechanical Energy”), Thomson asserted that the age of the earth is finite, but didn’t give an estimate.
2. Calculated [t66] the age of the habitable earth far less than Darwin’s estimate of hundreds of millions.²
3. Following Buffon³, Thompson imagined that the earth had cooled from a molten state.
4. Heat radiated from the earth’s surface to space.
5. => a temperature gradient from core to surface that diminished as the earth cooled with passage of time.
6. Gradient can be estimated from coal mine temperatures.
7. From this, Kelvin produced estimates of the age of the habitable earth ranging from 28 to 100 my.

D. Kelvin also calculated age of sun with comparable results.

E. Darwin had imagined effectively limitless amounts of time.
1. Had no response to Kelvin save to
   a. Strike estimates from later editions of *The Origin*.
   b. Emphasize mechanisms that would speed things up.
2. To Hooker, he wrote in 1867

   “I cannot think how you can attach so much weight to the physicists, seeing how Hopkins, Hennessey, Haughton, and Thomson have enormously disagreed about the rate of cooling of the crust; remembering Herschel's speculations about cold space,⁴ and bearing in mind all the recent speculations on change of axis, I will maintain to the death that your case of Fernando Po and

²See [http://www.me.rochester.edu/courses/ME223/webexamp/kelvin.pdf].

³ Buffon’s heated metal spheres of different size, observed the time required to cool, scaled up to the size of the earth. Estimated the earth 3,000,000 years old, later reduced to 75,000 years.

⁴ For an account of Herschel's views, see *Principles*, 1872, Edition XI., Volume I., page 283.
Abyssinia\textsuperscript{[5]} is worth ten times more than the belief of a dozen physicists.”

F. Kelvin’s calculations deeply disturbing to geologists. In 1895, Archibald Geikie later observed

“Geologists have not been slow to admit that they were in error in assuming that they had an eternity of past time for the evolution of the earth’s history. They have frankly acknowledged the validity of the physical arguments which go to place more or less definite limits to the antiquity of the earth. They were on the whole, disposed to acquiesce in the allowance of 100 millions of years granted to them by Lord Kelvin, for the … whole … of geological history. But the physicists have been insatiable and inexorable. \textit{As remorseless as Lear’s daughters, they have cut down their grant of years by successive slices, until some of them have brought the number to something less than ten millions.” [Emphasis added].}\textsuperscript{6}

G. As discussed by Powell [p01], geologists produced their own (marvelously inventive) estimates of the age of the earth.

1. All conformed to Kelvin’s maximum allowance.
2. All were wrong.

\textsuperscript{5} See \textit{The Origin}, 6\textsuperscript{th} edition, page 337: "Dr. Hooker has also lately shown that several of the plants living on the upper parts of the lofty island of Fernando Po and on the neighbouring Cameroon mountains, in the Gulf of Guinea, are closely related to those in the mountains of Abyssinia, and likewise to those of temperate Europe.” Darwin evidently means that such facts are better evidence “deep time” than the discordant conclusions of the physicists.

\textsuperscript{6} The “allowance of 100 millions of years” refers to Kelvin’s first estimate [t62] of 98 my.
“Geologists set about trying to measure the length of geologic time by their own methods ... . But after laboriously calculating the age of the earth ... [they] required an external reference. Yet only one reference existed: the apparently exquisite mathematical calculation of the leading scientist of the day, Lord Kelvin, who had determined the age of the earth to be 100 million years. ... . To use a geological method and reach the same conclusion as Kelvin not only validated one's scientific acumen, it confirmed the stature ... of geology. The combination proved irresistible.

“No matter what assumptions and approaches they used, the hourglass calculators wound up agreeing with Kelvin.”

3. Late in the 19th century, Kelvin’s fundamental assumption – cooling from a molten state – questioned.
   a. “Mathematics may be compared to a mill of exquisite workmanship, which grinds you stuff of any degree of fineness; but, nevertheless, what you get out depends upon what you put in.” – Huxley, 1869
   b. But this line of argument also proved a dead end.

4. “Mother wit”:
   a.“Huxley could not understand, much less counter, Kelvin's mathematics, so he had to fall back on 'mother-wit' and his considerable rhetorical skills.” [p01].
   
   b.“Biology takes her time from geology. The only reason we have for believing in the slow rate of change in living forms is that they persist through a series of deposits which, geology informs us, have taken a long while to make. If the geological clock is wrong, all the naturalist will have to do is to modify his notions of the rapidity of change accordingly.” – Huxley, 1869.
5. Only with the discovery of radioactive decay, was the true age of the earth – 4.6 billion years – determined.

a. As Rutherford later reminisced,

“I came into the room, which was half dark, and presently spotted Lord Kelvin in the audience and realized that I was in trouble at the last part of my speech dealing with the age of the earth, where my views conflicted with his. To my relief, Kelvin fell fast asleep, but as I came to the important point, I saw the old bird sit up, open an eye and cock a baleful glance at me! Then a sudden inspiration came, and I said Lord Kelvin had limited the age of the earth, provided no new source was discovered. That prophetic utterance refers to what we are considering tonight, radium! Behold, the old boy beamed upon me.” [p01]

b. Observation had replaced deduction:

“Close to the time of his speech to the Royal Society, Rutherford was walking the McGill campus. In his pocket he carried a small black object, a specimen of a uranium oxide mineral called pitchblende. Meeting a colleague, Rutherford said, ‘Adams, how old is the earth supposed to be?’ The answer came back at Kelvin’s earlier figure of 100 million years. ‘I know,’ said Rutherford quietly, ‘that this piece of pitchblende is 700 hundred million years old.’

7 "It seems, therefore, on the whole most probable that the sun has not illuminated the earth for 100,000,000 years … . As for the future, we may say … that inhabitants of the earth cannot continue to enjoy the light and heat essential to their life, for many million years longer, unless sources now unknown to us are prepared in the great storehouse of creation." [t62]
II. The Problem with Kelvin’s Calculation.

A. Rutherford’s reference to new sources of heat suggests that Kelvin’s calculations could be squared with modern estimates of the earth’s age by including heat generated by radioactive decay of crustal deposits of radioactive minerals.

1. Would steepen the temperature gradient at earth’s surface.

2. Long part of the history of science folk lore – repeated by Eiseley (Ch.9).

B. In fact, adding the heat so generated affects the calculated age of the earth very little.

C. What is really wrong with the calculation is that it assumes that the interior of the earth is homogeneous.

D. Current models assume a crus-
tal cap that sits atop a viscous interior wherein heat is transmitted by convection – see England et al. (2007).

E. And this had been proposed by John Perry, Kelvin’s former assistant back in 1895!

1. Think plate tectonics!

2. Following his allusion to Lear’s daughters, Geicke (1895) had observed,

“So here the matter rested for some years, neither side giving way, and with no prospect of agreement. … However, as readers of Nature will have observed, the question has been taken up anew from the physical side. Prof. Perry … finds that on assumption that the earth is not homogeneous as postulated by Lord Kelvin, but possesses a much higher conductivity and thermal capacity in its interior than in its crust, its age may be enormously greater than previous calculations have allowed.”

F. Kelvin was wrong, not because radioactivity had not yet been discovered, but because he used the wrong model.
III. What goes around …

A. Confirmation of “deep time” relieved evolutionists of the need for mechanisms that would speed things up.

B. But the problem of insufficient time would later arise in a different context.

C. With advent of radioactive dating came the ability to date fossils relative important events in earth’s history:

1. Origin of the Earth by accretion 4500-4600 Mya.

2. Bombardment phase (period of large-scale impacts; local or global re-melting of the earth’s surface) ends 4000-3800 Mya.

3. Earliest Life. $^{12}$C enriched organic matter (signature of photosynthesis) may date to 3800 Mya and the oldest known microfossils to 3500 Mya.

D. => a narrow “window of opportunity” for life to evolve.

1. Large scale impacts until 4000-3800 Mya.

2. 1$^{st}$ fossils 3500 Mya already complex.

Figure 3. A 3.5 billion year-old fossilized photosynthetic bacterium similar to contemporary cyanobacteria from Western Australia.
3. If $^{12}\text{C}$ enrichment $\Rightarrow$ biological activity, one has life emerging at end of bombardment period.

4. Otherwise maximum of 500,000 years to get from pre-life to cyanobacteria.

5. Along with likely absence of a strongly reducing environment,\(^8\) lends support to

a. Origin of life in protected environments – e.g., deep-sea hydrothermal vents.

b. Theories of extraterrestrial origin including “directed” panspermia, which has been advocated by no less an authority than Francis Crick.

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\(^8\) The more reducing the environment, the easier it is to synthesize biological molecules such as amino acids.
IV. While on the Subject of Time: The Cambrian Explosion.

A. Sudden appearance of fossils at the base of the Cambrian a major concern to Darwin.

1. From Chapter 9 (On the Imperfection of the Geological Record) of *The Origin*:

   “Most of the arguments which have convinced me that all the existing species of the same group have descended from one progenitor, apply with nearly equal force to the earliest known species. For instance, I cannot doubt that all the Silurian\(^9\) trilobites have descended from some one crustacean, which must have lived long before the Silurian age, and which probably differed greatly from any known animal.

   ... Consequently, if my theory be true, it is indisputable that before the lowest Silurian stratum was deposited, long periods elapsed, ...

   ... *To the question why we do not find records of these vast primordial periods, I can give no satisfactory answer.*” [Emphasis added].

2. Thereafter, Darwin discusses possible explanations:
   a. Lack of Precambrian fossiliferous rock due to metamorphosis.
   b. Infrequent / discontinuous preservation.

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\(^9\) In Darwin’s day, what we now call the Cambrian, was included in the Silurian.
B. We now know that the Cambrian explosion took place over some 10-15 million years as can be observed in locales where deposition was continuous:

1. The record (544 mya) begins with trace fossils (worm track, burrows, etc.) and small skeletal fossils representing a limited number of forms.

2. As one moves up the stratigraphic column, the abundance and complexity of both increase.

3. Fifteen million years into the Cambrian, one finds 80+ skeletal taxa.

4. Trilobites, the group most strongly associated with the Cambrian in popular lore, and brachiopods make their appearance no earlier than 530 Mya.

**Figure 5.** Estimated divergence times for selected metazoan phyla, based on seven genes, with standard errors indicated by shaded bars. The three estimated divergence times nest in agreement with well-corroborated phylogenetic relationships. Chordate-echinoderm and chordate-protostome divergence times are significantly different from each other. Divergence times among the three protostome phyla were not estimated. From Wray et al (1996).
5. Molecular genetics consistent with Precambrian divergence of major groups (Figure 5).

C. The Garden of Ediacara.
1. Since Darwin's time, a number of late Precambrian (565-543 Mya) metazoan assemblages have been discovered.

2. So-called “Ediacaran” faunas include soft-bodied forms and trace fossils.
   a. Manifest little evidence of body plans similar to those of existing phyla (Figure 6).
   b. Only modern group generally agreed to be represented is the cnidaria (coelenterates).
   c. McMenamin [m98] has proposed that Ediacaran life an independent, failed experiment.
      i. Ediacarans depended on algal symbiotes – hence the “Garden of Ediacara.”
      ii. No blastula stage – hence no development in conventional sense.
      iii. Composed of intercommunicating “cell families” – neither colonial nor metazoan.

3. Ediacara-like organisms types persisted into the mid-Cambrian – e.g., Burgess Shale.
D. Was the Cambrian Explosion Real?

1. If the molecular evidence to be believed, the various phyla that first appear in the lower stages of the Cambrian diverged long before that time.

2. Phylogenetic divergence of lineages does not necessitate morphological divergence, i.e., Cambrian taxa could date, absent hard parts to the Precambrian.

3. Either
   a. Most of the major taxa really did originate over a period of 10-15 million years, or
   b. Previously divergent lineages radiated into new niches and developed into contemporary phyla.
   c. But these organisms not Ediacarans.

4. Many factors have been suggested to account for explosive morphological change in the Cambrian:
   a. Increasing concentrations of oxygen made possible the secretion of hard parts.
   b. Increasing genome complexity, duplication of Hox genes, allowed for an evolutionary burst.
   c. Coevolutionary “arms race” => rapid change.
      i. Increasing presence of spines, rugosities, etc., in trilobites.
      ii. Shell thickening in mollusks.

5. Some or all of the above.
V. *The Origin in Review.*

A. Initial reception mixed.

1. *1st* round of reviews catalogued various the “deficiencies” one might expect.
   a. Limits to variability in contemporary species.
   b. Absence of species *in statu nascendi*.
   c. Absence of transitional forms in the fossil record.
   d. The Cambrian “explosion.”
   e. “Irreducible complexity” – structures that only work when fully formed –  *e.g.*, the vertebrate eye.
   f. Consistency not equivalent to proof –  *e.g.*, homology, development.
   g. Conflict with theology and the problem of man and his nature.
   h. *Etc.*

2. Even Huxley’s endorsements (1859) qualified.

   a. The persistence of ancient forms becomes an “unintelligible irregularity” when viewed from the perspective of separate acts of purposeful creation. But on assumption that

   “all living species are the result of the modification of other and simpler forms, the existence of these of these little altered persistent types … must indicate that they are but the final terms of an enormous series of modifications, which had their being in the great lapse of pregeologic time, and are now perhaps forever lost.”
b. “Lamarck guessed a solution, Vestiges perpetuated it; Darwin provided the answer.”

c. “Our object has been attained if we have given an intelligible, ... account of the established facts connected with species, and of the relation of the explanation of those facts offered by Mr. Darwin to the theoretical views held by his predecessors and ... to the requirements of scientific logic. We have ventured to point out that it does not, as yet, satisfy all those requirements; but we do not hesitate to assert that it is as superior to any preceding or contemporary hypothesis ... as was the hypothesis of Copernicus to the speculations of Ptolemy. But the planetary orbits turned out to be not quite circular after all, and, grand as was the service Copernicus rendered to science, Kepler and Newton had to come after him. What if the orbit of Darwinism should be a little too circular? What if species should offer residual phænomena, here and there, not explicable by natural selection?” [h60]

d. In fact, Huxley would continue to prefer *per saltum* to gradual change and to encourage Darwin to do some experiments that would actually derive one species from another.

B. Likewise, Asa Gray [g60] in correspondence with Darwin observed

1. “The moment I understood your premisses [*sic*], I felt sure you had a real foundation to hold on. Well, if one admits your premisses [*sic*], I do not see how he is to stop short of your conclusions, as a probable hypothesis at least.”

2. “It naturally happens that my review of your book does not exhibit anything like the full force of the impression the book has made
upon me. Under the circumstances I suppose I do your theory more good here, by bespeaking for it a fair and favourable consideration, and by standing non-committed as to its full conclusions, than I should if I announced myself a convert; nor could I say the latter, with truth.”

3. “Well, what seems to me the weakest point in the book is the attempt to account for the formation of organs, the making of eyes, etc., by natural selection. Some of this reads quite Lamarckian.”

4. The last point emphasized in Gray’s published review [g60], in which he compared the ideas of Darwin and Agassiz.

a. “From this generally accepted view the well-known theory of Agassiz and the recent one of Darwin diverge in exactly opposite directions.”

b. [The theory] of Agassiz … discards the idea of a common descent as the real bone of union among the individuals of a species, and also the idea of a local origin,— supposing, instead, that each species originated simultaneously, generally speaking over the whole geographical area it now occupies or has occupied, and in perhaps as many individuals as it numbered at any subsequent period.”

10 “[[I]ndependent, specific creation of each kind …, which reproduces its like from generation to generation … [A]ll species vary more or less … . But these variations are … limited if not transitory; so that the primordial differences between species … have not been effaced … . Consequently, whenever two reputed species are found to blend in nature through a series of intermediate forms, community of origin is inferred, and all the forms … are held to belong to one species.”
c. “Mr. Darwin, on the other hand, holds the orthodox view of the descent of all the individuals of a species not only from a local birth-place, but from a single ancestor or pair … . He goes farther, and this volume is a protracted argument intended to prove that … species … have descended, like varieties, from other species. Varieties, on this view, are incipient or possible species: species are varieties of a … wider and earlier divergence from the parent stock: the difference is one of degree, not of kind.” [Emphasis added]

d. “The ordinary view … looks to natural agencies for the actual distribution and perpetuation of species, to a supernatural for their origin.”

e. “The theory of Agassiz regards the origin of species and their present general distribution over the world as equally primordial, equally supernatural; that of Darwin, as equally derivative, equally natural.”

f. “… the whole relations of animals, &c. to surrounding nature and to each other, are regarded under the one view as ultimate facts … interpreted theologically;—under the other as complex facts, to be analyzed and interpreted scientifically. The one naturalist, perhaps too largely assuming the scientifically unexplained to be inexplicable, views the phenomena only in their supposed relation to the Divine mind. The other, naturally expecting many of these phenomena to be resolvable under investigation, views them in their relations to one another, and endeavors to explain them as far as he can (and perhaps farther) through natural causes.” [Emphasis added]
5. Bridging the divide: Gray argued that the operation of secondary causes in the production of new species not inconsistent

“with the idea of their being intellectually connected with one another through the Deity, i.e., as products of one mind, as indicating and realizing a preconceived plan.”

noting

“with pleasure the insertion [2nd edition], of an additional motto on the reverse of the title-page directly claiming the theistic view which we have vindicated for the doctrine.”

C. Especially offensive to Darwin’s associates, and undoubtedly to Darwin himself, was Owen’s self-serving review, published anonymously [o60].

D. Carpenter’s assessment [c60] most prescient:

“The history of every science shows that the great epochs of its progress are those not so much of new discoveries of facts, as of those new ideas which have served for the colligation of facts previously known into general principles, and which have thenceforward given a new direction to inquiry. It is in this point of view that we attach the highest value to Mr. Darwin's work. Naturalists have gone of quite long enough on the doctrine of the "permanence of species." Their catalogues are becoming more and more encumbered with these hypothetical "distinct creations." And the difficulty of distinguishing between true species and varieties increases, instead of diminishing, with the extension of their researches. The
doctrine of progressive modification by Natural Selection propounded by Mr. Darwin, will give a new direction to inquiry into the real genetic relationship of species, existing and extinct; and it has a claim to respectful consideration … because it brings into mutual reconciliation the antagonistic doctrines of two great schools—that of Unity of Type, as put forward by Geoffrey St. Hilaire and his followers of the Morphological School, and that of Adaptation to Conditions of Existence, which has been the leading principle of Cuvier and the Teleologists.”

IV. Slayer of Variation.

A. Fleeming Jenkin (1833-1885)

1. Scottish engineer; professor of engineering at Edinburgh.

2. Colleague and business associate of Kelvin.

3. Involved in post-Civil War transatlantic cable construction (Figure 7).

4. Inventor of telphers (cable cars), which he imagined would become the principal means of transport of people and goods (Figure 8).

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**Figure 7.** Top. Transatlantic cables construction in the 19th century. Bottom. The 1869 cable from Brest to Saint-Pierre was laid by the *Great Eastern*, with Jenkin and Kelvin on board.
5. An atheist til his later years

"'The longer I live, my dear Louis,' he wrote but a few months before his death, 'the more convinced I become of a direct care by God – which is reasonably impossible – but there it is.' And in his last year he took the communion." [r1s87]

B. Jenkin’s review of *The Origin* published anonymously in the *North British Review* (1867).

1. Darwin took Jenkins’ criticism very seriously as evidenced both in correspondence with Wallace, revisions to the *Origin* and later writings.

2. His son, Francis would later editorialize [d05]

“It is not a little remarkable that the criticisms, which my father ... felt to be the most valuable ever made on his views should have come, not from a professed naturalist but from a Professor of Engineering.” [Emphasis added]
C. By 1867, professionalization of the sciences had proceeded to the point that Jenkin felt obliged to justify his right to an opinion:

“The opponents of Darwin have been chiefly men having special knowledge similar to his own, and they have therefore naturally directed their attention to the cardinal facts of his theory.

“They have asserted that animals are not so similar but that specific differences can be detected, and that man can produce no varieties differing from the parent stock, as one species differs from another.”

“About the truth and extent of those facts none but men possessing a special knowledge of physiology and natural history have any right to an opinion; but the superstructure based on those facts enters the region of pure reason, and may be discussed apart from all doubt as to the fundamental facts.” [Emphasis added]

D. He also felt obliged to dissociate himself from religion:

“Some persons seem to have thought his theory dangerous to religion, morality, and what not. Others have tried to laugh it out of court. We can share neither the fears of the former nor the merriment of the latter; and, on the contrary, own to feeling the greatest admiration both for the ingenuity of the doctrine and for the temper in which it was broached, although, from a consideration of the following arguments, our opinion is adverse to its truth.”
E. Jenkin’s (lengthy and convoluted) review.

1. Summarizes Darwin’s argument and the case for descent with modification.
   a. “Small differences … between animals and their offspring.

   b. “Greater differences are observed between varieties known to be sprung form a common stock.

   c. “The differences between … species are sometimes hardly greater … than those between varieties owning a common origin.”

   d. “Even when species differ more widely, the difference … is one of degree only … . They [Darwin’s supporters] can see no clear … distinction by which to decide … whether two animals have sprung from a common ancestor or not.

   e. “They [Darwin’s supporters] feel warranted in concluding, that for aught the structure of animals shows to the contrary, they may be descended from a few ancestors only, --nay, even from a single pair.”
2. Natural Selection.

“Darwin shows that ... animals more favourably constituted than their fellows will survive in the struggle for life, will produce descendents resembling themselves. ... ; and so, generation after generation, nature... may be said to choose certain animals, even as man does when he desires to raise a special breed. ... All must agree that the process termed natural selection is in universal operation.” [Emphasis added]


“Geologists say their science shows no ground for doubting that the habitable world has existed for countless ages.”

4. Fossil Record.

“But if all beings are thus descended from a common ancestry, a complete historical record would show an unbroken chain of creatures ... We have no such record; but geology can produce vestiges ... [of] a few out of the innumerable links of the whole conceivable chain ....”

5. Five Questions.

a. Can natural selection choose special qualities, and so breed special varieties, as man does?

b. Does it appear that man has the power indefinitely to magnify the peculiarities which distinguish his breeds from the original stock?
c. Is there no other evidence than that of geology as to the age of the habitable earth?

d. How far, in the absence of other knowledge, does the mere difficulty in classifying organized beings justify us in expecting that they have had a common ancestor?

e. What value is to be attached to certain minor facts supposed to corroborate the new theory?


“Experience with domestic animals and cultivated plants shows that great variability exists.

“These differences are infinitely small as compared with the range required by his [Darwin’s] theory, but he assumes that by accumulation of successive difference any degree of variation may be produced; he [seems] to take for granted that if Sir John Sebright could with pigeons produce in six years a certain head and beak of say half the bulk possessed by the original stock, then in twelve years this bulk could be reduced to a quarter, in twenty-four to an eighth, and so farther.

“... but this seems no more accurate than to conclude that because we observe that a cannon-ball has traversed a mile in a minute, therefore in an hour it will be sixty miles off, and in the course of ages that it will reach the fixed stars.
“... As a matter of experience, have our racers improved in speed by one part in a thousand during the last twenty generations? Could we not double the speed of a cart-horse in twenty generations? Here is the analogy with our cannon-ball; the rate of variation in a given direction is not constant ...; it is a constantly diminishing rate, tending therefore to a limit.”

7. Limits to variation: Reversion to the mean.

“A given animal or plant appears to be contained, as it were, within a sphere of variation; one individual lies near one portion of the surface; another individual, of the same species, near another part of the surface; the average animal at the centre. Any individual may produce descendants varying in any direction, but is more likely to produce descendants varying towards the centre of the sphere, and the variations in that direction will be greater in amount than the variations towards the surface.

“What argument does Darwin offer showing that the law of variation will be different when the variation occurs slowly, not rapidly?

8. Continuing Deviation from the Mean.

“But not only do we require for Darwin's theory that time shall first permanently fix the variety near the outside of the assumed sphere of variation, we require that it shall give the power of varying beyond that sphere.

“Experiments conducted in a limited time point ... [to a] tendency to revert. ... [W]e are unaware of any reason for supposing that pouters [pigeons with distensible crops], after a thou-
sand generations of true breeding have acquired a fresh power of doubling their crops ... . *Why should we concede that a simple extension of time will reverse the rule?*

9. Inability of NS to produce new organs (see Lyell).

"We freely admit, that if an accumulation of slight improvements be possible, natural selection might improve hares as hares, and weasels as weasels, ... more than this, it may obliterate ... once useful organs ... for since that organ will weigh for nothing in the struggle of life, the average animal must be calculated as though it did not exist.

“...but the importance of this admission is much limited ...”

a. All variations must be in same direction.

“... first of all ... it should apply to variations which must occur in every individual, so that enormous numbers of individuals will exist, all having a little improvement in the same direction; ... [see below]

b. Inability of selection to create organs *de novo*.

“secondly, we require that the variation shall occur in an organ already useful ... . *Such a process of improvement ... could certainly never give organs ... to organisms which had never possessed them.* ... No doubt half the hares which are born have longer tails than the average of their ancestors; but as no large number of hares hang by their tails, it is inconceivable that any change of circumstances should breed hares with prehensile tails; ... Admitting, therefore,
that natural selection may improve organs already useful to
great numbers of a species, does not imply an admission
that it can create or develop new organs, and so original
species.

10. Loss of variation by chance.

“The advantage, whatever it may be, is utterly outbalanced by
numerical inferiority. ... However slight the advantage may be,
if it is shared by half the individuals produced, it will probably
be present in at least fifty-one [per cent] of the survivors, and
in a larger proportion of their offspring; but the chances are
against the preservation of any one 'sport' in a numerous tribe.

11. Loss of variation by blending.

a. In order to be preserved, favorable variations must
breed true. Gives a numerical example.

“[Assume that a sport] will breed and have a progeny ... intermediate between the average individual and the sport.
... after a few generations it would no longer be observed
and would count for no more in the struggle for life, than any
of the hundred trifling advantages which occur in the ordi-
nary organs.”

b. But if sports breed true,

“Let an animal be born with some useful peculiarity, and let
all his descendants retain his peculiarity in an eminent de-
gree, however, little of the first ancestor's blood be in them,
then it follows, from mere mathematics, that the descend-
ants of our gifted beast will probably exterminate the de-
cendants of his inferior brethren.”

c. In sum,
“... if in ... a given number of individuals there appears one
super-eminently gifted, and if the advantage accruing to the
descendants bears ... proportion to the amount of the an-
cestor's blood in their veins, the chances are considerable
that for the first few generations he will have many de-
scendants; but by degrees this advantage wanes, and after
many generations the chances are ...much against his hav-
ing any descendants at all alive .... ... If, on the contrary,
the advantage given by the sport is retained by all descend-
ants, independently ... the proportion of blood in their veins
... , then these descendants will shortly supplant the old
species entirely, after the manner required by Darwin.

12. But this is not Darwin’s theory.

“The appearance of a new specimen capable of perpetuating its peculiarity is precisely what might be termed a creation, the word being used to express our ignorance of how the thing happened. The substitution of the new specimens, descendants from the old species, would then be simply an example of strong race sup-
planting a weak one, by a process known long before the term 'natural selection' was invented. Perhaps this is the way in which new species are introduced, but it does not express the Darwinian theory of the gradual accumulation of infinitely minute differences of every-day occurrence, and apparently fortuitous in their charac-
ter.”


“He [the Darwinian] can invent trains of ancestors of whose existence there is no evidence; he can marshal hosts of equally imaginary foes; he can call up continents, floods, and peculiar atmospheres; he can dry up oceans, split islands, and parcel out eternity at will; surely with these advantages he must be a dull fellow if he cannot scheme some series of animals and circumstances explaining our assumed difficulty quite naturally. Feeling the difficulty of dealing with adversaries who command so huge a domain of fancy, we will abandon these arguments, and trust to those which at least cannot be assailed by mere efforts of imagination.’ " – Shades of Cuvier – see Lecture 2; also Gould and Lewontin.

15. Time. Darwin’s estimate of the age of the Weald; Thomson’s arguments; no reason for assuming uniformity; etc.

16. Patterns of similarity in things not descended from each other – chemical elements.

“It is very curious to see how man’s contrivances … fall into series, presenting the difficulty complained of by naturalists in classifying birds and beasts, or

Figure 9. Phylogenetic tree of cornets. Vertical branches correspond to periods of manufacture of particular models (M); curved lines, to potential instances of information transfer among makers. Triangles indicate key innovations in design. For details, see [te0?].
chemists in arranging compounds. It is this difficulty which pro-
duces litigation under the Patent Laws.”

a. Limited number of possible forms. Design constraints.

“This difficulty [patent infringement] results from the ac-
tion of man's mind contriving machines to produce a com-
mon result according to definite laws, the laws of mechan-
ics.”

b. Correlation of parts.

“It is difficult to suppose that every stripe on a zebra or quagga ... is useful to it. It seems possible, even proba-
ble, that these things are the unavoidable consequences of
the elementary combination which will produce the quagga,
or a beast like it.” – Discuss.

17. Geographic distribution.

“The peculiarities of geographic distribution seem very difficult of
explanation on any theory. Darwin calls in alternately winds, tides,
birds, beasts, all animated nature, as the diffusers of species, and
then a good many of the same agencies as impenetrable barriers.
There are some impenetrable barriers between the Galapagos Is-
lands, but not between New Zealand and South America. Conti-
nents are created to join Australia and the Cape of Good Hope,
while a sea as broad as the British Channel is elsewhere a valid
line of demarcation.” – Discuss.
18. Lack of transitional fossils.


“If we are told ... that God works by laws, then we answer, 'Why the special Darwinian law?' A plausible theory should not be accepted while unproven; and if the arguments of this essay be admitted, Darwin's theory ... is not only without sufficient support from evidence, but is proved false by a cumulative proof.

F. Contemporary response to Jenkin’s review.

1. Vorzimmer [v63].
   a. Darwin believed he had already dealt with blending, but conceded that “single differences” of no import.
   b. Reliance on “individual differences” drove him to emphasize Lamarckian mechanisms.

2. Gould [g85].
   a. Rejects sphere metaphor – it can be reconstituted about previously peripheral points.
   b. Nonetheless believes ∃ important constraints (developmental, genetic) to variation.
   c. Accepts the argument that “large-scale” evolution (long-term trends, post-mass extinction adaptive radiations) cannot be extrapolated from micro-evolutionary processes.
d. Lauds Jenkin’s appreciation of the fact that “nearly any static situation can arise via several historical routes” – the “invertibility” problem.”

3. Morris [m94]:
   a. Kelvin’s limitations on available time more important Jenkin’s swamping argument.
   b. By publishing in a forum that addressed the general, literate public, the same audience to which The Origin was directed, Jenkin forced Darwin to confront Kelvin’s arguments.

G. Bulmer [b04]

1. Rejected swamping argument as a mathematical consequence of improper assumptions.
   a. Observes that Jenkin assumed each pair produces a single surviving offspring => extinction of population and new variation.
   b. Replacing this with two surviving offspring => population size unchanged (no extinction); new variation diluted but preserved.
   c. “Phenotype” of the new variation diluted by an amount < 1/N – consequence of its selective advantage.
   d. Cites Davis (1871) as having pointed this out shortly after the publication of Jenkin’s review.
2. In short, new character spreads, but diluted – blending slows, but does not abolish evolutionary improvement.

3. More frequent recurrent “mutation” required to achieve a given result than if inheritance particulate.

4. In modern terms, \((\frac{dN}{dt}) \propto V_g\), which is more quickly exhausted.

5. Absent selection, blending abolishes \(V_g\) by a factor of 50% each generation – nothing for selection to work on when environment changes, i.e., new selective pressures.

6. Bulmer also distinguishes between phenotypic blending and physical blending, in which regard he notes that ideas of particulate inheritance not unknown to Darwin and his contemporaries – e.g., Galton.
V. Darwin’s reaction as related by his son, Francis in [d05].

A. While preparing the fifth edition of the 'Origin,' he wrote to Wallace (January 22, 1869) as follows:

"I have been interrupted in my regular work in preparing a new edition of the 'Origin,' … . I always thought [multiple] individual differences more important than single variations, but now I have come to the conclusion that they are of paramount importance, … . Fleeming Jenkin's arguments have convinced me."

1. This was revised on February 2 – again to Wallace:

"I must have expressed myself atrociously; I meant to say exactly the reverse … . F. Jenkin argued … against single variations ever being perpetuated, and has convinced me, though not in quite so broad a manner as here put. I always thought individual differences more important; but I was blind and thought that single variations might be preserved much oftener than I now see is possible or probable. ... I believe I was mainly deceived by single variations offering such simple illustrations, as when man selects."

2. Francis writes

“"My father's copy of the paper (ripped out of the volume as usual, and tied with a bit of string) is annotated in pencil in many places."

3. Contra Eiseley, Morris [m94] suggests that the real significance of Jenkin’s article was that it called general attention to the arguments of Thomson regarding the age of the habitable earth.
4. Hence Darwin’s suggestion in the 6th edition that

“the world at a very early period was subjected to more rapid and violent changes in its physical conditions than those now occurring; and such changes would have tended to induce changes at a corresponding rate in the organisms which then existed.”

B. Darwin had long recognized [v63] difficulty posed by blending.

1. From the 1842 “Sketch”:

“Each parent transmits its peculiarities, therefore if varieties allowed freely to cross, except by the chance of two characterized by same peculiarity happening to marry, such varieties will be constantly demolished.”

2. Countered this difficulty by arguing for sterility between differentiated races.

3. How does this tie in with Bowler’s claim that Darwin and Wallace differed with regard to their formulations of DwM via NS in 1858?

C. Additions to the 6th Edition.

1. Admission:
“… until reading an able and valuable article in the 'North British Review' (1867), I did not appreciate how rarely single variations, whether slight or strongly-marked, could be perpetuated.”

2. Loss by blending of single variations:

The justice of these remarks cannot, I think, be disputed. If, for instance, a bird of some kind could procure its food more easily by having its beak curved, and if one were born with its beak strongly curved, ... nevertheless there would be a very poor chance of this one individual perpetuating its kind to the exclusion of the common form;


“In such cases, if the varying individual did not actually transmit to its offspring its newly acquired character, it would undoubtedly transmit to them, as long as the existing conditions remained the same, a still stronger tendency to vary in the same manner. There can also be little doubt that the tendency to vary in the same manner has often been so strong that all the individuals of the same species have been similarly modified without the aid of any form of selection. ... [I]f the variation were of a beneficial nature, the original form would soon be supplanted by the modified form, through the survival of the fittest.

4. Effective population size.

“To the effects of intercrossing in eliminating variations ... , I shall have to recur; but ... most animals and plants keep to their proper homes, and do not needlessly wander about; ... Conse-
quently each newly-formed variety would generally be at first local, ...; so that similarly modified individuals would ... often breed together. If the new variety were successful in its battle for life, it would slowly spread from a central district, competing with and conquering the unchanged individuals on the margins of an ever-increasing circle.”

D. Relation to Theory of Punctuated Equilibrium.

1. Gould and Eldredge imagined that stabilizing selection in large populations impedes continuing gradual change.
   a. Emphasized co-adaptedness of entire genome.

   b. In terms of adaptive topographies, this corresponds to inability to evolve through valleys of low fitness.

2. Stabilizing selection relaxed in small populations (peripheral or on islands), where maladaptive mutations can accumulate consequent to “sampling error.”

3. With subsequent increase in population size, new gene combinations refined.
   a. Selective pressures on the periphery of a species’ range different than at the center.

   b. Most evolutionary change therefore associated with speciation events.
Evolution on a 2-D adaptive landscape. Dotted lines are contours of equal fitness. Plus signs indicate fitness maxima; minus signs, minima. **Left.** Increased mutation or reduced selection leads to increased genetic variability. **Center.** Increased selection or reduced mutation reduces variability. **Right.** An environmental shift can place a population on a new peak, which selection then causes the population to climb. Reduced population size has the same effect as increasing mutation / reducing selection. From Simpson. 1944. *Tempo and Mode in Evolution.*
E. Darwin, by way of contrast, argues that favorable mutations can only accumulate in small populations because blending would eliminate them in large populations.

4. Today, we imagine
   a. Tension between gene flow (cohesive) and local selection (disruptive).
   b. Differentiation of geographically isolated populations as the result of chance or local selection.
   c. Reproductive isolation evolves subsequent to re-establishment of gene flow.

Figure 10. Contemporary model of geographic (allopatric) speciation.
VI. Pangene
sis.

A. In Variation of Animals and Plants Under Domestication, Darwin proposed his "provisional hypothesis of pangene
sis."

1. “It is almost universally admitted that cells ... propagate themselves by self-division ... , and [are] ... converted into the various tissues and substances of the body.

2. “... I assume that cells, before their conversion into ... "formed material," throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment multiply by self-division, subsequently becoming developed into cells like those from which they were derived.

3. “These granules ... may be called ... gemmules. They are ... transmitted from the parents to the offspring, and are generally developed in the generation which immediately succeeds, but are often transmitted in a dormant state during many generations and are then developed.

4. “Their development ... depend[s] on their union with other partially developed cells or gemmules which precede them in the regular course of growth.

5. “Gemmules are ... thrown off by every cell or unit, not only during the adult state, but during all the stages of development.
6. “… gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation either into buds or into the sexual elements.

7. “Variability often depends … on the reproductive organs being injuriously affected by changed conditions; and in this case the gemmules derived from the various parts of the body are probably aggregated in an irregular manner, some superfluous and others deficient.

8. “Whether a superabundance of gemmules, together with fusion during development, would lead to the increased size of any part cannot be told; but … their partial deficiency, without necessarily leading to the entire abortion of the part, might cause considerable modifications.”

9. “It is generally … necessary that an organism should be exposed during several generations to changed conditions or habits, in order that any modification … of the offspring should ensue. … I can account for the fact … by the assumption … that gemmules derived from each cell before it had undergone … modification are transmitted in large numbers to successive generations, but that the gemmules derived from the same cells after modification, naturally go on increasing under the same favouring conditions, until at last they become sufficiently numerous to overpower and supplant the old gemmules.

10. “… variability depends on at least two distinct … causes.

   a. Firstly, on the deficiency, superabundance, fusion, and transposition of gemmules, and on the redevelopment of those which have long been dormant. In these cases the gemmules
themselves have undergone no modification; but the mutations in the above respects will amply account for much fluctuating variability. (Inherent variability including atavisms)

b. “Secondly, in the cases in which the organisation has been modified by changed conditions, the increased use or disuse of parts, or any other cause, the gemmules cast off from the modified units of the body will be themselves modified, and, when sufficiently multiplied, will be developed into new and changed structures.” (Environmental effects; use and disuse)

B. #9 is key: Darwin imagined a “struggle for existence” among varying gemmules within organisms, even as he imagined competition among varying individuals within populations.

C. Darwin imagined pangenesis accounted for
   1. Blending
   2. Origin of variation.
   3. Atavisms (See Interlude 3)
   4. Inheritance of acquired characteristics.

D. Importantly – if gemmules in different individuals respond similarly to changed environmental circumstances, we get production of multiple variations that vary in same direction.
1. This plus more rapid environmental change in past would constitute Darwin’s response to Kelvin / Jenkin.

2. This is the context of comment in the 1880 letter to *Nature* quoted previously:

   “I AM sorry to find that Sir Wyville Thomson does not understand the principle of natural selection … . If he had done so, he could not have written [that] … ‘The character of the abyssal fauna refuses to give the least support to the theory which refers the evolution of species to extreme variation guided only by natural selection.’ … Can Sir Wyville Thomson name any one who has said that the evolution of species depends only on natural selection? As far as concerns myself, *I believe that no one has brought forward so many observations on the effects of the use and disuse of parts, as I have done in my "Variation of Animals and Plants under Domestication"; and these observations were made for this special object. I have likewise there adduced a considerable body of facts, showing the direct action of external conditions on organisms;” [Emphasis Added]

E. Invalidation of the theory.

1. Galton’s blood transfusion experiments on true-breeding rabbits of different color failed to affect color of the offspring.

2. Weismann’s mutilation experiments on mice – “he cut off their tails with a carving knife” – pointed to sequestration the germ line.