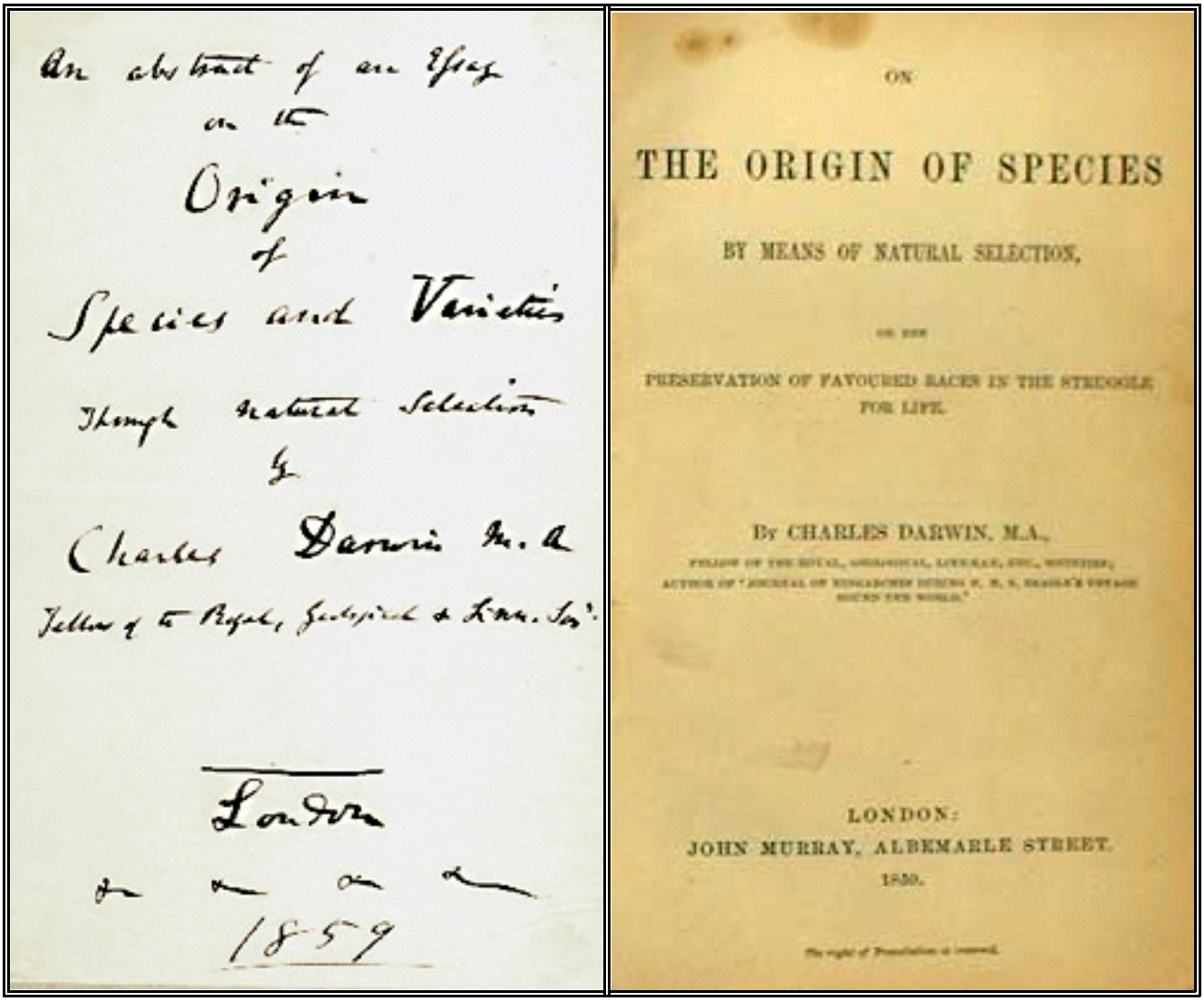
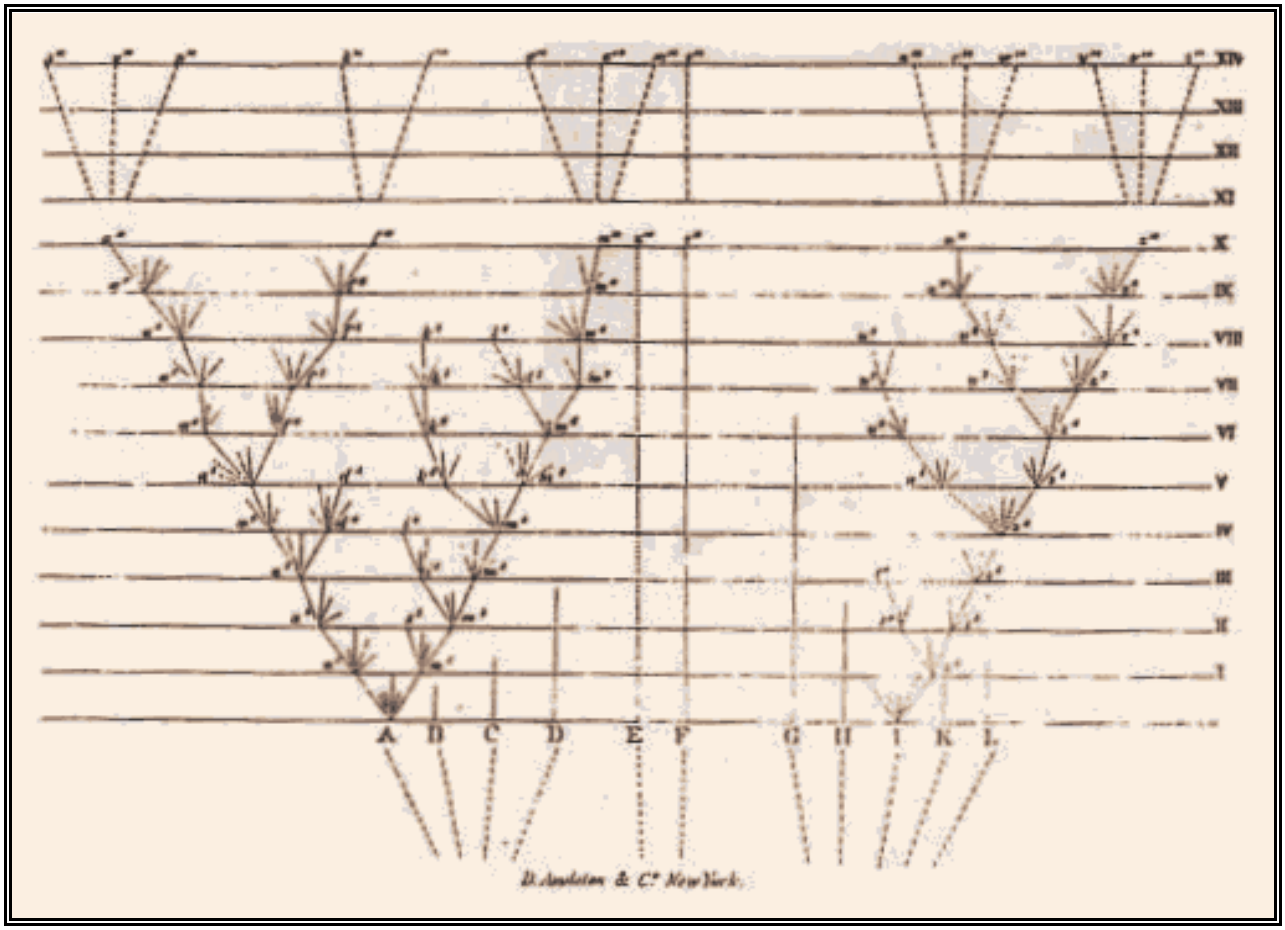


On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life

Charles Darwin, M.A.

Charles Darwin's 'Origin of Species' is unquestionably one of the most culturally transformative achievements in human intellectual history. This annotated abridgement is intended to make Darwin's ideas more accessible to a broader audience and to provide historical context and connections to current evolutionary thinking. This work may be freely copied and distributed but please do not delete or modify editorial comments or footnotes. This is an evolving 'social text' and suggestions or criticisms are welcome and should be directed to Dann Siems, Department of Biology, Bemidji State University, Bemidji MN 56601 – dsiems@bemidjistate.edu.



Lone figure from 'Origin of Species'

A Summary of the Logic of Natural Selection

Three inductions from observation and two necessary deductive conclusion

If Inductions 1-3 (derived directly from observation) are true then the Deductions (A & B) necessarily follow. The inductions derived from observations are corroborated by empirical evidence therefore evolution by natural selection is inevitable; all that remains as controversial it to determine its relative significance as a causal process.

Induction 1 – Adults on average produce (many) more offspring than required for their own replacement
Induction 2 – Populations remain relatively constant in number (at least they don't increase continuously)
Deduction A – Therefore, it follows that some (many) offspring must fail to survive and/or to reproduce.
Induction 3 – Within any population there are heritable variations in form and physiology (ie., species have no immutable essence)
Deduction B – Any heritable variations which enhance prospects for survival and reproduction will increase in frequency over time within a population (this is Natural Selection)

IMPORTANT NOTE: Deduction A in no way implies the inevitability of competition. Many offspring fall prey to predators, are victims of pathogens or parasites, or are victims of environmental events. The widespread belief (past and present!) that natural selection requires competition reflects cultural rather than biological foundations!

Table I. Structure and origins of Darwin's strategy of argument(s) in "The Origin of Species"

Part	Strategy	Tactic	Chapters
I. Variation and selection under domestication	*Vera causa* existence [after Herschel]	Establish accepted idea	*I. Variation under domestication*
		Argue from analogy	*II. Variation under nature* *III. Struggle for existence*
II. Variation and selection in nature	*Vera causa* competence	Make case	*IV. Natural selection* *V. Laws of variation*
		Consider difficulties	*VI. Difficulties of the theory* *VII*. Miscellaneous objections (added in 2nd edition)* *VII. Instinct* *VIII. Hybridism* *IX. Imperfections of the geological record*
III. Explanatory trials of the theory	*Vera causa* responsibility	Present evidence favoring responsibility	*X. Geological succession* *XI. Geographic distribution*
	Consilience of inductions [after Whewell]	Make sense of a large class of otherwise disparate facts	*XII. Geographic distribution* *XIII. Mutual affinities of organic beings*
Recapitulation	Allay fears, Convert ready	Humility & Reverie [after Humboldt]	*XIV. Recapitulation and conclusions*

Darwin built his case in the 'Origin of Species' specifically to address Victorian expectations concerning the nature of sound scientific practices. In particular, Darwin presents a *vera causa* (= 'true cause') argument in Chapters 1-11 that is a direct response to the practices advocated by John Herschel in "Preliminary Discourse on the Study of Natural Philosophy" (1830). In a *vera causa* approach, one must first demonstrate the existence of some potentially causal process, then demonstrate that the process is in principle competent to explain the phenomenon of interest, and finally that the process is in fact responsible. In Chapters 12 & 13 Darwin follows the approach put forth by William Whewell, the first philosopher of science, in his "History (1837) and Philosophy (1840) of the Inductive Sciences." Whewell (who incidently had coined the then rather controversial term 'scientist' in 1833) argued that the quality and utility of a scientific theory could be judged based on its capacity to makes sense of large class of otherwise apparently unrelated facts and coincidences. In carefully and intentionally structuring his argument in this way, Darwin was actively seeking the approval of Herschel and Whewell as a strategy for enhancing the likelihood of a positive scientific and public reaction to his theory of evolution by natural selection. In the final chapter, Darwin echoes the 'nature reveries' of Humboldt's "Personal Narrative of Travels to Equinoctial Regions of the New Continent" which Darwin had read as a youth and which shaped his rather Romantic views of nature throughout his life. Table adapted primarily from Hodge, M. 1977. The Structure and strategy and Darwin's 'Long Argument.' British Journal for the History of Science 10: 237-246 and Waters, K. The arguments in the Origin of Species. pp. 116-140. In: Hodge, M. & Radick, G. The Cambridge Companion to Darwin. Cambridge University Press. 2003; see also Sloan, P.R. 1991. The sense of sublimity: Darwin on nature and the divine. Osiris 16: 251-269. Janet Browne's (2007) "Darwin's 'Origin of Species': A Biography" provides a concise analysis of the context and development of Darwin's theory.

On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.[1] [2]

Charles Darwin, M.A.

Fellow of the Royal, Geological, Linnæan, etc. societies;
Author of Journal of researches during H. M. S. Beagle's Voyage round the world.
London: John Murray, Albemarle Street, 1859
– Edited and annotated by Dann Siems (2007)[3] –

Preface – An Historical Sketch

I WILL here give a brief sketch of the progress of opinion on the Origin of Species. Until recently the great majority of naturalists believed that species were immutable productions, and had been separately created. This view has been ably maintained by many authors. Some few naturalists, on the other hand, have believed that species undergo modification, and that the existing forms of life are the descendants by true generation of pre-existing forms. [...]

Lamarck was the first man whose conclusions on the subject excited much attention. This justly-celebrated naturalist first published his views in 1801; he much enlarged them in 1809 in his "Philosophie Zoologique,' and subsequently, in 1815, in the Introduction to his "Hist. Nat. des Animaux sans Vertébres.' In these works he upholds the doctrine that species, including man, are descended from other species. He first did the eminent service of arousing attention to the probability of all change in the organic, as well as in the inorganic world,

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[1] The first edition of this work (1250 copies) was published on November 24th, 1859. In seeking support for his theory, Darwin sent complimentary copies to one hundred leading men of science. A second edition (3000 copies) following quickly on January 7th, 1860. A Preface first appeared in the third edition (2000 copies) published in 1861 but the preface version reproduced here is from the 6th edition published in 1872 (3000 copies; 4th edition 1500 copies) Interestingly, Herbert Spencer's phrase "survival of the fittest" did not appear in the Origin until the 5th edition published in 1869 (2000 copies). Spencer had coined this language in his 1864 book "Principles of Biology" where he wrote: "This survival of the fittest, which I have here sought to express in mechanical terms, is that which Mr. Darwin has called 'natural selection', or the preservation of favoured races in the struggle for life." Although many of Darwin's contemporaries urged him to use "survival of the fittest" as a synonym for natural selection in the Origin, Darwin consistently resisted these entreaties believing Spencer's phrase simplistic and misleading. [Note that only 12,750 copies of the Origin were printed in the first decade; however, it is likely that most, if not all members of the Royal Society had a copy or were familiar with its contents].

[2] First edition full text is available on-line at http://www.talkorigins.org/faqs/origin.html. John van Wyhe provides another excellent on-line first edition at http://darwin-online.org.uk/; this site has the advantage of preserving original page numbering.

[3] Selections reproduced here are intended to provide an abridged overview of the style and structure of Darwin's argument. **This abridgement was developed to provide background information for students participating in a 'Reacting to the Past' series game entitled "Charles Darwin, the Copley Medal, and the Rise of Naturalism." Game players should pay particular attention to the introductory remarks at the head of each chapter as they highlight the conceptual content and the strategic rhetorical role of subsequent material. In addition, GAME NOTES specific to various issues are interspersed throughout the text as are CHARACTER ALERTS specific to particular roles.** Editorial comments and annotations are presented in *[italicized brackets]* or footnotes and include brief descriptions of deleted material, contextual commentary, and connections to contemporary evolutionary theory. Contact: Dann Siems, Bemidji State University, Bemidji MN 56601 (dsiems@bemidjistate.edu).

being the result of law, and not of miraculous interposition. Lamarck seems to have been chiefly led to his conclusion on the gradual change of species, by the difficulty of distinguishing species and varieties, by the almost perfect gradation of forms in certain groups, and by the analogy of domestic productions. With respect to the means of modification, he attributed something to the direct action of the physical conditions of life, something to the crossing of already existing forms, and much to use and disuse, that is, to the effects of habit. To this latter agency he seemed to attribute all the beautiful adaptations in nature; — such as the long neck of the giraffe for browsing on the branches of trees. But he likewise believed in a law of progressive development; and as all the forms of life thus tend to progress, in order to account for the existence at the present day of simple productions, he maintains that such forms are now spontaneously generated.

[...] It is curious how largely my grandfather, Dr Erasmus Darwin, anticipated the views and erroneous grounds of opinion of Lamarck in his 'Zoonomia' [...] published in 1794. According to Isid. Geoffroy Saint Hilaire there is no doubt that Goethe was an extreme partisan of similar views, as shown in the Introduction to a work written in 1794 and 1795, but not published till long afterwards. [...] It is rather a singular instance of the manner in which similar views arise at about the same time, that Goethe in Germany, Dr Darwin in England, and Geoffroy Saint-Hilaire [...] in France; came to the same conclusion on the origin of species, in the years 1794-5.

[There follows a compilation of thirty-four examples of others who apparently espoused evolutionary views and even some who recognized the principle of natural selection between 1800 and 1859. Interestingly, Darwin does not claim that he was the first to propose the idea of natural selection and he even uses prior recognition of the principle by others to support the legitimacy of his argument. Only several of the excerpts most relevant to present concerns are included here. ***GAME NOTE:*** *Look for references to your character (or an ally or adversary) of your character here. Darwin's comments on Owen are particularly revealing.]*

The 'Vestiges of Creation' appeared in 1844. In the tenth and much improved edition (1853) the anonymous author[4] says (p. 155):- 'The proposition determined on after much consideration is, that the several series of animated beings, from the simplest and oldest up to the highest and most recent, are, under the providence of God, the results, first, of an impulse which has been imparted to the forms of life, advancing them, in definite times, by generation, through grades of organisation terminating in the highest dicotyledons and vertebrata, these grades being few in number, and generally marked by intervals of organic character, which we find to be a practical difficulty in ascertaining affinities; second, of another impulse connected with the vital forces, tending, in the course of generations, to modify organic structures in accordance with external circumstances, as food, the nature of the habitat, and the meteoric agencies, these being the "adaptations" of the natural theologian.' The author apparently believes that organisation progresses by sudden leaps, but that the effects produced by the conditions of life are gradual. He argues with much force on general grounds that species are not immutable productions. [...] The work, from its powerful and brilliant style, though displaying in the earlier editions little accurate knowledge and a great want of scientific caution, immediately had a very wide circulation. In my opinion it has done excellent service in this country in calling attention to the subject, in removing prejudice, and in thus preparing the ground for the reception of analogous views. [...]

Professor Owen, in 1849 ('Nature of Limbs,' p. 86), wrote as follows:- "The archetypal idea was manifested in the flesh under diverse such modifications, upon this planet, long prior to the existence of those animal species that actually exemplify it. To what natural laws or secondary causes the orderly succession and progression of such organic phenomena may have been committed, we, as yet, are ignorant." In his Address to the British Association, in 1858, he speaks (p. li.) of "the axiom of the continuous operation of creative power, or of the ordained becoming of living things." Farther on (p. xc.), after referring to geographical distribution, he adds, "These phenomena shake our confidence in the conclusion that the Apteryx of New Zealand and the Red Grouse

[4] Revealed to be Robert Chambers in 1884. This work was widely read on both sides the Atlantic and brought natural history to public attention. For more see http://www.ucmp.berkeley.edu/history/chambers.html.

of England were distinct creations in and for those islands respectively. Always, also, it may be well to bear in mind that by the word 'creation' the zoologist means 'a process he knows not what.'" He amplifies this idea by adding that when such cases as that of the Red Grouse are enumerated by the zoologists as evidence of distinct creation of the bird in and for such islands, he chiefly expresses that he knows not how the Red Grouse came to be there, and there exclusively; signifying also, by this mode of expressing such ignorance, his belief that both the bird and the islands owed their origin to a great first Creative Cause.' If we interpret these sentences given in the same Address, one by the other, it appears that this eminent philosopher felt in 1858 his confidence shaken that the Apteryx and the Red Grouse first appeared in their respective homes, 'he knew not how,' or by some process 'he knew not what.'

This Address was delivered after the papers by Mr Wallace and myself on the Origin of Species, presently to be referred to, had been read before the Linnean Society. When the first edition of this work was published, I was so completely deceived, as were many others, by such expressions as 'the continuous operation of creative power,' that I included Professor Owen with other palaeontologists as being firmly convinced of the immutability of species; but it appears ('Anat. of Vertebrates,' vol. iii. p. 796) that this was on my part a preposterous error. In the last edition of this work I inferred, and the inference still seems to me perfectly just, from a passage beginning with the words 'no doubt the type-form,' &c. (Ibid. vol. i. p. xxxv.), that Professor Owen admitted that natural selection may have done something in the formation of a new species; but this it appears (Ibid. vol. nl. p. 798) is inaccurate and without evidence. I also gave some extracts from a correspondence between Professor Owen and the Editor of the 'London Review,' from which it appeared manifest to the Editor as well as to myself, that Professor Owen claimed to have promulgated the theory of natural selection before I had done so; and I expressed my surprise and satisfaction at this announcement; but as far as it is possible to understand certain recently published passages (Ibid. vol. iii. p. 798) I have either partially or wholly again fallen into error. It is consolatory to me that others find Professor Owen's controversial writings as difficult to understand and to reconcile with each other, as I do. As far as the mere enunciation of the principle of natural selection is concerned, it is quite immaterial whether or not Professor Owen preceded me, for both of us, as shown in this historical sketch, were long ago preceded by Dr Wells and Mr Matthews. [...]

The 'Philosophy of Creation' has been treated in a masterly manner by the Rev. Baden Powell, in his "Essays on the Unity of Worlds," 1855. Nothing can be more striking than the manner in which he shows that the introduction of new species is "a regular, not a casual phenomenon," or, as Sir John Herschel expresses it, "a natural in contradistinction to a miraculous, process."[5]

[...] Professor Huxley gave a lecture before the Royal Institution on the "Persistent Types of Animal Life." Referring to such cases, he remarks, "It is difficult to comprehend the meaning of such facts as these, if we suppose that each species of animal and plant, or each great type of organisation, was formed and placed upon the surface of the globe at long intervals by a distinct act of creative power; and it is well to recollect that such an assumption is as unsupported by tradition or revelation as it is opposed to the general analogy of nature. If, on the other hand, we view 'Persistent Types' in relation to that hypothesis which supposes the species living at any time to be the result of the gradual modification of pre-existing species a hypothesis which, though unproven, and sadly damaged by some of its supporters, is yet the only one to which physiology lends any countenance; their existence would seem to show that the amount of modification which living beings have undergone during geological time is but very small in relation to the whole series of changes which they have suffered.'

... Dr Hooker published his 'Introduction to the Australian Flora.' In the first part of this great work he admits the truth of the descent and modification of species, and supports this doctrine by many original observations.

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[5] Baden-Powell was also one of seven contributors to "Essay & Reviews" (1860) which precipitated the events that are central to our Re-Acting Game. Incidently, Baden-Powell's son later founded the Boy Scouts.

CONTENTS

INTRODUCTION

*[**GAME NOTE:** Before proceeding with the text itself, pay particularly close attention to the structure of Darwin's argument [see 'Summary of the Logic of Natural Selection' and 'Table I : Structure of Darwin's argument' at the beginning of this document]. Note especially that Darwin devotes four (or, in later editions, five) chapters to considering "the most apparent and gravest difficulties" facing his theory. This self-critical approach is an important forerunner to the now standard practice of placing one's own "pet hypotheses" at maximum jeopardy.]*

WHEN on board H.M.S. Beagle, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species — that mystery of mysteries, as it has been called by one of our greatest philosophers. On my return home, it occurred to me, in 1837, that something might perhaps be made out on this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it. After five years' work I allowed myself to speculate on the subject, and drew up some short notes; these I enlarged in 1844 into a sketch of the conclusions, which then seemed to me probable: from that period to the present day I have steadily pursued the same object. I hope that I may be excused for entering on these personal details, as I give them to show that I have not been hasty in coming to a decision. *[**GAME NOTE:** Why is Darwin so concerned not to be perceived as 'hasty?']*

My work is now nearly finished; but as it will take me two or three more years to complete it, and as my health is far from strong, I have been urged to publish this Abstract. I have more especially been induced to do this, as Mr Wallace, who is now studying the natural history of the Malay archipelago, has arrived at almost exactly the same general conclusions that I have on the origin of species. Last year he sent to me a memoir on this subject, with a request that I would forward it to Sir Charles Lyell, who sent it to the Linnean Society, and it is published in the third volume of the journal of that Society. Sir C. Lyell and Dr Hooker, who both knew of my work — the latter having read my sketch of 1844 — honoured me by thinking it advisable to publish, with Mr Wallace's excellent memoir, some brief extracts from my manuscripts.[6]

This Abstract, which I now publish, must necessarily be imperfect. I cannot here give references and authorities for my several statements; and I must trust to the reader reposing some confidence in my accuracy. No doubt errors will have crept in, though I hope I have always been cautious in trusting to good authorities alone. I can here give only the general conclusions at which I have arrived, with a few facts in illustration, but which, I hope, in most cases will suffice. No one can feel more sensible than I do of the necessity of hereafter publishing in detail all the facts, with references, on which my conclusions have been grounded; and I hope in a future work to do this. For I am well aware that scarcely a single point is discussed in this volume on which facts cannot be adduced, often apparently leading to conclusions directly opposite to those at which I have arrived. A fair result can be obtained only by fully stating and balancing the facts and arguments on both sides of each question; and this cannot possibly be here done.

I much regret that want of space prevents my having the satisfaction of acknowledging the generous assistance which I have received from very many naturalists, some of them personally unknown to me. I cannot, however, let this opportunity pass without expressing my deep obligations to Dr Hooker, who for the last fifteen years has aided me in every possible way by his large stores of knowledge and his excellent judgement.

In considering the Origin of Species, it is quite conceivable that a naturalist, reflecting on the mutual affinities of

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[6] Papers were read 1 July 1858. Darwin's paper was read by George Busk, a member of the X-Club who later would nominate Darwin for the Royal Society's Copley Medal. Copies of both papers are available on-line at: http://www.darwingame.org/Darwin and Wallace 1858.pdf.

organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified so as to acquire that perfection of structure and co-adaptation which most justly excites our admiration. Naturalists continually refer to external conditions, such as climate, food, &c., as the only possible cause of variation. In one very limited sense, as we shall hereafter see, this may be true; but it is preposterous to attribute to mere external conditions, the structure, for instance, of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees. In the case of the misseltoe, which draws its nourishment from certain trees, which has seeds that must be transported by certain birds, and which has flowers with separate sexes absolutely requiring the agency of certain insects to bring pollen from one flower to the other, it is equally preposterous to account for the structure of this parasite, with its relations to several distinct organic beings, by the effects of external conditions, or of habit, or of the volition of the plant itself.

The author of the 'Vestiges of Creation' would, I presume, say that, after a certain unknown number of generations, some bird had given birth to a woodpecker, and some plant to the misseltoe, and that these had been produced perfect as we now see them; but this assumption seems to me to be no explanation, for it leaves the case of the coadaptations of organic beings to each other and to their physical conditions of life, untouched and unexplained.

It is, therefore, of the highest importance to gain a clear insight into the means of modification and coadaptation. At the commencement of my observations it seemed to me probable that a careful study of domesticated animals and of cultivated plants would offer the best chance of making out this obscure problem. Nor have I been disappointed; in this and in all other perplexing cases I have invariably found that our knowledge, imperfect though it be, of variation under domestication, afforded the best and safest clue. I may venture to express my conviction of the high value of such studies, although they have been very commonly neglected by naturalists.

From these considerations, I shall devote the first chapter of this Abstract to Variation under Domestication. We shall thus see that a large amount of hereditary modification is at least possible, and, what is equally or more important, we shall see how great is the power of man in accumulating by his Selection successive slight variations. I will then pass on to the variability of species in a state of nature; but I shall, unfortunately, be compelled to treat this subject far too briefly, as it can be treated properly only by giving long catalogues of facts. *[**GAME NOTE:** Why does Darwin note the need for 'long catalogues of facts?' Remember that Darwin intended the "Origin" as a brief abstract of his theory. If your character needs these additional examples you may find it helpful to refer to some of his other works (e.g., on barnacles or orchids). To understand more fully the importance of 'catalogues of fact' refer to section on "Playing a Natural Philosopher" in your Game Book.]* We shall, however, be enabled to discuss what circumstances are most favourable to variation. In the next chapter the Struggle for Existence amongst all organic beings throughout the world, which inevitably follows from their high geometrical powers of increase, will be treated of. This is the doctrine of Malthus, applied to the whole animal and vegetable kingdoms. As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form. *[**GAME NOTE:** Is a competitive 'struggle for existence' <u>necessarily</u> a consequence of surplus reproduction? See additional comments in Chapter III notes.]*

This fundamental subject of Natural Selection will be treated at some length in the fourth chapter; and we shall then see how Natural Selection almost inevitably causes much Extinction of the less improved forms of life and induces what I have called Divergence of Character. In the next chapter I shall discuss the complex and little known laws of variation and of correlation of growth. In the four succeeding chapters, the most apparent and gravest difficulties on the theory will be given: namely, first, the difficulties of transitions, or understanding how

a simple being or a simple organ can be changed and perfected into a highly developed being or elaborately constructed organ; secondly the subject of Instinct, or the mental powers of animals, thirdly, Hybridism, or the infertility of species and the fertility of varieties when intercrossed; and fourthly, the imperfection of the Geological Record. In the next chapter I shall consider the geological succession of organic beings throughout time; in the eleventh and twelfth, their geographical distribution throughout space; in the thirteenth, their classification or mutual affinities, both when mature and in an embryonic condition. In the last chapter I shall give a brief recapitulation of the whole work, and a few concluding remarks.)

No one ought to feel surprise at much remaining as yet unexplained in regard to the origin of species and varieties, if he makes due allowance for our profound ignorance in regard to the mutual relations of all the beings which live around us. Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world. Still less do we know of the mutual relations of the innumerable inhabitants of the world during the many past geological epochs in its history. Although much remains obscure, and will long remain obscure, I can entertain no doubt, after the most deliberate study and dispassionate judgement of which I am capable, that the view which most naturalists entertain, and which I formerly entertained — namely, that each species has been independently created — is erroneous.[7] I am fully convinced that species are not immutable; but that those belonging to what are called the same genera are lineal descendants of some other and generally extinct species, in the same manner as the acknowledged varieties of any one species are the descendants of that species. Furthermore, I am convinced that Natural Selection has been the main but not exclusive means of modification.

*[**GAME NOTE:** Darwin provided a convenient sketch of the topics considered in each chapter. I have used bold-faced type to indicate those sections from which excerpts have been drawn. Players may what to consult an on-line, full text version to review relevant sections not included here.]*

CHAPTER I
VARIATION UNDER DOMESTICATION

Causes of Variability – Effects of Habit and the Use of Disuse of Parts – Correlation of Growth – **Inheritance** – Character of Domestic Varieties – **Difficulty of distinguishing between Varieties and Species** – Origin of Domestic Varieties from one or more Species – **Domestic pigeons, their Differences and Origin** – **Principle of Selection anciently followed, its Effects** – **Methodical and Unconscious Selection** – Unknown Origin of our Domestic Productions – Circumstances favourable to Man's power of Selection

*[**GAME NOTE:** Darwin's strategy in Chapter I is to establish that considerable variation exists in domesticated populations and that this variation is not an anomaly but instead is an inevitable result of processes of heredity and development. The existence and extent of this variation within species was a problem for those who believed that each individual was a manifestation of some immutable underlying ideal type or essence. Since natural*

[7] In an 1844 letter to J.D. Hooker in which he revealed his evolutionary ideas for the first time, Darwin wrote, "I am almost convinced (quite contrary to the opinion I started with) that species are not (it is like confessing a murder) immutable. Heaven forfend me from Lamarck nonsense of a 'tendency to progression' 'adaptations from the slow willing of animals' &c, but the conclusions I am led to are not widely different than his – though the means of change are wholly so – I think I have found out (here's presumption!) the simple way by which species become exquisitely adapted to various ends." See R. Colp. (1986) "Confessing a Murder" – Darwin's First Revelations about Transmutation. Isis 77: 8-32 for more details on this letter. This paper also provides a good introduction to Darwin's earliest thinking about transmutation and is particularly insightful with respect to Darwin's personal reluctance to press his views publically. This work also offers a revealing portrayal of the relationship between Charles and Emma and shows that while she was long aware of his ideas she remained more than a little skeptical.

theology presumes that a perfect creator created a perfect creation, these deviations from the ideal type were often regarded as consequences of the 'sin' of Adam and Eve. Earlier transmutationists (such as Darwin's grandfather Erasmus) held that species change essence over time – for Darwin, species lacked any 'essence' whatsoever! Because variation within populations is a necessary precondition for natural selection, Darwin goes to great length here to establish its existence. Darwin then shows here how breeders have used these variations to effect desired changes through a process of selective mating. Note that establishing existence of such phenomena is the first step in presenting a vera causa *argument.]*

[...] It has been disputed at what period of time the causes of variability, whatever they may be, generally act; whether during the early or late period of development of the embryo, or at the instant of conception. Geoffroy St Hilaire's experiments show that unnatural treatment of the embryo causes monstrosities; and monstrosities cannot be separated by any clear line of distinction from mere variations. But I am strongly inclined to suspect that the most frequent cause of variability may be attributed to the male and female reproductive elements having been affected prior to the act of conception.

[...] There are many laws regulating variation, some few of which can be dimly seen, and will be hereafter briefly mentioned. I will here only allude to what may be called correlation of growth. Any change in the embryo or larva will almost certainly entail changes in the mature animal. In monstrosities, the correlations between quite distinct parts are very curious; and many instances are given in Isidore Geoffroy St Hilaire's great work on this subject. Breeders believe that long limbs are almost always accompanied by an elongated head. Some instances of correlation are quite whimsical; thus cats with blue eyes are invariably deaf; colour and constitutional peculiarities go together, of which many remarkable cases could be given amongst animals and plants. From the facts collected by Heusinger, it appears that white sheep and pigs are differently affected from coloured individuals by certain vegetable poisons. Hairless dogs have imperfect teeth; long-haired and coarse-haired animals are apt to have, as is asserted, long or many horns; pigeons with feathered feet have skin between their outer toes; pigeons with short beaks have small feet, and those with long beaks large feet. Hence, if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly unconsciously modify other parts of the structure, owing to the mysterious laws of the correlation of growth.

[...] Any variation which is not inherited is unimportant for us. But the number and diversity of inheritable deviations of structure, both those of slight and those of considerable physiological importance, is endless. [...] No breeder doubts how strong is the tendency to inheritance: like produces like is his fundamental belief: doubts have been thrown on this principle by theoretical writers alone. When a deviation appears not unfrequently, and we see it in the father and child, we cannot tell whether it may not be due to the same original cause acting on both; but when amongst individuals, apparently exposed to the same conditions, any very rare deviation, due to some extraordinary combination of circumstances, appears in the parent say, once amongst several million individuals and it reappears in the child, the mere doctrine of chances almost compels us to attribute its reappearance to inheritance. Every one must have heard of cases of albinism, prickly skin, hairy bodies, &c. appearing in several members of the same family. If strange and rare deviations of structure are truly inherited, less strange and commoner deviations may be freely admitted to be inheritable. Perhaps the correct way of viewing the whole subject, would be, to look at the inheritance of every character whatever as the rule, and non-inheritance as the anomaly. ***[GAME NOTE:*** *Why does Darwin want to characterize inheritance of traits as a general rule in his consideration of domestic animals? Primarily because by so doing , it will be easier to argue from analogy in the case of plants and animals in the state of nature in the subsequent chapter.* ***Character Alert:*** *Friend of Mill and the Disciple of Bacon especially will want to pay attention to Darwin's rhetorical strategy and all players should ponder the role of argument from analogy discussed in the Game Book]*

The laws governing inheritance are quite unknown; [8] no one can say why the same peculiarity in different individuals of the same species, and in individuals of different species, is sometimes inherited and sometimes not so; why the child often reverts in certain characters to its grandfather or grandmother or other much more remote ancestor; why a peculiarity is often transmitted from one sex to both sexes or to one sex alone, more commonly but not exclusively to the like sex. A[n]...important rule...is that, at whatever period of life a peculiarity first appears, it tends to appear in the offspring at a corresponding age, though sometimes earlier. [...H]ereditary diseases and some other facts make me believe that the rule has a wider extension, and that when there is no apparent reason why a peculiarity should appear at any particular age, yet that it does tend to appear in the offspring at the same period at which it first appeared in the parent. I believe this rule to be of the highest importance in explaining the laws of embryology.

[...] ...there are hardly any domestic races, either amongst animals or plants, which have not been ranked by some competent judges as mere varieties, and by other competent judges as the descendants of aboriginally distinct species. If any marked distinction existed between domestic races and species, this source of doubt could not so perpetually recur.

On the Breeds of the Domestic Pigeon

*[**GAME NOTE:** Pigeons were particularly important to the development or Darwin's ideas so I have included rather extensive excerpts from the following section . Players in both A and X faction should read this section closely and may want to cite specific examples in Royal Society discussions.]*

Believing that it is always best to study some special group, I have, after deliberation, taken up domestic pigeons. I have kept every breed which I could purchase or obtain, and have been most kindly favoured with skins from several quarters of the world, more especially by the Hon. W. Elliot from India, and by the Hon. C. Murray from Persia. Many treatises in different languages have been published on pigeons, and some of them are very important, as being of considerably antiquity. I have associated with several eminent fanciers, and have been permitted to join two of the London Pigeon Clubs. The diversity of the breeds is something astonishing.[9] Compare the English carrier and the short-faced tumbler, and see the wonderful difference in their beaks, entailing corresponding differences in their skulls. The carrier, more especially the male bird, is also remarkable from the wonderful development of the carunculated skin about the head, and this is accompanied by greatly elongated eyelids, very large external orifices to the nostrils, and a wide gape of mouth. The short-faced tumbler has a beak in outline almost like that of a finch; and the common tumbler has the singular and strictly inherited habit of flying at a great height in a compact flock, and tumbling in the air head over heels. The runt is a bird of great size, with long, massive beak and large feet; some of the sub-breeds of runts have very long necks, others very long wings and tails, others singularly short tails. The barb is allied to the carrier, but, instead of a very long beak, has a very short and very broad one. The pouter has a much elongated body, wings, and legs; and its enormously developed crop, which it glories in inflating, may well excite astonishment and even laughter. The turbit has a very short and conical beak, with a line of reversed feathers down the breast; and it has the habit of continually expanding slightly the upper part of the oesophagus. The Jacobin has the feathers so much reversed along the back of the neck that they form a hood, and it has, proportionally to its size, much elongated wing and

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[8] Darwin had no clear notion of how inheritance worked at the level of physical processes. Darwin believed that 'gemmules' of parents somehow blended in offspring; this fundamental misunderstanding severely weakened his theory and as P. Bowler [(1983) The eclipse of Darwinism. John Hopkins University Press: Baltimore MD] has shown, natural selection had fallen out of favor by 1900 and was only resurrected following the rediscovery of Mendel's notion of particulate inheritance. Another interesting consequence of Darwin's misunderstanding was his lifelong belief in the Lamarckian notion of inheritance of acquired characters through habitual use or disuse.

[9] Many, if not most, of Darwin's mid-nineteenth century gentleman-readers would have been at least generally familiar with the astonishing diversity of various domestic pigeon breeds. Since most twenty-first century readers are not, I have included a Victorian era illustration as a back cover for this abridgement.

tail feathers. The trumpeter and laugher, as their names express, utter a very different coo from the other breeds. The fantail has thirty or even forty tail-feathers, instead of twelve or fourteen, the normal number in all members of the great pigeon family; and these feathers are kept expanded, and are carried so erect that in good birds the head and tail touch; the oil-gland is quite aborted. Several other less distinct breeds might have been specified.

In the skeletons of the several breeds, the development of the bones of the face in length and breadth and curvature differs enormously. The shape, as well as the breadth and length of the ramus of the lower jaw, varies in a highly remarkable manner. The number of the caudal and sacral vertebrae vary; as does the number of the ribs, together with their relative breadth and the presence of processes. The size and shape of the apertures in the sternum are highly variable; so is the degree of divergence and relative size of the two arms of the furcula. The proportional width of the gape of mouth, the proportional length of the eyelids, of the orifice of the nostrils, of the tongue (not always in strict correlation with the length of beak), the size of the crop and of the upper part of the oesophagus; the development and abortion of the oil-gland; the number of the primary wing and caudal feathers; the relative length of wing and tail to each other and to the body; the relative length of leg and of the feet; the number of scutellae on the toes, the development of skin between the toes, are all points of structure which are variable. The period at which the perfect plumage is acquired varies, as does the state of the down with which the nestling birds are clothed when hatched. The shape and size of the eggs vary. The manner of flight differs remarkably; as does in some breeds the voice and disposition. Lastly, in certain breeds, the males and females have come to differ to a slight degree from each other.

Altogether at least a score of pigeons might be chosen, which if shown to an ornithologist, and he were told that they were wild birds, would certainly, I think, be ranked by him as well-defined species. Moreover, I do not believe that any ornithologist would place the English carrier, the short-faced tumbler, the runt, the barb, pouter, and fantail in the same genus; more especially as in each of these breeds several truly-inherited sub-breeds, or species as he might have called them, could be shown him. [...] Great as the differences are between the breeds of pigeons, I am fully convinced that the common opinion of naturalists is correct, namely, that all have descended from the rock-pigeon (Columba livia), including under this term several geographical races or sub-species, which differ from each other in the most trifling respects. *[**GAME NOTE:** Darwin then listed reasons which led him to this conclusion – if this is important for your character you may want to consult a full text version on-line.]*

[...] I have discussed the probable origin of domestic pigeons at some, yet quite insufficient, length; because when I first kept pigeons and watched the several kinds, knowing well how true they bred, I felt fully as much difficulty in believing that they could ever have descended from a common parent, as any naturalist could in coming to a similar conclusion in regard to the many species of finches, or other large groups of birds, in nature. One circumstance has struck me much; namely, that all the breeders of the various domestic animals and the cultivators of plants, with whom I have ever conversed, or whose treatises I have read, are firmly convinced that the several breeds to which each has attended, are descended from so many aboriginally distinct species. Ask, as I have asked, a celebrated raiser of Hereford cattle, whether his cattle might not have descended from long horns, and he will laugh you to scorn. I have never met a pigeon, or poultry, or duck, or rabbit fancier, who was not fully convinced that each main breed was descended from a distinct species. [...] Innumerable other examples could be given. The explanation, I think, is simple: from long-continued study they are strongly impressed with the differences between the several races; and though they well know that each race varies slightly, for they win their prizes by selecting such slight differences, yet they ignore all general arguments, and refuse to sum up in their minds slight differences accumulated during many successive generations. May not those naturalists who, knowing far less of the laws of inheritance than does the breeder, and knowing no more than he does of the intermediate links in the long lines of descent, yet admit that many of our domestic races have descended from the same parents may they not learn a lesson of caution, when they deride the idea of species in a state of nature being lineal descendants of other species? **[*GAME NOTE:** Darwin's rhetoric here is intended to move fellow naturalists toward at least entertaining the possibility that natural selection might be sufficient to produce multiple species from a common ancestor. For some however, his speculative tone in comments like this one marked a departure from the well-established inductive methods of science.*]

Selection

Let us now briefly consider the steps by which domestic races have been produced, either from one or from several allied species. Some little effect may, perhaps, be attributed to the direct action of the external conditions of life, and some little to habit; but he would be a bold man who would account by such agencies for the differences of a dray and race horse, a greyhound and bloodhound, a carrier and tumbler pigeon. One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. Some variations useful to him have probably arisen suddenly, or by one step; many botanists, for instance, believe that the fuller's teazle, with its hooks, which cannot be rivalled by any mechanical contrivance, is only a variety of the wild Dipsacus; and this amount of change may have suddenly arisen in a seedling. So it has probably been with the turnspit dog; and this is known to have been the case with the ancon sheep. But when we compare the dray-horse and race-horse, the dromedary and camel, the various breeds of sheep fitted either for cultivated land or mountain pasture, with the wool of one breed good for one purpose, and that of another breed for another purpose; when we compare the many breeds of dogs, each good for man in very different ways; when we compare the gamecock, so pertinacious in battle, with other breeds so little quarrelsome, with 'everlasting layers' which never desire to sit, and with the bantam so small and elegant; when we compare the host of agricultural, culinary, orchard, and flower-garden races of plants, most useful to man at different seasons and for different purposes, or so beautiful in his eyes, we must, I think, look further than to mere variability. We cannot suppose that all the breeds were suddenly produced as perfect and as useful as we now see them; indeed, in several cases, we know that this has not been their history. The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds.

The great power of this principle of selection is not hypothetical. It is certain that several of our eminent breeders have, even within a single lifetime, modified to a large extent some breeds of cattle and sheep. In order fully to realise what they have done, it is almost necessary to read several of the many treatises devoted to this subject, and to inspect the animals. Breeders habitually speak of an animal's organisation as something quite plastic, which they can model almost as they please. [...] That most skilful breeder, Sir John Sebright, used to say, with respect to pigeons, that 'he would produce any given feather in three years, but it would take him six years to obtain head and beak.' In Saxony the importance of the principle of selection in regard to merino sheep is so fully recognised, that men follow it as a trade: the sheep are placed on a table and are studied, like a picture by a connoisseur; this is done three times at intervals of months, and the sheep are each time marked and classed, so that the very best may ultimately be selected for breeding.

[...] It may be objected that the principle of selection has been reduced to methodical practice for scarcely more than three-quarters of a century; it has certainly been more attended to of late years, and many treatises have been published on the subject; and the result , has been, in a corresponding degree, rapid and important. But it is very far from true that the principle is a modern discovery. I could give several references to the full acknowledgement of the importance of the principle in works of high antiquity. In rude and barbarous periods of English history choice animals were often imported, and laws were passed to prevent their exportation: the destruction of horses under a certain size was ordered, and this may be compared to the 'roguing' of plants by nurserymen. The principle of selection I find distinctly given in an ancient Chinese encyclopaedia. Explicit rules are laid down by some of the Roman classical writers. From passages in Genesis, it is clear that the colour of domestic animals was at that early period attended to. Savages now sometimes cross their dogs with wild canine animals, to improve the breed, and they formerly did so, as is attested by passages in Pliny. The savages in South Africa match their draught cattle by colour, as do some of the Esquimaux their teams of dogs. Livingstone shows how much good domestic breeds are valued by the negroes of the interior of Africa who have not associated with Europeans. Some of these facts do not show actual selection, but they show that the breeding of domestic animals was carefully attended to in ancient times, and is now attended to by the lowest savages. It would have been a strange fact, indeed, had attention not been paid to breeding, for the inheritance of good and bad qualities is so obvious.

At the present time, eminent breeders try by methodical selection, with a distinct object in view, to make a new strain or sub-breed, superior to anything existing in the country. But, for our purpose, a kind of Selection, which may be called Unconscious, and which results from every one trying to possess and breed from the best individual animals, is more important. Thus, a man who intends keeping pointers naturally tries to get as good dogs as he can, and afterwards breeds from his own best dogs, but he has no wish or expectation of permanently altering the breed.

[...] Youatt gives an excellent illustration of the effects of a course of selection, which may be considered as unconsciously followed, in so far that the breeders could never have expected or even have wished to have produced the result which ensued namely, the production of two distinct strains. The two flocks of Leicester sheep kept by Mr Buckley and Mr Burgess, as Mr Youatt remarks, 'have been purely bred from the original stock of Mr Bakewell for upwards of fifty years. There is not a suspicion existing in the mind of any one at all acquainted with the subject that the owner of either of them has deviated in any one instance from the pure blood of Mr Bakewell's flock, and yet the difference between the sheep possessed by these two gentlemen is so great that they have the appearance of being quite different varieties.'

[...] Variability is governed by many unknown laws, more especially by that of correlation of growth. Something may be attributed to the direct action of the conditions of life. Something must be attributed to use and disuse. The final result is thus rendered infinitely complex. In some cases, I do not doubt that the intercrossing of species, aboriginally distinct, has played an important part in the origin of our domestic productions.[10] When in any country several domestic breeds have once been established, their occasional intercrossing, with the aid of selection, has, no doubt, largely aided in the formation of new sub-breeds; but the importance of the crossing of varieties has, I believe, been greatly exaggerated, both in regard to animals and to those plants which are propagated by seed. In plants which are temporarily propagated by cuttings, buds, &c., the importance of the crossing both of distinct species and of varieties is immense; for the cultivator here quite disregards the extreme variability both of hybrids and mongrels, and the frequent sterility of hybrids; but the cases of plants not propagated by seed are of little importance to us, for their endurance is only temporary. Over all these causes of change I am convinced that the accumulative action of selection, whether applied methodically and more quickly, or unconsciously and more slowly, but more efficiently, is by far the predominant power.

CHAPTER II
VARIATION UNDER NATURE

> **Variability – Individual differences** – Doubtful species – Wide ranging, much diffused, and common species vary most – Species of the larger genera in any country vary more than the species of the smaller genera – Many of the species of the larger genera resemble varieties in being very closely, but unequally, related to each other, and in having restricted ranges

*[**GAME NOTE:** In this chapter, Darwin establishes the unexpectedly high degree of variation present in populations in nature. He argues that differences among species are, in principle, similar to those commonly observed among sub-species and varieties. In many respects, **this is Darwin's key insight as it marks the transition from typological to population thinking** (see Mayr, E. 1976. Typological versus populational thinking. In: Mary, E. Evolution and the Diversity of Life. Harvard University Press: Cambridge UK.) Note also Darwin's comments on Lubbock's recent work.]*

Before applying the principles arrived at in the last chapter to organic beings in a state of nature, we must briefly discuss whether these latter are subject to any variation. To treat this subject at all properly, a long catalogue of

[10] Recent work suggests that Darwin underestimated the importance of reconnecting or "anastomosing" lineages. In a particularly telling example, eukaryote cells contain mitochondrial endosymbionts descended from purple bacteria.

dry facts should be given; but these I shall reserve for my future work. Nor shall I here discuss the various definitions which have been given of the term species.[11] No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. Generally the term includes the unknown element of a distinct act of creation. The term 'variety' is almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved. ***[GAME NOTE:*** *Another implied but absent 'long catalogue of dry facts.' For A-men, this can be taken as a further indication that Darwin's theory amounts to speculative hand-waving; for X men, absence of (abundant) evidence is not evidence of absence in principle but rather a call for further research. How you interpret such passages depends on your game objectives. Ultimately, the merit of Darwin's work and his viability as a candidate for the Copley Medal will hinge on the perceived balance of his inductive observations and deductive speculations]*.

[...] Again, we have many slight differences which may be called individual differences, such as are known frequently to appear in the offspring from the same parents, or which may be presumed to have thus arisen, from being frequently observed in the individuals of the same species inhabiting the same confined locality. No one supposes that all the individuals of the same species are cast in the very same mould. These individual differences are highly important for us, as they afford materials for natural selection to accumulate, in the same manner as man can accumulate in any given direction individual differences in his domesticated productions. These individual differences generally affect what naturalists consider unimportant parts; but I could show by a long catalogue of facts, that parts which must be called important, whether viewed under a physiological or classificatory point of view, sometimes vary in the individuals of the same species. I am convinced that the most experienced naturalist would be surprised at the number of the cases of variability, even in important parts of structure, which he could collect on good authority, as I have collected, during a course of years. It should be remembered that systematists are far from pleased at finding variability in important characters, and that there are not many men who will laboriously examine internal and important organs, and compare them in many specimens of the same species. I should never have expected that the branching of the main nerves close to the great central ganglion of an insect would have been variable in the same species; I should have expected that changes of this nature could have been effected only by slow degrees: yet quite recently Mr Lubbock has shown a degree of variability in these main nerves in Coccus, which may almost be compared to the irregular branching of the stem of a tree. This philosophical naturalist, has also quite recently shown that the muscles in the larvae of certain insects are very far from uniform. Authors sometimes argue in a circle when they state that important organs never vary; for these same authors practically rank that character as important (as some few naturalists have honestly confessed) which does not vary; and, under this point of view, no instance of any important part varying will ever be found: but under any other point of view many instances assuredly can be given.[12]

[...] Certainly no clear line of demarcation has as yet been drawn between species and sub-species that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage.

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[11] The 'species problem' remains challenging; see e.g., M.C. McKitrick and R. M. Zink. 1988. Species concepts in ornithology. Condor 90: 1-13. No fewer than thirty definitions of the term species occur in the evolutionary literature and these are often contradictory. The once favored 'biological species concept' based on reproductive isolation has fallen out of favor in recent years as abundant counter-evidence has accumulated.

[12] Such arguments are called tautologies and natural selection itself, particularly in its misleading "survival of the fittest" formulation, has often and sometimes justifiably, been criticized as a tautology. For example, if we define fitness in terms of survival and reproduction and then attribute observed differences in survival and reproduction to differences in fitness, we have explained nothing. For a more detailed critique and solution to this problem see Mills, S.K. & Beatty, J.H. 1979. The propensity interpretation of fitness. Philosophy of Science 46: 263-268.

Hence I look at individual differences, though of small interest to the systematist, as of high importance for us, as being the first step towards such slight varieties as are barely thought worth recording in works on natural history. And I look at varieties which are in any degree more distinct and permanent, as steps leading to more strongly marked and more permanent varieties; and at these latter, as leading to sub-species, and to species. The passage from one stage of difference to another and higher stage may be, in some cases, due merely to the long-continued action of different physical conditions in two different regions; but I have not much faith in this view; and I attribute the passage of a variety, from a state in which it differs very slightly from its parent to one in which it differs more, to the action of natural selection in accumulating (as will hereafter be more fully explained) differences of structure in certain definite directions. Hence I believe a well-marked variety may be justly called an incipient species; but whether this belief be justifiable must be judged of by the general weight of the several facts and views given throughout this work.

Finally then varieties have the same general characters as species, for they cannot be distinguished from species, except, firstly, by the discovery of intermediate linking forms, and the occurrence of such links cannot affect the actual characters of the forms which they connect; and except, secondly, by a certain amount of difference, for two forms, if differing very little, are generally ranked as varieties, notwithstanding that intermediate linking forms have not been discovered; but the amount of difference considered necessary to give to two forms the rank of species is quite indefinite. In genera having more than the average number of species in any country, the species of these genera have more than the average number of varieties. In large genera the species are apt to be closely, but unequally, allied together, forming little clusters round certain species. Species very closely allied to other species apparently have restricted ranges. In all these several respects the species of large genera present a strong analogy with varieties. And we can clearly understand these analogies, if species have once existed as varieties, and have thus originated: whereas, these analogies are utterly inexplicable if each species has been independently created.

CHAPTER III
STRUGGLE FOR EXISTENCE

Bears on natural selection – **The term used in a wide sense** – Geometrical powers of increase – Rapid increase of naturalised animals and plants – Nature of the checks to increase – **Competition universal** – Effects of climate – Protection from the number of individuals – Complex relations of all animals and plants throughout nature – Struggle for life most severe between individuals and varieties of the same species; often severe between species of the same genus – The relation of organism to organism the most important of all relations

*[**GAME NOTE:** Chapter 3 is critical for an understanding of Darwin's theory and it would be well worth your time to peruse the full text of this chapter on-line. Pay attention to the way in which struggle for existence is related to geometrical increases in population and thus to seemingly inevitable competition. Although Darwin notes that he uses the term struggle for existence in 'a large and metaphorical sense' and indeed provides numerous examples where struggle is related not to competition but to predation, parasitism, or environmental conditions, he nonetheless adopts the then prevailing Malthusian view that competition is universal. In effect, he reads an interpretation of human culture back into nature in spite of his own evidence to the contrary. As a result, many readers presume (wrongly) that natural selection requires competition among individuals. More recent work suggests that 'surplus reproduction' is an evolutionary response to high mortality rates due to pathogens, parasites, predators, and environmental events and that competition a relatively rare, negative-negative ecological interaction that tends to be eliminated by natural selection.[13]*

***Character Alert:** All players – but especially the Malthusian Mathematician and the Civil Engineer – should pay particular attention to Darwin's emphasis on a "universal struggle for life" – for Darwin and his contemporaries human events such as the Irish potato famines of the late 1840s demonstrated that even if 'struggles for existence' were intermittent , they were nonetheless profoundly important for understanding differences in survival among populations. For example, many members of the Royal Society believed that the potato famines killed so many Irish because of the innate inferiority of the Celtic race relative to the Saxons (e.g., Knox, R. 1850.]*

Before entering on the subject of this chapter, I must make a few preliminary remarks, to show how the struggle for existence bears on Natural Selection. It has been seen in the last chapter that amongst organic beings in a state of nature there is some individual variability; indeed I am not aware that this has ever been disputed. It is immaterial for us whether a multitude of doubtful forms be called species or sub-species or varieties; what rank, for instance, the two or three hundred doubtful forms of British plants are entitled to hold, if the existence of any well-marked varieties be admitted. But the mere existence of individual variability and of some few well-marked varieties, though necessary as the foundation for the work, helps us but little in understanding how species arise in nature. How have all those exquisite adaptations of one part of the organisation to another part, and to the conditions of life, and of one distinct organic being to another being, been perfected? We see these beautiful co-adaptations most plainly in the woodpecker and missletoe; and only a little less plainly in the humblest parasite which clings to the hairs of a quadruped or feathers of a bird; in the structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world.

[...] Nothing is easier than to admit in words the truth of the universal struggle for life, or more difficult at least I have found it so than constantly to bear this conclusion in mind. Yet unless it be thoroughly engrained in the mind, I am convinced that the whole economy of nature, with every fact on distribution, rarity, abundance,

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[13] For more on this see Connell, J.H. 1980. Diversity and the co-evolution of competitors, or the ghost of competition past. Oikos 35: 131-138; also Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population control, and competition. American Naturalist 94: 421-425.

extinction, and variation, will be dimly seen or quite misunderstood. We behold the face of nature bright with gladness, we often see superabundance of food; we do not see, or we forget, that the birds which are idly singing round us mostly live on insects or seeds, and are thus constantly destroying life; or we forget how largely these songsters, or their eggs, or their nestlings are destroyed by birds and beasts of prey; we do not always bear in mind, that though food may be now superabundant, it is not so at all seasons of each recurring year.

I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which on an average only one comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground. The missletoe is dependent on the apple and a few other trees, but can only in a far-fetched sense be said to struggle with these trees, for if too many of these parasites grow on the same tree, it will languish and die. But several seedling missletoes, growing close together on the same branch, may more truly be said to struggle with each other. As the missletoe is disseminated by birds, its existence depends on birds; and it may metaphorically be said to struggle with other fruit-bearing plants, in order to tempt birds to devour and thus disseminate its seeds rather than those of other plants. In these several senses, which pass into each other, I use for convenience sake the general term of struggle for existence. *[**GAME NOTE:** Some critical analysis of Darwin's "Struggle for Existence" metaphor might pay dividends in the context of the game – for either faction or for careful non-partisans seeking to advance their case on ancillary issues (ie., race, gender, social welfare).]*

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase.[14] Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them.[15] [***Character Alert**: Malthusian Mathematician and Civil Engineer*]

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[14] It can be argued (and this is an emerging view among 21st evolutionary ecologists) that observed high reproductive rates are an effect rather than a cause of struggle for existence in the face of predators, parasites, pathogens and environmental caprice. Note that destruction of eggs or seeds in no way implies competition as a necessary fate. The 'doctrine of Malthus' was derived not from 'nature' but from interpretations of human experience in industrial and imperial nineteenth century English culture. D.H. Abbott [(1988) Natural suppression of fertility. Zoological Journal of the Linnean Society 60: 7-28] documents numerous cases where individual reproduction is not maximized in natural systems. Others have shown that reproductive tactics are quite plastic and can be adjusted in response to various environmental cues (see e.g., D.P. Siems and R.S. Sikes (1995) Tactical trade-offs between growth and reproduction. Environmental Biology of Fishes 53: 319-329).

[15] Reverend Thomas Malthus wrote "An essay on the principle of population as it affects the future improvement of society" in 1798 (Johnson: London). This work was an attack on 'the Poor Laws,' early attempts to provide a economic safety net for industrial England's economically disenfranchised. For Malthus, poverty was inevitable and was part of God's inscrutable plan – providing for the welfare of impoverished classes would only aggravate problems by encouraging higher birth rates among inferior stock. Darwin, who read for amusement a 6th edition (1828) copy of Malthus in 1838, was a generous contributor to various progressive social causes and thus found the views of Malthus morally repugnant. Nonetheless, he rather uncritically adopted the (mistaken) Malthusian notion that food supplies increase arithmetically while populations increase geometrically.

There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair. Even slow-breeding man has doubled in twenty-five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny.[16] Linnaeus has calculated that if an annual plant produced only two seeds and there is no plant so unproductive as this and their seedlings next year produced two, and so on, then in twenty years there would be a million plants. The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pairs of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair ***[GAME NOTE**: Elephant example provides a useful paper and pencil demonstration lab exercise especially for the X-man faction – consult with your Gamemaster on how to conduct such a demonstration]*.

[...] In looking at Nature, it is most necessary to keep the foregoing considerations always in mind never to forget that every single organic being around us may be said to be striving to the utmost to increase in numbers; that each lives by a struggle at some period of its life; that heavy destruction inevitably falls either on the young or old, during each generation or at recurrent intervals. Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount. The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force.

What checks the natural tendency of each species to increase in number is most obscure. Look at the most vigorous species; by as much as it swarms in numbers, by so much will its tendency to increase be still further increased. We know not exactly what the checks are in even one single instance. [...] Here I will make only a few remarks, just to recall to the reader's mind some of the chief points. Eggs or very young animals seem generally to suffer most, but this is not invariably the case. With plants there is a vast destruction of seeds, [...] Seedlings, also, are destroyed in vast numbers by various enemies; for instance, on a piece of ground three feet long and two wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of the 357 no less than 295 were destroyed, chiefly by slugs and insects. ***[GAME NOTE:** Here is an excellent empirical example you may wish to cite in your debates; it is worth noting however that observed 83% mortality rate was due primarily to herbivory rather than competition for resources]*

[...] The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species.

[...] Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought, I believe to be the most effective of all checks. I estimated that the winter of 1854-55 destroyed four-fifths of the birds in my own grounds; and this is a tremendous destruction, when we remember that ten per cent. is an extraordinarily severe mortality from epidemics with man. The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food. Even when climate, for instance extreme cold, acts directly, it will be the

[16] The human population of industrializing England had doubled in a quarter century with much of the increase occurring within the poorest classes of newly urbanized workers. In 1825 London was already the world's largest city with a population of 1.35 million; by 1875 London's population had reached 4.25 million. For a sense of living conditions in London see http://www.fidnet.com/~dap1955/dickens/dickens_london.html.

least vigorous, or those which have got least food through the advancing winter, which will suffer most. [...] [17]

[...] When a species...increases inordinately in numbers in a small tract, epidemics — at least this seems generally to occur with our game animals — often ensue: and here we have a limiting check independent of the struggle for life. But even some of these so-called epidemics appear to be due to parasitic worms, which have from some cause, possibly in part through facility of diffusion amongst the crowded animals, been disproportionably favoured: and here comes in a sort of struggle between the parasite and its prey.

[...] Many cases are on record showing how complex and unexpected are the checks and relations between organic beings, which have to struggle together in the same country. I will give only a single instance, which, though a simple one, has interested me. In Staffordshire, on the estate of a relation where I had ample means of investigation, there was a large and extremely barren heath, which had never been touched by the hand of man; but several hundred acres of exactly the same nature had been enclosed twenty-five years previously and planted with Scotch fir. The change in the native vegetation of the planted part of the heath was most remarkable, more than is generally seen in passing from one quite different soil to another: not only the proportional numbers of the heath-plants were wholly changed, but twelve species of plants (not counting grasses and carices) flourished in the plantations, which could not be found on the heath. The effect on the insects must have been still greater, for six insectivorous birds were very common in the plantations, which were not to be seen on the heath; and the heath was frequented by two or three distinct insectivorous birds. Here we see how potent has been the effect of the introduction of a single tree, nothing whatever else having been done, with the exception that the land had been enclosed, so that cattle could not enter. But how important an element enclosure is, I plainly saw near Farnham, in Surrey. Here there are extensive heaths, with a few clumps of old Scotch firs on the distant hill-tops: within the last ten years large spaces have been enclosed, and self-sown firs are now springing up in multitudes, so close together that all cannot live. When I ascertained that these young trees had not been sown or planted, I was so much surprised at their numbers that I went to several points of view, whence I could examine hundreds of acres of the unenclosed heath, and literally I could not see a single Scotch fir, except the old planted clumps. But on looking closely between the stems of the heath, I found a multitude of seedlings and little trees, which had been perpetually browsed down by the cattle. In one square yard, at a point some hundreds yards distant from one of the old clumps, I counted thirty-two little trees; and one of them, judging from the rings of growth, had during twenty-six years tried to raise its head above the stems of the heath, and had failed. No wonder that, as soon as the land was enclosed, it became thickly clothed with vigorously growing young firs. Yet the heath was so extremely barren and so extensive that no one would ever have imagined that cattle would have so closely and effectually searched it for food.

Not that in nature the relations can ever be as simple as this. Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time, though assuredly the merest trifle would often give the victory to one organic being over another. Nevertheless so profound is our ignorance, and so high our presumption, that we marvel when we hear of the extinction of an organic being; and as we do not see the cause, we invoke cataclysms to desolate the world, or invent laws on the duration of the forms of life!

[...] Look at a plant in the midst of its range, why does it not double or quadruple its numbers? We know that it can perfectly well withstand a little more heat or cold, dampness or dryness, for elsewhere it ranges into slightly hotter or colder, damper or drier districts. In this case we can clearly see that if we wished in imagination to give the plant the power of increasing in number, we should have to give it some advantage over its competitors, or over the animals which preyed on it. On the confines of its geographical range, a change of constitution with

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[17] Winter 'starvation' in white-tail deer provides an interesting example. Artificially high deer population levels (intentionally achieved as a management goal) coupled with reductions of natural predators creates a situation where high mortality occurs during cold, snowy winters. Although overall food supplies remain adequate, snow depth greatly reduces mobility resulting in local depletion of food and increased death rates among youngest and oldest sectors of the population. Most death are a result of exposure, secondary infections, and predation.

respect to climate would clearly be an advantage to our plant; but we have reason to believe that only a few plants or animals range so far, that they are destroyed by the rigour of the climate alone. Not until we reach the extreme confines of life, in the arctic regions or on the borders of an utter desert, will competition cease.[18]

It is good thus to try in our imagination to give any form some advantage over another. Probably in no single instance should we know what to do, so as to succeed. It will convince us of our ignorance on the mutual relations of all organic beings; a conviction as necessary, as it seems to be difficult to acquire. All that we can do, is to keep steadily in mind that each organic being is striving to increase at a geometrical ratio; that each at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life, and to suffer great destruction. When we reflect on this struggle, we may console ourselves with the full belief, that the war of nature is not incessant, that no fear is felt, that death is generally prompt, and that the vigorous, the healthy, and the happy survive and multiply.

CHAPTER IV
NATURAL SELECTION

> **Natural Selection** – its power compared with man's selection – its power on characters of trifling importance – its power at all ages and on both sexes – **Sexual Selection** – On the generality of intercrosses between individuals of the same species – Circumstances favourable and unfavourable to Natural Selection, namely, intercrossing, isolation, number of individuals – Slow action – Extinction caused by Natural Selection – **Divergence of Character**, related to the diversity of inhabitants of any small area, and to naturalisation – Action of Natural Selection, through Divergence of Character and Extinction, on the descendants from a common parent – **Explains the Grouping of all organic beings**

*[**GAME NOTE:** This chapter presents the core idea of Darwin's theory of natural selection. The theory is deductively certain provided that its premises are correct so you should try to pick out both the logical structure of the argument and the nature of Darwin's assumptions. Read critically and look for places where assumptions seem dubious. **CHARACTER ALERT:** understanding this chapter is critical for all players!]*

How will the struggle for existence, discussed too briefly in the last chapter, act in regard to variation? Can the principle of selection, which we have seen is so potent in the hands of man, apply in nature? I think we shall see that it can act most effectually. Let it be borne in mind in what an endless number of strange peculiarities our domestic productions, and, in a lesser degree, those under nature, vary; and how strong the hereditary tendency is. Under domestication, it may be truly said that the, whole organisation becomes in some degree plastic. Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element, as perhaps we see in the species called polymorphic.[19]

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[18] Darwin's examples in this chapter primarily focus on effects of predation and disease but here he makes a (culturally-induced?) shift in focus and concludes that competition ceases only at the 'extreme confines of life." Among his cited examples, competition is only apparent among firs within human constructed exclosures!

[19] Recent work suggests that much of the genetic and biochemical variation in populations is in fact neutral with respect to natural selection. For more on this see Kimura, M. 1989. The neutral theory of molecular evolution and

We shall best understand the probable course of natural selection by taking the case of a country undergoing some physical change, for instance, of climate. The proportional numbers of its inhabitants would almost immediately undergo a change, and some species might become extinct. We may conclude, from what we have seen of the intimate and complex manner in which the inhabitants of each country are bound together, that any change in the numerical proportions of some of the inhabitants, independently of the change of climate itself, would most seriously affect many of the others. If the country were open on its borders, new forms would certainly immigrate, and this also would seriously disturb the relations of some of the former inhabitants. Let it be remembered how powerful the influence of a single introduced tree or mammal has been shown to be. But in the case of an island, or of a country partly surrounded by barriers, into which new and better adapted forms could not freely enter, we should then have places in the economy of nature which would assuredly be better filled up, if some of the original inhabitants were in some manner modified; for, had the area been open to immigration, these same places would have been seized on by intruders. In such case, every slight modification, which in the course of ages chanced to arise, and which in any way favoured the individuals of any of the species, by better adapting them to their altered conditions, would tend to be preserved; and natural selection would thus have free scope for the work of improvement.

[...] It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapses of ages, and then so imperfect is our view into long past geological ages, that we only see that the forms of life are now different from what they formerly were.

Sexual Selection

[***CHARACTER ALERT:*** *Paleontologist and Astronomer*] ... this leads me to say a few words on what I call Sexual Selection. This depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection. Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny. But in many cases, victory will depend not on general vigour, but on having special weapons, confined to the male sex.

[...] Amongst birds, the contest is often of a more peaceful character. All those who have attended to the subject, believe that there is the severest rivalry between the males of many species to attract by singing the females. The rock-thrush of Guiana, birds of paradise, and some others, congregate; and successive males display their gorgeous plumage and perform strange antics before the females, which standing by as spectators, at last choose the most attractive partner. [...] It may appear childish to attribute any effect to such apparently weak means: I cannot here enter on the details necessary to support this view; but if man can in a short time give elegant carriage and beauty to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect.[20]

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the worldview of the neutralists. Genome 31: 24-31. Random changes in the frequencies of different forms of a given gene (i.e., alleleles) are referred to as genetic drift. Genetic drift inevitably produces changes in form and physiology that are not related to any particular adaptive advantages.

[20] Because Darwin's notion of sexual selection included active female choice as an agent every bit as important as male-male contest competition, it was a difficult idea for even his supporters to accept. Recent DNA-based paternity studies in several species reveal that winners of male-male competition do not necessarily end up fathering more offspring and also suffer reduced life-spans due directly to injury and indirectly to stress related physiological problems [see e.g., R. M. Sapolsky. (1990) Stress in the wild. Scientific American. Jan: 116-123].

Illustrations of the action of Natural Selection

In order to make it clear how, as I believe, natural selection acts, I must beg permission to give one or two imaginary illustrations. Let us take the case of a wolf, which preys on various animals, securing some by craft, some by strength, and some by fleetness; and let us suppose that the fleetest prey, a deer for instance, had from any change in the country increased in numbers, or that other prey had decreased in numbers, during that season of the year when the wolf is hardest pressed for food. I can under such circumstances see no reason to doubt that the swiftest and slimmest wolves would have the best chance of surviving, and so be preserved or selected, provided always that they retained strength to master their prey at this or at some other period of the year, when they might be compelled to prey on other animals. I can see no more reason to doubt this, than that man can improve the fleetness of his greyhounds by careful and methodical selection, or by that unconscious selection which results from each man trying to keep the best dogs without any thought of modifying the breed.

*[**GAME NOTE:** Darwin next presents several hypothetical cases of how natural selection might be expected to operate. Because some of these examples were overly simplistic they were subject to great skepticism and occasional ridicule. **CHARACTER ALERT:** A-men should consult the full text to glean some of these examples as illustrations of Darwin's speculative deviations from the time-proven, inductive methods of science].*

I am well aware that this doctrine of natural selection, exemplified in the above imaginary instances, is open to the same objections which were at first urged against Sir Charles Lyell's noble views on 'the modern changes of the earth, as illustrative of geology;' but we now very seldom hear the action, for instance, of the coast-waves, called a trifling and insignificant cause, when applied to the excavation of gigantic valleys or to the formation of the longest lines of inland cliffs. Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications, each profitable to the preserved being; and as modern geology has almost banished such views as the excavation of a great valley by a single diluvial wave, so will natural selection, if it be a true principle, banish the belief of the continued creation of new organic beings, or of any great and sudden modification in their structure.

*[**GAME NOTE:** Next follows an extended digression on inter-crossing that was not viewed central to Darwin's main argument. Following that Darwin offers a rather rambling section describing circumstances supposed to be favorable for natural selection; I have included only part of his summary here.]*

That natural selection will always act with extreme slowness, I fully admit. Its action depends on there being places in the polity of nature, which can be better occupied by some of the inhabitants of the country undergoing modification of some kind. The existence of such places will often depend on physical changes, which are generally very slow, and on the immigration of better adapted forms having been checked. But the action of natural selection will probably still oftener depend on some of the inhabitants becoming slowly modified; the mutual relations of many of the other inhabitants being thus disturbed. Nothing can be effected, unless favourable variations occur, and variation itself is apparently always a very slow process. [...] Many will exclaim that these several causes are amply sufficient wholly to stop the action of natural selection. I do not believe so. On the other hand, I do believe that natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time. I further believe, that this very slow, intermittent action of natural selection accords perfectly well with what geology tells us of the rate and manner at which the inhabitants of this world have changed.

Slow though the process of selection may be, if feeble man can do much by his powers of artificial selection, I can see no limit to the amount of change, to the beauty and infinite complexity of the coadaptations between all organic beings, one with another and with their physical conditions of life, which may be effected in the long

course of time by nature's power of selection.[21]

Extinction caused by Natural Selection

[...] Natural selection acts solely through the preservation of variations in some way advantageous, which consequently endure. But as from the high geometrical powers of increase of all organic beings, each area is already fully stocked with inhabitants, it follows that as each selected and favoured form increases in number, so will the less favoured forms decrease and become rare. Rarity, as geology tells us, is the precursor to extinction. We can, also, see that any form represented by few individuals will, during fluctuations in the seasons or in the number of its enemies, run a good chance of utter extinction. But we may go further than this; for as new forms are continually and slowly being produced, unless we believe that the number of specific forms goes on perpetually and almost indefinitely increasing, numbers inevitably must become extinct.[22]

Divergence of Character

The principle, which I have designated by this term, is of high importance on my theory, and explains, as I believe, several important facts. In the first place, varieties, even strongly-marked ones, though having somewhat of the character of species as is shown by the hopeless doubts in many cases how to rank them yet certainly differ from each other far less than do good and distinct species.[23] Nevertheless, according to my view, varieties are species in the process of formation, or are, as I have called them, incipient species. How, then, does the lesser difference between varieties become augmented into the greater difference between species? That this does habitually happen, we must infer from most of the innumerable species throughout nature presenting well-marked differences; whereas varieties, the supposed prototypes and parents of future well-marked species, present slight and ill-defined differences. Mere chance, as we may call it, might cause one variety to differ in some character from its parents, and the offspring of this variety again to differ from its parent in the very same character and in a greater degree; but this alone would never account for so habitual and large an amount of difference as that between varieties of the same species and species of the same genus.

[...] The truth of the principle, that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances. In an extremely small area, especially if freely open to immigration, and where the contest between individual and individual must be severe, we always find great diversity in its inhabitants. For instance, I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other. So it is with the plants and insects on small and uniform islets; and so in small ponds of fresh water. Farmers find that they can raise most food by a rotation of plants belonging to the most different orders: nature follows what may be

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[21] Darwin's debt to Lyell and other geologist is apparent here. For an extended analysis of the importance of the emergence of the notion of 'deep time' see Gould, S.J. 1989. Time's arrow, time's cycle. Harvard University Press: Boston MA.

[22] The idea that competitive interactions lead to extinctions is known as competitive exclusion. The formal mathematical theory of competitive exclusion was developed by G.F. Gause (1934) in a "The Struggle for Existence," (Williams and Wilkins: Baltimore MD). After numerous failed attempts, Gause was eventually able to develop a laboratory system with micro-organisms that produced results consistent with his theory. However, competitive exclusion has never been conclusively demonstrated in any natural system!

[23] Character displacement (W.L. Brown and E.O. Wilson. 1956. Character Displacement. Systematic Zoology 5: 49-64) is the usual result of a range overlap between species with similar resource requirements. Here species diverge, over a few generations, in ways that minimize competition for shared resources. For a more recent analysis see P.A. Abrams (1986) Character displacement and niche shift analyzed using consumer resource models of competition. Theoretical Population Biology 29: 107-159.

called a simultaneous rotation. Most of the animals and plants which live close round any small piece of ground, could live on it (supposing it not to be in any way peculiar in its nature), and may be said to be striving to the utmost to live there; but, it is seen, that where they come into the closest competition with each other, the advantages of diversification of structure, with the accompanying differences of habit and constitution, determine that the inhabitants, which thus jostle each other most closely, shall, as a general rule, belong to what we call different genera and orders.[24]

The accompanying diagram[25] will aid us in understanding this rather perplexing subject. Let A to L represent the species of a genus large in its own country; these species are supposed to resemble each other in unequal degrees, as is so generally the case in nature, and as is represented in the diagram by the letters standing at unequal distances. I have said a large genus, because we have seen in the second chapter, that on an average more of the species of large genera vary than of small genera; and the varying species of the large genera present a greater number of varieties. We have, also, seen that the species, which are the commonest and the most widely-diffused, vary more than rare species with restricted ranges. Let (A) be a common, widely-diffused, and varying species, belonging to a genus large in its own country. The little fan of diverging dotted lines of unequal lengths proceeding from (A), may represent its varying offspring. The variations are supposed to be extremely slight, but of the most diversified nature; they are not supposed all to appear simultaneously, but often after long intervals of time; nor are they all supposed to endure for equal periods. Only those variations which are in some way profitable will be preserved or naturally selected. And here the importance of the principle of benefit being derived from divergence of character comes in; for this will generally lead to the most different or divergent variations (represented by the outer dotted lines) being preserved and accumulated by natural selection. When a dotted line reaches one of the horizontal lines, and is there marked by a small numbered letter, a sufficient amount of variation is supposed to have been accumulated to have formed a fairly well-marked variety, such as would be thought worthy of record in a systematic work. [...]

Summary of Chapter

If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organisation, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection. Natural selection, on the principle of qualities being inherited at corresponding ages, can modify the egg, seed, or young, as easily as the adult. Amongst many animals, sexual selection will give its aid to ordinary selection, by assuring to the most vigorous and best adapted males the greatest number of offspring. Sexual selection will also give characters useful to the males alone, in their struggles with other males.

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[24] This is a fascinating conjecture, to my knowledge so far untested. Potentially great dissertation topic!

[25] The diagram mentioned here is the only illustration in the 'Origin' and it is reproduced inside the front cover of the present abridgement. Darwin presented an extended discussion of this diagram that is worth careful study. In the interest of brevity I have omitted most of that text here but curious readers are encouraged to consult one of the on-line versions of noted earlier.

The affinities of all the beings of the same class have sometimes been represented by a great tree.[26] I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species. At each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs and branches, in the same manner as species and groups of species have tried to overmaster other species in the great battle for life. The limbs divided into great branches, and these into lesser and lesser branches, were themselves once, when the tree was small, budding twigs; and this connexion of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups. Of the many twigs which flourished when the tree was a mere bush, only two or three, now grown into great branches, yet survive and bear all the other branches; so with the species which lived during long-past geological periods, very few now have living and modified descendants. From the first growth of the tree, many a limb and branch has decayed and dropped off; and these lost branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only from having been found in a fossil state. [...] As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications.

CHAPTER V
LAWS OF VARIATION

> Effects of external conditions – Use and disuse, combined with natural selection; organs of flight and of vision – Acclimatisation – Correlation of growth – Compensation and economy of growth – False correlations – Multiple, rudimentary, and lowly organised structures variable – Parts developed in an unusual manner are highly variable: specific character more variable than generic: secondary sexual characters variable – Species of the same genus vary in an analogous manner – Reversions to long-lost characters – **Summary**

[***GAME NOTE**: Darwin's misunderstanding of genetics posed perhaps the greatest single weakness of his theory. Consequently, both his adversaries and his supporters will want to pay close attention to this chapter.*] Our ignorance of the laws of variation is profound. [...] The external conditions of life, as climate and food, &c., seem to have induced some slight modifications. Habit in producing constitutional differences, and use in strengthening, and disuse in weakening and diminishing organs, seem to have been more potent in their effects. Homologous parts tend to vary in the same way, and homologous parts tend to cohere. Modifications in hard parts and in external parts sometimes affect softer and internal parts. When one part is largely developed, perhaps it tends to draw nourishment from the adjoining parts; and every part of the structure which can be saved without detriment to the individual, will be saved. Changes of structure at an early age will generally affect parts subsequently developed; and there are very many other correlations of growth, the nature of which we are utterly unable to understand. Multiple parts are variable in number and in structure, perhaps arising from such parts not having been closely specialized to any particular function, so that their modifications have not been closely checked by natural selection. It is probably from this same cause that organic beings low in the scale of nature are more variable than those which have their whole organisation more specialized, and are higher in the scale. Rudimentary organs, from being useless, will be disregarded by natural selection, and hence probably are variable. Specific characters that is, the characters which have come to differ since the several species of the

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[26] The great tree of life has been called the 'dominant visual metaphor' in evolutionary biology. Inside the back cover, I have provided a representative 1874 image of a "Lebensbaum" from the German biologist Ernst Haeckel (1834-1919), the self-described "apostle of Darwin in Germany." Note that the image can be as misleading as it can be informative. The position of man at the pinnacle of the tree has no biological justification. On a related note, the "Tree of Life" project (http://tolweb.org/tree/phylogeny.html), a distributed attempt to provide a systematic overview of earth's diverse biota, is one of the more interesting and useful internet applications.

same genus branched off from a common parent are more variable than generic characters, or those which have long been inherited, and have not differed within this same period. [...] Secondary sexual characters are highly variable, and such characters differ much in the species of the same group. Variability in the same parts of the organisation has generally been taken advantage of in giving secondary sexual differences to the sexes of the same species, and specific differences to the several species of the same genus. Any part or organ developed to an extraordinary size or in an extraordinary manner, in comparison with the same part or organ in the allied species, must have gone through an extraordinary amount of modification since the genus arose; and thus we can understand why it should often still be variable in a much higher degree than other parts; for variation is a long-continued and slow process, and natural selection will in such cases not as yet have had time to overcome the tendency to further variability and to reversion to a less modified state. But when a species with any extraordinarily-developed organ has become the parent of many modified descendants which on my view must be a very slow process, requiring a long lapse of time in this case, natural selection may readily have succeeded in giving a fixed character to the organ, in however extraordinary a manner it may be developed. Species inheriting nearly the same constitution from a common parent and exposed to similar influences will naturally tend to present analogous variations, and these same species may occasionally revert to some of the characters of their ancient progenitors. Although new and important modifications may not arise from reversion and analogous variation, such modifications will add to the beautiful and harmonious diversity of nature.

Whatever the cause may be of each slight difference in the offspring from their parents and a cause for each must exist it is the steady accumulation, through natural selection, of such differences, when beneficial to the individual, that gives rise to all the more important modifications of structure, by which the innumerable beings on the face of this earth are enabled to struggle with each other, and the best adapted to survive.

CHAPTER VI
DIFFICULTIES ON THEORY

> **Difficulties on the theory of descent with modification** – Transitions – **Absence or rarity of transitional varieties** – Transitions in habits of life – Diversified habits in the same species – Species with habits widely different from those of their allies – **Organs of extreme perfection** – Means of transition – Cases of difficulty – Natura non facit saltum – Organs of small importance – Organs not in all cases absolutely perfect – The law of Unity of Type and of the Conditions of Existence embraced by the theory of Natural Selection

*[**GAME NOTE:** In this characteristically self-critical chapter, Darwin considers objections to his theory in detail. Here I have reproduced only his general overview and students are encouraged to peruse the full text of this chapter on-line. Pay particular attention to his strategy for resolving (dismissing?) apparent difficulties.]*

Long before having arrived at this part of my work, a crowd of difficulties will have occurred to the reader. Some of them are so grave that to this day I can never reflect on them without being staggered; but, to the best of my judgment, the greater number are only apparent, and those that are real are not, I think, fatal to my theory.

These difficulties and objections may be classed under the following heads: Firstly, why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion instead of the species being, as we see them, well defined?

Secondly, is it possible that an animal having, for instance, the structure and habits of a bat, could have been formed by the modification of some animal with wholly different habits? Can we believe that natural selection could produce, on the one hand, organs of trifling importance, such as the tail of a giraffe, which serves as a fly-flapper, and, on the other hand, organs of such wonderful structure, as the eye, of which we hardly as yet fully understand the inimitable perfection?

Thirdly, can instincts be acquired and modified through natural selection? What shall we say to so marvelous an instinct as that which leads the bee to make cells, which have practically anticipated the discoveries of profound mathematicians?

Fourthly, how can we account for species, when crossed, being sterile and producing sterile offspring, whereas, when varieties are crossed, their fertility is unimpaired?

The two first heads shall be here discussed (with) Instinct and Hybridism in separate chapters.

[...] as by this theory innumerable transitional forms must have existed, why do we not find them embedded in countless numbers in the crust of the earth? It will be much more convenient to discuss this question in the chapter on the Imperfection of the geological record; and I will here only state that I believe the answer mainly lies in the record being incomparably less perfect than is generally supposed; the imperfection of the record being chiefly due to organic beings not inhabiting profound depths of the sea, and to their remains being embedded and preserved to a future age only in masses of sediment sufficiently thick and extensive to withstand an enormous amount of future degradation; and such fossiliferous masses can be accumulated only where much sediment is deposited on the shallow bed of the sea, whilst it slowly subsides. These contingencies will concur only rarely, and after enormously long intervals. Whilst the bed of the sea is stationary or is rising, or when very little sediment is being deposited, there will be blanks in our geological history. The crust of the earth is a vast museum; but the natural collections have been made only at intervals of time immensely remote.

[...] Organs of extreme perfection and complication. To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree. Yet reason tells me, that if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if further, the eye does vary ever so slightly, and the variations be inherited, which is certainly the case; and if any variation or modification in the organ be ever useful to an animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real. How a nerve comes to be sensitive to light, hardly concerns us more than how life itself first originated; but I may remark that several facts make me suspect that any sensitive nerve may be rendered sensitive to light, and likewise to those coarser vibrations of the air which produce sound.

CHAPTER VII
INSTINCT

Instincts comparable with habits, but different in their origin – Instincts graduated – Aphides and ants – Instincts variable – Domestic instincts, their origin – Natural instincts of the cuckoo, ostrich, and parasitic bees – Slave-making ants – Hive-bee, its cell-making instinct – Difficulties on the theory of the Natural Selection of instincts – Neuter or sterile insects – **Summary**

*[**GAME NOTE:** For this and several subsequent chapters I have simply reproduced Darwin's own chapter summary. While this approach greatly reduces the total amount of reading it fails to do full justice to the breadth and depth of Darwin's evidence and readers are encouraged to consult the full text concerning specific examples. **CHARACTER ALERT:** The Anthropologist and the Ethnologist will want to consult the section on Slave Making Ants. As a hint to all characters – using an on-line version of the text and your browsers "Find in Page" feature will allow you to rapidly find Darwin's views on specific topics.]*

I have endeavoured briefly in this chapter to show that the mental qualities of our domestic animals vary, and that the variations are inherited. Still more briefly I have attempted to show that instincts vary slightly in a state of

nature. No one will dispute that instincts are of the highest importance to each animal. Therefore I can see no difficulty, under changing conditions of life, in natural selection accumulating slight modifications of instinct to any extent, in any useful direction. In some cases habit or use and disuse have probably come into play. I do not pretend that the facts given in this chapter strengthen in any great degree my theory; but none of the cases of difficulty, to the best of my judgment, annihilate it.[27] On the other hand, the fact that instincts are not always absolutely perfect and are liable to mistakes; that no instinct has been produced for the exclusive good of other animals, but that each animal takes advantage of the instincts of others; that the canon in natural history, of 'natura non facit saltum' is applicable to instincts as well as to corporeal structure, and is plainly explicable on the foregoing views, but is otherwise inexplicable, all tend to corroborate the theory of natural selection.

This theory is, also, strengthened by some few other facts in regard to instincts; as by that common case of closely allied, but certainly distinct, species, when inhabiting distant parts of the world and living under considerably different conditions of life, yet often retaining nearly the same instincts. For instance, we can understand on the principle of inheritance, how it is that the thrush of South America lines its nest with mud, in the same peculiar manner as does our British thrush: how it is that the male wrens (Troglodytes) of North America, build 'cock-nests,' to roost in, like the males of our distinct Kitty-wrens, a habit wholly unlike that of any other known bird. Finally, it may not be a logical deduction, but to my imagination it is far more satisfactory to look at such instincts as the young cuckoo ejecting its foster-brothers, ants making slaves, [...] not as specially endowed or created instincts, but as small consequences of one general law, leading to the advancement of all organic beings, namely, multiply, vary, let the strongest live and the weakest die.

CHAPTER VIII
HYBRIDISM

Distinction between the sterility of first crosses and of hybrids – Sterility various in degree, not universal, affected by close interbreeding, removed by domestication – Laws governing the sterility of hybrids – Sterility not a special endowment, but incidental on other differences – Causes of the sterility of first crosses and of hybrids – Parallelism between the effects of changed conditions of life and crossing – Fertility of varieties when crossed and of their mongrel offspring not universal – Hybrids and mongrels compared independently of their fertility – **Summary**

[***GAME ADVISORY***: *In this chapter Darwin is struggling with the implications of the fact that species, which seems so obviously distinctive, have no fixed essence. This sense of impermanence was perhaps the most disconcerting aspect of Darwin's work for his contemporaries.*] First crosses between forms sufficiently distinct to be ranked as species, and their hybrids, are very generally, but not universally, sterile. The sterility is of all degrees, and is often so slight that the two most careful experimentalists who have ever lived, have come to diametrically opposite conclusions in ranking forms by this test. The sterility is innately variable in individuals of the same species, and is eminently susceptible of favourable and unfavourable conditions. The degree of sterility does not strictly follow systematic affinity, but is governed by several curious and complex laws. It is generally different, and sometimes widely different, in reciprocal crosses between the same two species. It is not always equal in degree in a first cross and in the hybrid produced from this cross.

In the same manner as in grafting trees, the capacity of one species or variety to take on another, is incidental on generally unknown differences in their vegetative systems, so in crossing, the greater or less facility of one species to unite with another, is incidental on unknown differences in their reproductive systems. There is no more reason to think that species have been specially endowed with various degrees of sterility to prevent them

[27] Darwin appreciation of the distinction between confirmation and falsification anticipates the work of Karl Popper and his claim that science is ultimately a process of "conjectures and refutations."

crossing and blending in nature, than to think that trees have been specially endowed with various and somewhat analogous degrees of difficulty in being grafted together...

The sterility of first crosses between pure species, which have their reproductive systems perfect, seems to depend on several circumstances; in some cases largely on the early death of the embryo. The sterility of hybrids, which have their reproductive systems imperfect, and which have had this system and their whole organisation disturbed by being compounded of two distinct species, seems closely allied to that sterility which so frequently affects pure species, when their natural conditions of life have been disturbed. This view is supported by a parallelism of another kind; namely, that the crossing of forms only slightly different is favourable to the vigour and fertility of their offspring; and that slight changes in the conditions of life are apparently favourable to the vigour and fertility of all organic beings. It is not surprising that the degree of difficulty in uniting two species, and the degree of sterility of their hybrid-offspring should generally correspond, though due to distinct causes; for both depend on the amount of difference of some kind between the species which are crossed. Nor is it surprising that the facility of effecting a first cross, the fertility of the hybrids produced, and the capacity of being grafted together though this latter capacity evidently depends on widely different circumstances should all run, to a certain extent, parallel with the systematic affinity of the forms which are subjected to experiment; for systematic affinity attempts to express all kinds of resemblance between all species.

First crosses between forms known to be varieties, or sufficiently alike to be considered as varieties, and their mongrel offspring, are very generally, but not quite universally, fertile. Nor is this nearly general and perfect fertility surprising, when we remember how liable we are to argue in a circle with respect to varieties in a state of nature; and when we remember that the greater number of varieties have been produced under domestication by the selection of mere external differences, and not of differences in the reproductive system. In all other respects, excluding fertility, there is a close general resemblance between hybrids and mongrels. Finally, then, the facts briefly given in this chapter do not seem to me opposed to, but even rather to support the view, that there is no fundamental distinction between species and varieties.

CHAPTER IX
ON THE IMPERFECTIONS OF THE GEOLOGICAL RECORD

On the absence of intermediate varieties at the present day - On the nature of extinct intermediate varieties; on their number - On the vast lapse of time, as inferred from the rate of deposition and of denudation - On the poorness of our palaeontological collections - On the intermittence of geological formations - On the absence of intermediate varieties in any one formation - **On their sudden appearance in the lowest known fossiliferous strata**

[***CHARACTER ALERT***: *Geologist, Paleontologist, Owen, Huxley – each of you should be conversant with what was known of the fossil record in the 1860s – you need to serve as authorities on such matters in both General and Council Sessions.*] In the first place it should always be borne in mind what sort of intermediate forms must, on my theory, have formerly existed. I have found it difficult, when looking at any two species, to avoid picturing to myself, forms directly intermediate between them. But this is a wholly false view; we should always look for forms intermediate between each species and a common but unknown progenitor; and the progenitor will generally have differed in some respects from all its modified descendants. To give a simple illustration: the fantail and pouter pigeons have both descended from the rock-pigeon; if we possessed all the intermediate varieties which have ever existed, we should have an extremely close series between both and the rock-pigeon; but we should have no varieties directly intermediate between the fantail and pouter; none, for instance, combining a tail somewhat expanded with a crop somewhat enlarged, the characteristic features of these two breeds. These two breeds, moreover, have become so much modified, that if we had no historical or indirect evidence regarding their origin, it would not have been possible to have determined from a mere comparison of their structure with that of the rock-pigeon, whether they had descended from this species or from some other allied species, such as C. oenas.

So with natural species, if we look to forms very distinct, for instance to the horse and tapir, we have no reason to suppose that links ever existed directly intermediate between them, but between each and an unknown common parent. The common parent will have had in its whole organisation much general resemblance to the tapir and to the horse; but in some points of structure may have differed considerably from both, even perhaps more than they differ from each other. Hence in all such cases, we should be unable to recognise the parent-form of any two or more species, even if we closely compared the structure of the parent with that of its modified descendants, unless at the same time we had a nearly perfect chain of the intermediate links.

[...] The abrupt manner in which whole groups of species suddenly appear in certain formations, has been urged by several palaeontologists, for instance, by Agassiz, Pictet, and by none more forcibly than by Professor Sedgwick, as a fatal objection to the belief in the transmutation of species. If numerous species, belonging to the same genera or families, have really started into life all at once, the fact would be fatal to the theory of descent with slow modification through natural selection. For the development of a group of forms, all of which have descended from some one progenitor, must have been an extremely slow process; and the progenitors must have lived long ages before their modified descendants. But we continually over-rate the perfection of the geological record, and falsely infer, because certain genera or families have not been found beneath a certain stage, that they did not exist before that stage. We continually forget how large the world is, compared with the area over which our geological formations have been carefully examined; we forget that groups of species may elsewhere have long existed and have slowly multiplied before they invaded the ancient archipelagoes of Europe and of the United States. We do not make due allowance for the enormous intervals of time, which have probably elapsed between our consecutive formations, longer perhaps in some cases than the time required for the accumulation of each formation. These intervals will have given time for the multiplication of species from some one or some few parent-forms; and in the succeeding formation such species will appear as if suddenly created.

CHAPTER X
ON THE GEOLOGICAL SUCCESSION OF ORGANIC BEINGS

On the slow and successive appearance of new species - On their different rates of change - Species once lost do not reappear - Groups of species follow the same general rules in their appearance and disappearance as do single species - On Extinction - On simultaneous changes in the forms of life throughout the world - On the affinities of extinct species to each other and to living species - On the state of development of ancient forms - On the succession of the same types within the same areas - **Summary of preceding and present chapters**

[***GAME NOTE:*** *Absence of evidence is not evidence of absence – X-men can interpret Darwin's theory as a guide to interesting empirical studies. A-men can make the case the sparsity of evidence points to the recklessly speculative nature of Darwin's work.*] I have attempted to show that the geological record is extremely imperfect; that only a small portion of the globe has been geologically explored with care; that only certain classes of organic beings have been largely preserved in a fossil state; that the number both of specimens and of species, preserved in our museums, is absolutely as nothing compared with the incalculable number of generations which must have passed away even during a single formation; that, owing to subsidence being necessary for the accumulation of fossiliferous deposits thick enough to resist future degradation, enormous intervals of time have elapsed between the successive formations; that there has probably been more extinction during the periods of subsidence, and more variation during the periods of elevation, and during the latter the record will have been least perfectly kept; that each single formation has not been continuously deposited; that the duration of each formation is, perhaps, short compared with the average duration of specific forms; that migration has played an important part in the first appearance of new forms in any one area and formation; that widely ranging species are those which have varied most, and have oftenest given rise to new species; and that varieties have at first often been local. All these causes taken conjointly, must have tended to make the geological record extremely imperfect, and will to a large extent explain why we do not find interminable varieties, connecting together all the extinct and existing forms of life by the finest graduated steps.

He who rejects these views on the nature of the geological record, will rightly reject my whole theory. For he may ask in vain where are the numberless transitional links which must formerly have connected the closely allied or representative species, found in the several stages of the same great formation. He may disbelieve in the enormous intervals of time which have elapsed between our consecutive formations; he may overlook how important a part migration must have played, when the formations of any one great region alone, as that of Europe, are considered; he may urge the apparent, but often falsely apparent, sudden coming in of whole groups of species. He may ask where are the remains of those infinitely numerous organisms which must have existed long before the first bed of the Silurian system was deposited: I can answer this latter question only hypothetically, by saying that as far as we can see, where our oceans now extend they have for an enormous period extended, and where our oscillating continents now stand they have stood ever since the Silurian epoch; but that long before that period, the world may have presented a wholly different aspect; and that the older continents, formed of formations older than any known to us, may now all be in a metamorphosed condition, or may lie buried under the ocean.[28]

Passing from these difficulties, all the other great leading facts in palaeontology seem to me simply to follow on the theory of descent with modification through natural selection. We can thus understand how it is that new species come in slowly and successively; how species of different classes do not necessarily change together, or at the same rate, or in the same degree; yet in the long run that all undergo modification to some extent. The extinction of old forms is the almost inevitable consequence of the production of new forms.[29] [...] Groups of species increase in numbers slowly, and endure for unequal periods of time; for the process of modification is necessarily slow, and depends on many complex contingencies. The dominant species of the larger dominant groups tend to leave many modified descendants, and thus new sub-groups and groups are formed. As these are formed, the species of the less vigorous groups, from their inferiority inherited from a common progenitor, tend to become extinct together, and to leave no modified offspring on the face of the earth. But the utter extinction of a whole group of species may often be a very slow process, from the survival of a few descendants, lingering in protected and isolated situations. When a group has once wholly disappeared, it does not reappear; for the link of generation has been broken.

We can understand how the spreading of the dominant forms of life, which are those that oftenest vary, will in the long run tend to people the world with allied, but modified, descendants; and these will generally succeed in taking the places of those groups of species which are their inferiors in the struggle for existence. Hence, after long intervals of time, the productions of the world will appear to have changed simultaneously. [...]

The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life, and are, in so far, higher in the scale of nature; and this may account for that vague yet ill-defined sentiment, felt by many palaeontologists, that organisation on the whole has progressed. If it should hereafter be proved that ancient animals resemble to a certain extent the embryos of more recent animals of the same class, the fact will be intelligible. The succession of the same types of structure within the same areas during the later geological periods ceases to be mysterious, and is simply explained by inheritance.

If the geological record be as imperfect as I believe it to be, and it may at least be asserted that the record cannot be proved to be much more perfect, the main objections to the theory of natural selection are greatly diminished

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[28] Numerous pre-Silurian fossil beds have since been discovered. S.J. Gould [(1989) Wonderful life: the Burgess Shale and the nature of history. W.W. Norton: New York NY] provides a particularly rich and accessible account of the diversity of one of the best studied pre-Silurian (actually pre-Cambrian, 530 m.y.a.) sites.

[29] From a purely logical perspective, it makes at least as much sense to argue that the production of new forms is the almost inevitable consequence of the opportunity provided by extinction of old forms; this is especially important in light of relatively recent realization that there have been at least seven great extinction events in earth's history (independent of species interactions! – see http://en.wikipedia.org/wiki/Extinction_event for more details).

or disappear. On the other hand, all the chief laws of palaeontology plainly proclaim, as it seems to me, that species have been produced by ordinary generation: old forms having been supplanted by new and improved forms of life, produced by the laws of variation still acting round us, and preserved by Natural Selection.

CHAPTER XI
GEOGRAPHICAL DISTRIBUTION

Present distribution cannot be accounted for by differences in physical conditions - Importance of barriers - Affinity of the productions of the same continent - Centres of creation - **Means of dispersal, by changes of climate and of the level of the land, and by occasional means** - Dispersal during the Glacial period co-extensive with the world

[***GAME NOTE**: Recall that, like Darwin, many of you have traveled rather extensively and have been personally struck by the patterns he is seeking to interpret here. Depending on your objectives, you may elect to confirm or contrast his observations with your own.*] In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions. Of late, almost every author who has studied the subject has come to this conclusion. The case of America alone would almost suffice to prove its truth: for if we exclude the northern parts where the circumpolar land is almost continuous, all authors agree that one of the most fundamental divisions in geographical distribution is that between the New and Old Worlds;[30] yet if we travel over the vast American continent, from the central parts of the United States to its extreme southern point, we meet with the most diversified conditions; the most humid districts, arid deserts, lofty mountains, grassy plains, forests, marshes, lakes, and great rivers, under almost every temperature. There is hardly a climate or condition in the Old World which cannot be paralleled in the New at least as closely as the same species generally require; for it is a most rare case to find a group of organisms confined to any small spot, having conditions peculiar in only a slight degree; for instance, small areas in the Old World could be pointed out hotter than any in the New World, yet these are not inhabited by a peculiar fauna or flora. Notwithstanding this parallelism in the conditions of the Old and New Worlds, how widely different are their living productions!

In the southern hemisphere, if we compare large tracts of land in Australia, South Africa, and western South America, between latitudes 25° and 35°, we shall find parts extremely similar in all their conditions, yet it would not be possible to point out three faunas and floras more utterly dissimilar. Or again we may compare the productions of South America south of lat. 35° with those north of 25°, which consequently inhabit a considerably different climate, and they will be found incomparably more closely related to each other, than they are to the productions of Australia or Africa under nearly the same climate. Analogous facts could be given with respect to the inhabitants of the sea.

A second great fact which strikes us in our general review is, that barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions. We see this in the great difference of nearly all the terrestrial productions of the New and Old Worlds, excepting in the northern parts, where the land almost joins, and where, under a slightly different climate, there might have been free migration for the northern temperate forms, as there now is for the strictly arctic productions. We see the same fact in the great difference between the inhabitants of Australia, Africa, and South America under the same latitude: for these countries are almost as much isolated from each other as is possible. On each continent, also, we see the same fact; for on the opposite sides of lofty and continuous mountain-ranges, and of great deserts, and sometimes even of large rivers, we find different productions; though as mountain

[30] Remember that Darwin's work here far pre-dates the notion of continental drift which was first clearly articulated by Alfred Wegener in 1912 and later incorporated into the larger theory of plate tectonics.

chains, deserts, &c., are not as impassable, or likely to have endured so long as the oceans separating continents, the differences are very inferior in degree to those characteristic of distinct continents.[31]

[...] Considering that the several above means of transport, and that several other means, which without doubt remain to be discovered, have been in action year after year, for centuries and tens of thousands of years, it would I think be a marvellous fact if many plants had not thus become widely transported. These means of transport are sometimes called accidental, but this is not strictly correct: the currents of the sea are not accidental, nor is the direction of prevalent gales of wind. It should be observed that scarcely any means of transport would carry seeds for very great distances; for seeds do not retain their vitality when exposed for a great length of time to the action of seawater; nor could they be long carried in the crops or intestines of birds. These means, however, would suffice for occasional transport across tracts of sea some hundred miles in breadth, or from island to island, or from a continent to a neighbouring island, but not from one distant continent to another. The floras of distant continents would not by such means become mingled in any great degree; but would remain as distinct as we now see them to be. The currents, from their course, would never bring seeds from North America to Britain, though they might and do bring seeds from the West Indies to our western shores, where, if not killed by so long an immersion in salt-water, they could not endure our climate. Almost every year, one or two land-birds are blown across the whole Atlantic Ocean, from North America to the western shores of Ireland and England; but seeds could be transported by these wanderers only by one means, namely, in dirt sticking to their feet, which is in itself a rare accident. Even in this case, how small would the chance be of a seed falling on favourable soil, and coming to maturity! But it would be a great error to argue that because a well-stocked island, like Great Britain, has not, as far as is known (and it would be very difficult to prove this), received within the last few centuries, through occasional means of transport, immigrants from Europe or any other continent, that a poorly-stocked island, though standing more remote from the mainland, would not receive colonists by similar means. I do not doubt that out of twenty seeds or animals transported to an island, even if far less well-stocked than Britain, scarcely more than one would be so well fitted to its new home, as to become naturalised. But this, as it seems to me, is no valid argument against what would be effected by occasional means of transport, during the long lapse of geological time, whilst an island was being upheaved and formed, and before it had become fully stocked with inhabitants. On almost bare land, with few or no destructive insects or birds living there, nearly every seed, which chanced to arrive, would be sure to germinate and survive.

CHAPTER XII
GEOGRAPHICAL DISTRIBUTION (Continued)

Distribution of fresh-water productions - On the inhabitants of oceanic islands - Absence of Batrachians and of terrestrial Mammals - On the relations of the inhabitants of islands to those of the nearest mainland - On colonisation from the nearest source with subsequent modification - **Summary of the last and present chapters**

[***GAME NOTE:*** *Darwin is showing here that his theory produces what Whewell championed as a 'consilience of inductions' – an ability of a theory to make coherent sense of an other large class of disparate facts.* ***CHARACTER ALERT:*** *Inductivist (Baconian) Philosopher and Friend of Mill*] In these chapters I have endeavoured to show, that if we make due allowance for our ignorance of the full effects of all the changes of climate and of the level of the land, which have certainly occurred within the recent period, and of other similar changes which may have occurred within the same period; if we remember how profoundly ignorant we are with respect to the many and curious means of occasional transport, a subject which has hardly ever been properly

[31] There has been considerable work on the relative significance of migration versus separation of populations by geological events. Because earth's crust has proven far more dynamic than Darwin supposed, he generally over-estimated the significance of migration and underestimated the role of vicariance events (e.g., emergence of the isthmus of Panama, plate tectonics more generally).

experimentised on; if we bear in mind how often a species may have ranged continuously over a wide area, and then have become extinct in the intermediate tracts, I think the difficulties in believing that all the individuals of the same species, wherever located, have descended from the same parents, are not insuperable. And we are led to this conclusion, which has been arrived at by many naturalists under the designation of single centres of creation, by some general considerations, more especially from the importance of barriers and from the analogical distribution of sub-genera, genera, and families.

If the difficulties be not insuperable in admitting that in the long course of time the individuals of the same species, and likewise of allied species, have proceeded from some one source; then I think all the grand leading facts of geographical distribution are explicable on the theory of migration (generally of the more dominant forms of life), together with subsequent modification and the multiplication of new forms. We can thus understand the high importance of barriers, whether of land or water, which separate our several zoological and botanical provinces. We can thus understand the localisation of sub-genera, genera, and families; and how it is that under different latitudes, for instance in South America, the inhabitants of the plains and mountains, of the forests, marshes, and deserts, are in so mysterious a manner linked together by affinity, and are likewise linked to the extinct beings which formerly inhabited the same continent. Bearing in mind that the mutual relations of organism to organism are of the highest importance, we can see why two areas having nearly the same physical conditions should often be inhabited by very different forms of life; for according to the length of time which has elapsed since new inhabitants entered one region; according to the nature of the communication which allowed certain forms and not others to enter, either in greater or lesser numbers; according or not, as those which entered happened to come in more or less direct competition with each other and with the aborigines; and according as the immigrants were capable of varying more or less rapidly, there would ensue in different regions, independently of their physical conditions, infinitely diversified conditions of life, there would be an almost endless amount of organic action and reaction, and we should find, as we do find, some groups of beings greatly, and some only slightly modified, some developed in great force, some existing in scanty numbers in the different great geographical provinces of the world.

On these same principles, we can understand, as I have endeavoured to show, why oceanic islands should have few inhabitants, but of these a great number should be endemic or peculiar; and why, in relation to the means of migration, one group of beings, even within the same class, should have all its species endemic, and another group should have all its species common to other quarters of the world. We can see why whole groups of organisms, as batrachians and terrestrial mammals, should be absent from oceanic islands, whilst the most isolated islands possess their own peculiar species of aërial mammals or bats. We can see why there should be some relation between the presence of mammals, in a more or less modified condition, and the depth of the sea between an island and the mainland. We can clearly see why all the inhabitants of an archipelago, though specifically distinct on the several islets, should be closely related to each other, and likewise be related, but less closely, to those of the nearest continent or other source whence immigrants were probably derived. We can see why in two areas, however distant from each other, there should be a correlation, in the presence of identical species, of varieties, of doubtful species, and of distinct but representative species.

[...] On my theory these several relations throughout time and space are intelligible; for whether we look to the forms of life which have changed during successive ages within the same quarter of the world, or to those which have changed after having migrated into distant quarters, in both cases the forms within each class have been connected by the same bond of ordinary generation; and the more nearly any two forms are related in blood, the nearer they will generally stand to each other in time and space; in both cases the laws of variation have been the same, and modifications have been accumulated by the same power of natural selection.

CHAPTER XIII

MUTUAL AFFINITIES OF ORGANIC BEINGS: MORPHOLOGY: EMBRYOLOGY: RUDIMENTARY ORGANS

CLASSIFICATION, groups subordinate to groups - Natural system - Rules and difficulties in classification, explained on the theory of descent with modification - Classification of varieties - Descent always used in classification - Analogical or adaptive characters - Affinities, general, complex and radiating - Extinction separates and defines groups - MORPHOLOGY, between members of the same class, between parts of the same individual - EMBRYOLOGY, laws of, explained by variations not supervening at an early age, and being inherited at a corresponding age - RUDIMENTARY ORGANS; their origin explained - **Summary**

In this chapter I have attempted to show, that the subordination of group to group in all organisms throughout all time; that the nature of the relationship, by which all living and extinct beings are united by complex, radiating, and circuitous lines of affinities into one grand system; the rules followed and the difficulties encountered by naturalists in their classifications; the value set upon characters, if constant and prevalent, whether of high vital importance, or of the most trifling importance, or, as in rudimentary organs, of no importance; the wide opposition in value between analogical or adaptive characters, and characters of true affinity; and other such rules; all naturally follow on the view of the common parentage of those forms which are considered by naturalists as allied, together with their modification through natural selection, with its contingencies of extinction and divergence of character. In considering this view of classification, it should be borne in mind that the element of descent has been universally used in ranking together the sexes, ages, and acknowledged varieties of the same species, however different they may be in structure. If we extend the use of this element of descent, the only certainly known cause of similarity in organic beings, we shall understand what is meant by the natural system: it is genealogical in its attempted arrangement, with the grades of acquired difference marked by the terms varieties, species, genera, families, orders, and classes.

On this same view of descent with modification, all the great facts in Morphology become intelligible, whether we look to the same pattern displayed in the homologous organs, to whatever purpose applied, of the different species of a class; or to homologous parts constructed on the same pattern in each individual animal and plant.

On the principle of successive slight variations, not necessarily or generally supervening at a very early period of life, and being inherited at a corresponding period, we can understand the great leading facts in Embryology; namely, the resemblance in an individual embryo of the homologous parts, which when matured will become widely different from each other in structure and function; and the resemblance in different species of a class of the homologous parts or organs, though fitted in the adult members for purposes as different as possible. Larvae are active embryos, which have become specially modified in relation to their habits of life, through the principle of modifications being inherited at corresponding ages. On this same principle and bearing in mind, that when organs are reduced in size, either from disuse or selection, it will generally be at that period of life when the being has to provide for its own wants, and bearing in mind how strong is the principle of inheritance the occurrence of rudimentary organs and their final abortion, present to us no inexplicable difficulties; on the contrary, their presence might have been even anticipated. The importance of embryological characters and of rudimentary organs in classification is intelligible, on the view that an arrangement is only so far natural as it is genealogical.[32]

[**Closing paragraph added to later editions:** Finally, the several classes of facts which have been considered in this chapter, seem to me to proclaim so plainly, that the innumerable species, genera and families, with which this

[32] For an update on the relationship between evolution and development see J. Gerhart and M. Kirshner [(1997) Cells, embryos, and evolution: toward a cellular and developmental understanding of phenotypic variation and evolutionary adaptability. Blackwell Science: Malden MA.]

world is peopled, are all descended , each within its own class or group, from common parents, and have all been modified in the course of descent, that I should without hesitation adopt this view, even if it were unsupported by other arguments.][33]

CHAPTER XIV
RECAPITULATION AND CONCLUSION

Recapitulation of the difficulties on the theory of Natural Selection – Recapitulation of the general and special circumstances in its favour – Causes of the general belief in the immutability of species – How far the theory of natural selection may be extended – Effects of its adoption on the study of Natural history – Concluding remarks

*[**GAME NOTES:** Excerpts presented here are drawn primarily from Darwin's concluding remarks; readers may wish to read the entire final chapter on-line for Darwin' s full recapitulation of his "long argument."]*

As this whole volume is one long argument, it may be convenient to the reader to have the leading facts and inferences briefly recapitulated. [...] That many and grave objections may be advanced against the theory of descent with modification through natural selection, I do not deny. I have endeavoured to give to them their full force. Nothing at first can appear more difficult to believe than that the more complex organs and instincts should have been perfected not by means superior to, though analogous with, human reason, but by the accumulation of innumerable slight variations, each good for the individual possessor. Nevertheless, this difficulty, though appearing to our imagination insuperably great, cannot be considered real if we admit the following propositions, namely, -- that gradations in the perfection of any organ or instinct, which we may consider, either do now exist or could have existed, each good of its kind, -- that all organs and instincts are, in ever so slight a degree, variable, -- and, lastly, that there is a struggle for existence leading to the preservation of each profitable deviation of structure or instinct. The truth of these propositions cannot, I think, be disputed. [...]

[...] As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modification; it can act only by very short and slow steps. Hence the canon of `Natura non facit saltum,' which every fresh addition to our knowledge tends to make more strictly correct, is on this theory simply intelligible. We can plainly see why nature is prodigal in variety, though niggard in innovation. But why this should be a law of nature if each species has been independently created, no man can explain.[34]

Many other facts are, as it seems to me, explicable on this theory. How strange it is that a bird, under the form of woodpecker, should have been created to prey on insects on the ground; that upland geese, which never or rarely swim, should have been created with webbed feet; that a thrush should have been created to dive and feed on sub-aquatic insects; and that a petrel should have been created with habits and structure fitting it for the life of an auk or grebe! and so on in endless other cases. But on the view of each species constantly trying to increase in number, with natural selection always ready to adapt the slowly varying descendants of each to any unoccupied or ill-occupied place in nature, these facts cease to be strange, or perhaps might even have been anticipated.

As natural selection acts by competition, it adapts the inhabitants of each country only in relation to the degree of perfection of their associates; so that we need feel no surprise at the inhabitants of any one country, although on the ordinary view supposed to have been specially created and adapted for that country, being beaten and

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[33] This addition clearly reflects a Darwin's commitment to Whewell's 'consilience of inductions.' It is also interesting to note that Darwin here explicitly restricts his theory to changes within group or class.

[34] See N. Eldredge and S.J. Gould [(1972) Punctuated equilibrium: an alternative to phyletic gradualism. In: Schopf, T. Models in Paleobiology. W.H. Freeman: San Francisco CA] for a discussion of how gradual changes in genes can produce more abrupt changes in form. The on-going exchange between gradualists and proponents of punctuated equilibrium continues to be one of the most dynamic and contentious arenas of evolutionary theory.

supplanted by the naturalised productions from another land. *[Naturalizing and justifying the British Empire?]* Nor ought we to marvel if all the contrivances in nature be not, as far as we can judge, absolutely perfect; and if some of them be abhorrent to our ideas of fitness. We need not marvel at the sting of the bee causing the bee's own death; at drones being produced in such vast numbers for one single act, and being then slaughtered by their sterile sisters; at the astonishing waste of pollen by our fir-trees; at the instinctive hatred of the queen bee for her own fertile daughters; at ichneumonidae feeding within the live bodies of caterpillars; and at other such cases. The wonder indeed is, on the theory of natural selection, that more cases of the want of absolute perfection have not been observed.

The fact, as we have seen, that all past and present organic beings constitute one grand natural system, with group subordinate to group, and with extinct groups often falling in between recent groups, is intelligible on the theory of natural selection with its contingencies of extinction and divergence of character.[35] On these same principles we see how it is, that the mutual affinities of the species and genera within each class are so complex and circuitous. We see why certain characters are far more serviceable than others for classification; -- why adaptive characters, though of paramount importance to the being, are of hardly any importance in classification; why characters derived from rudimentary parts, though of no service to the being, are often of high classificatory value; and why embryological characters are the most valuable of all. The real affinities of all organic beings are due to inheritance or community of descent. The natural system is a genealogical arrangement, in which we have to discover the lines of descent by the most permanent characters, however slight their vital importance may be.

The framework of bones being the same in the hand of a man, wing of a bat, fin of the porpoise, and leg of the horse, -- the same number of vertebrae forming the neck of the giraffe and of the elephant, -- and innumerable other such facts, at once explain themselves on the theory of descent with slow and slight successive modifications. The similarity of pattern in the wing and leg of a bat, though used for such different purposes, -- in the jaws and legs of a crab, -- in the petals, stamens, and pistils of a flower, is likewise intelligible on the view of the gradual modification of parts or organs, which were alike in the early progenitor of each class. On the principle of successive variations not always supervening at an early age, and being inherited at a corresponding not early period of life, we can clearly see why the embryos of mammals, birds, reptiles, and fishes should be so closely alike, and should be so unlike the adult forms. We may cease marvelling at the embryo of an air-breathing mammal or bird having branchial slits and arteries running in loops, like those in a fish which has to breathe the air dissolved in water, by the aid of well-developed branchiae.

Disuse, aided sometimes by natural selection, will often tend to reduce an organ, when it has become useless by changed habits or under changed conditions of life; and we can clearly understand on this view the meaning of rudimentary organs. But disuse and selection will generally act on each creature, when it has come to maturity and has to play its full part in the struggle for existence, and will thus have little power of acting on an organ during early life; hence the organ will not be much reduced or rendered rudimentary at this early age. The calf, for instance, has inherited teeth, which never cut through the gums of the upper jaw, from an early progenitor having well-developed teeth; and we may believe, that the teeth in the mature animal were reduced, during successive generations, by disuse or by the tongue and palate having been fitted by natural selection to browse without their aid; whereas in the calf, the teeth have been left untouched by selection or disuse, and on the principle of inheritance at corresponding ages have been inherited from a remote period to the present day. On the view of each organic being and each separate organ having been specially created, how utterly inexplicable it is that parts, like the teeth in the embryonic calf or like the shrivelled wings under the soldered wing-covers of some beetles, should thus so frequently bear the plain stamp of inutility! Nature may be said to have taken pains to reveal, by rudimentary organs and by homologous structures, her scheme of modification, which it seems that

[35] Systematics is slowly but surely being re-built on an explicitly evolutionary or "cladistic" foundation as first advocated by W. Hennig (1966) in "Phylogenetic Systematics" [University of Illinois Press: Urbana IL].

we wilfully will not understand.[36] [...]

[...] I have now recapitulated the chief facts and considerations which have thoroughly convinced me that species have changed, and are still slowly changing by the preservation and accumulation of successive slight favourable variations. Why, it may be asked, have all the most eminent living naturalists and geologists rejected this view of the mutability of species? It cannot be asserted that organic beings in a state of nature are subject to no variation; it cannot be proved that the amount of variation in the course of long ages is a limited quantity; no clear distinction has been, or can be, drawn between species and well-marked varieties. It cannot be maintained that species when intercrossed are invariably sterile, and varieties invariably fertile; or that sterility is a special endowment and sign of creation. The belief that species were immutable productions was almost unavoidable as long as the history of the world was thought to be of short duration; and now that we have acquired some idea of the lapse of time, we are too apt to assume, without proof, that the geological record is so perfect that it would have afforded us plain evidence of the mutation of species, if they had undergone mutation.

But the chief cause of our natural unwillingness to admit that one species has given birth to other and distinct species, is that we are always slow in admitting any great change of which we do not see the intermediate steps. The difficulty is the same as that felt by so many geologists, when Lyell first insisted that long lines of inland cliffs had been formed, and great valleys excavated, by the slow action of the coast-waves. The mind cannot possibly grasp the full meaning of the term of a hundred million years; it cannot add up and perceive the full effects of many slight variations, accumulated during an almost infinite number of generations.

Although I am fully convinced of the truth of the views given in this volume under the form of an abstract, I by no means expect to convince experienced naturalists whose minds are stocked with a multitude of facts all viewed, during a long course of years, from a point of view directly opposite to mine. It is so easy to hide our ignorance under such expressions as the `plan of creation,' `unity of design,' &c., and to think that we give an explanation when we only restate a fact. Any one whose disposition leads him to attach more weight to unexplained difficulties than to the explanation of a certain number of facts will certainly reject my theory. A few naturalists, endowed with much flexibility of mind, and who have already begun to doubt on the immutability of species, may be influenced by this volume; but I look with confidence to the future, to young and rising naturalists, who will be able to view both sides of the question with impartiality. Whoever is led to believe that species are mutable will do good service by conscientiously expressing his conviction; for only thus can the load of prejudice by which this subject is overwhelmed be removed.

Several eminent naturalists have of late published their belief that a multitude of reputed species in each genus are not real species; but that other species are real, that is, have been independently created. This seems to me a strange conclusion to arrive at. They admit that a multitude of forms, which till lately they themselves thought were special creations, and which are still thus looked at by the majority of naturalists, and which consequently have every external characteristic feature of true species, – they admit that these have been produced by variation, but they refuse to extend the same view to other and very slightly different forms. Nevertheless they do not pretend that they can define, or even conjecture, which are the created forms of life, and which are those produced by secondary laws. They admit variation as a vera causa in one case, they arbitrarily reject it in another, without assigning any distinction in the two cases. The day will come when this will be given as a curious illustration of the blindness of preconceived opinion. These authors seem no more startled at a miraculous act of creation than at an ordinary birth. But do they really believe that at innumerable periods in the earth's history certain elemental atoms have been commanded suddenly to flash into living tissues? Do they believe that at each supposed act of creation one individual or many were produced? Were all the infinitely numerous kinds of animals and plants created as eggs or seed, or as full grown? and in the case of mammals, were they created

[36] For a classic and wonderfully insightful extension of these ideas see F. Jacob (1977) Evolution and tinkering. Science 196: 1161-1166.

bearing the false marks of nourishment from the mother's womb? Although naturalists very properly demand a full explanation of every difficulty from those who believe in the mutability of species, on their own side they ignore the whole subject of the first appearance of species in what they consider reverent silence.

It may be asked how far I extend the doctrine of the modification of species. The question is difficult to answer, because the more distinct the forms are which we may consider, by so much the arguments fall away in force. But some arguments of the greatest weight extend very far. All the members of whole classes can be connected together by chains of affinities, and all can be classified on the same principle, in groups subordinate to groups. Fossil remains sometimes tend to fill up very wide intervals between existing orders. Organs in a rudimentary condition plainly show that an early progenitor had the organ in a fully developed state; this in some instances necessarily implies an enormous amount of modification in the descendants. Throughout whole classes various structures are formed on the same pattern, and at an embryonic age the species closely resemble each other. Therefore I cannot doubt that the theory of descent with modification embraces all the members of the same class. I believe that animals have descended from at most only four or five progenitors, and plants from an equal or lesser number.

Analogy would lead me one step further, namely, to the belief that all animals and plants have descended from some one prototype. But analogy may be a deceitful guide. Nevertheless all living things have much in common, in their chemical composition, their germinal vesicles, their cellular structure, and their laws of growth and reproduction. [...] Therefore I should infer from analogy that probably all the organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed.

When the views entertained in this volume on the origin of species [...] are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. [...] Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected. [...] In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.

[...] When we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond his comprehension; when we regard every production of nature as one which has had a history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, [...] how far more interesting, I speak from experience, will the study of natural history become! [...] In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history.[37]

Authors of the highest eminence seem to be fully satisfied with the view that each species has been independently created. To my mind it accords better with what we know of the laws impressed on matter by the Creator, that the production and extinction of the past and present inhabitants of the world should have been due to secondary causes, like those determining the birth and death of the individual. When I view all beings not as special creations, but as the lineal descendants of some few beings which lived long before the first bed of the Silurian system was deposited, they seem to me to become ennobled. [...] As all the living forms of life are the lineal descendants of those which lived long before [...], we may feel certain that the ordinary succession by generation

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[37] The recent emergence of evolutionary psychology marks the fulfillment of this possibility. For a concise introductory overview of evolutionary psychology see http://en.wikipedia.org/wiki/Evolutionary_psychology.

has never once been broken, and that no cataclysm has desolated the whole world. Hence we may look with some confidence to a secure future of equally inappreciable length. And as natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection.

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. [...] There is grandeur in this view of life, with its several powers, having been originally breathed[38] 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.[39]

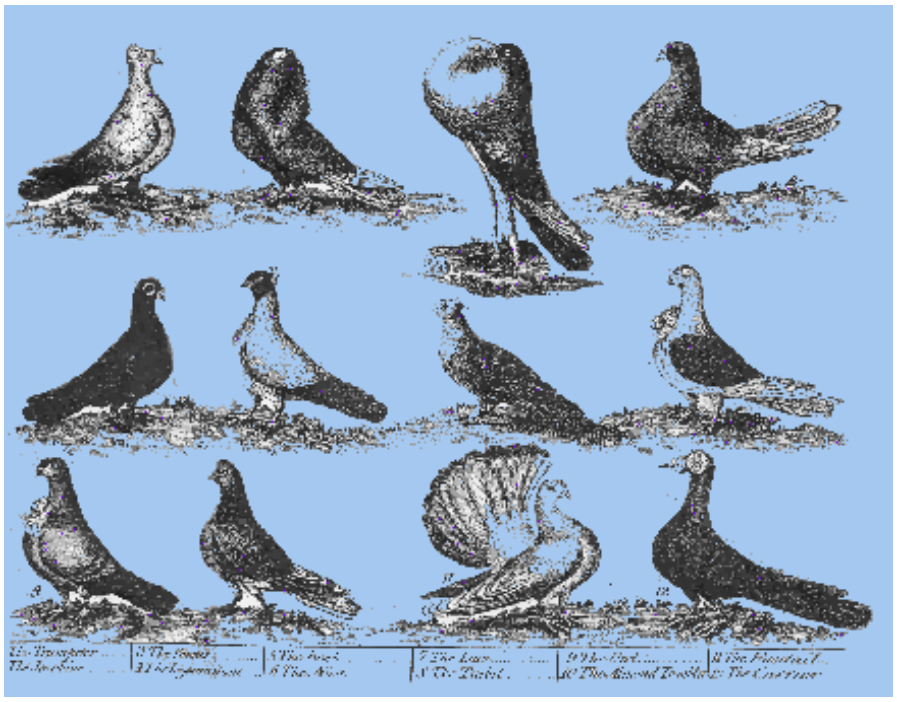
[38] Darwin added the phrase 'by the creator' here in the second and all subsequent edition. He did this to "conciliate angry clerics" but as a letter of 29 March 1863 to Hooker reveals he regretted his decision: "I have long since regretted that I truckled to public opinion and used the Pentateuchal term of creation, by which I really meant 'appeared' by some wholly unknown process." In the same letter Darwin wrote, "It is mere rubbish, thinking at present of the origin of life; one might as well think of the origin of matter.".

[39] See P.R. Sloan [(2001) The sense of sublimity: Darwin on nature and divinity. Osiris 16: 251-269] for insightful analysis of Darwin's 'nature reveries' and his philosophical and theological affinity with Alexander von Humboldt.

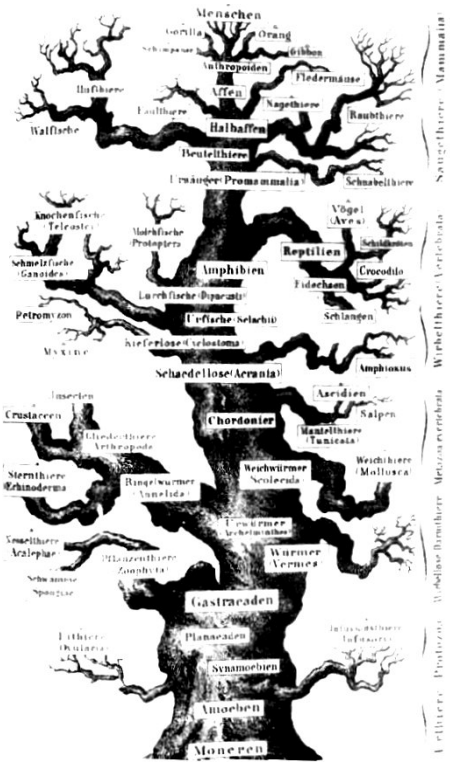
GLOSSARY

I am indebted to the kindness of Mr. W. S. Dallas for this Glossary, which has been given because several readers have complained to me that some of the terms used were unintelligible to them. Mr. Dallas has endeavoured to give the explanations of the terms in as popular a form as possible.

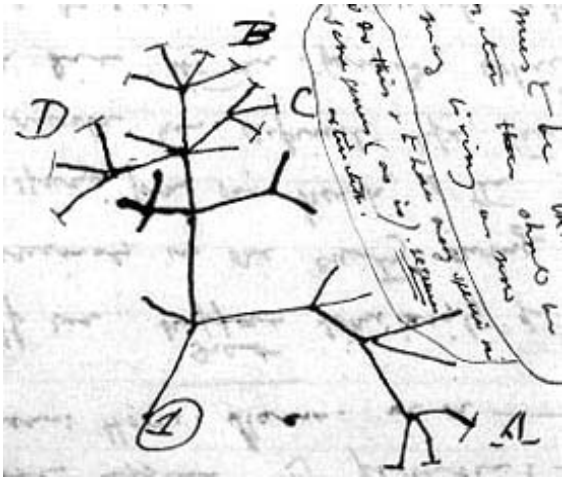
*[**GAME NOTE:** The first edition did not include a glossary but talk.origins has reproduced the glossary from the sixth edition which is available on-line at http://www.talkorigins.org/faqs/origin/glossary.html. Players may wish to use the space below to develop their own glossary of unfamiliar terms.]*



From Daniel Girton. (n.d.) The Complete Pigeon Fancier. London: Alexander Hogg



Ernst Haeckel's 1874 "Lebensbaum"
("Tree of Life") image



Darwin 1837 – B Notebook