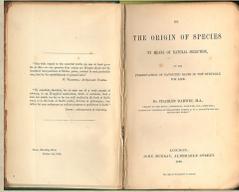


## Darwin's *On the Origin of Species*



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## In search of a mechanism

- What is Darwin lacking?
  - A mechanism—no understanding of how these patterns arose
- September 1838: for amusement Darwin read the *Essay on Population* (1798) by Rev. Thomas Robert Malthus (1766-1834)



» Malthus, along with Adam Smith and others interested in political economy, sought to discover the *laws of society*

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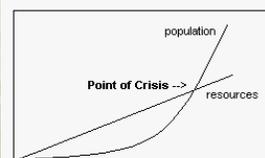
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## Malthus' laws of population

- Law 1: Food Supply grows *arithmetically*: 2, 4, 6, 8, 10, 12 . . .
- Law 2: Population tends to grow *geometrically*: 2, 4, 8, 16, 32, 64, 128 . . .
- 1<sup>st</sup> consequence: Populations always tend to outrun food supplies
- 2<sup>nd</sup> consequence: More offspring born than can survive
- 3<sup>rd</sup> consequent: There will always be competition for food (and other) resources



Malthus' Basic Theory

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## From competition to selection

- Overproduction means only some will survive
- That doesn't yet imply selection as survival might only depend on luck, chance, etc.
  - Must add that survival depends upon the organism's *abilities to deal with the demands of competition*
  - Also, that there is *variability* among the competitors
  - And that this variability is *heritable*—offspring will possess those very traits that improved the parents' ability to deal with environment demands
- Evolution by natural selection requires heritable variation in fitness

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## Developing the idea—Darwin's notes on natural selection

- 15-page "Essay" of 1842
- 100+ page "Essay" of 1844
- Circulated among some associates (Lyell, Joseph Dalton, Hooker)
  - They urged him to publish, but Darwin was cautious
- Chambers' *Vestiges* was published in 1844
- Darwin then detoured to work on systematics of barnacles (*Cirripedia*)—a detailed two volume work that established Darwin's reputation in biology



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## Goaded into publication

- Darwin received a letter in 1857 from Alfred Russel Wallace, a young naturalist living in Malaysia
- Wallace had also read Malthus and written a paper on "natural selection"
- Lyell and Hooker arranged for papers of both Darwin and Wallace to be read before the Linnaean Society in July 1858 and published in Society's *Proceedings* in August
- There was no significant response to these papers
- Darwin began feverishly writing his "Abstract," which he sent to his publisher, John Murray in June, 1859
- Published on November 1, 1859 and the first run of 1250 copies sold out that day



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## Structure of the *Origin*—an abstract!

1. Variation Under Domestication
2. Variation Under Nature
3. Struggle for Existence
4. Natural Selection
5. Laws of Variation
6. Difficulties on Theory
7. Instinct
8. Hybridism
9. On the Imperfection of the Geological Record
10. On The Geological Succession of Organic Beings
11. Geographical Distribution
12. Geographical Distribution continued
13. Mutual Affinities of Organic Beings: Morphology: Embryology: Rudimentary Organs
14. Recapitulation and Conclusion

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## Variation under domestication

- Why start with variability under domestication (artificial selection)?
- Where did these varieties come from?
  - Why does hybridization alone not account for the varieties that exist?
  - Source of domesticated species:
    - “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”
  - Often the differences are so minor as to be undetected except by the skilled breeder
  - “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” in producing change in domestic species



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## Inherited variability

- Why interest only in *inherited* variability?
- “The laws governing inheritance are quite unknown; 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.”

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## Reversion

- “Having alluded to the subject of reversion, I may here refer to a statement often made by naturalists namely, that our domestic varieties, when run wild, gradually but certainly revert in character to their aboriginal stocks. Hence it has been argued that no deductions can be drawn from domestic races to species in a state of nature. I have in vain endeavoured to discover on what decisive facts the above statement has so often and so boldly been made.”
- Why is Darwin concerned about this?

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## Variation under nature

- “I [will not] here discuss the various definitions which have been given of the term species. No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species.
- Variability in both unimportant and important characteristics, including internal ones:
  - “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”



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## Varieties and incipient species

Difference between species and varieties not sharp:

- What one researcher identifies as a species, another identifies as a variety:
  - “From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience sake.”

- Why is this significant for Darwin?

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## Struggle for existence



- The challenge of adaptation: “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?”
- “Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow inevitably from the struggle for life.”

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## Generality of struggle

- “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.”
- Malthus’ principle: “A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. 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.”

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## Natural Selection

- 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.

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### Contrasts with artificial selection

- “Man can act only on external and visible characters: nature cares nothing for appearances, except in so far as they may be useful to any being. She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life.”
- “Man selects only for his own good; Nature only for that of the being which she tends.”

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### The power of natural selection

- “Why, if man can by patience select variations most useful to himself, should nature fail in selecting variations useful, under changing conditions of life, to her living products? What limit can be put to this power, acting during long ages and rigidly scrutinising the whole constitution, structure, and habits of each creature, — favouring the good and rejecting the bad? I can see no limit to this power, in slowly and beautifully adapting each form to the most complex relations of life. The theory of natural selection, even if we looked no further than this, seems to me to be in itself probable.”

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### Creating separate species

- “As each species tends by its geometrical ratio of reproduction to increase inordinately in number; and as the modified descendants of each species will be enabled to increase by so much the more as they become more diversified in habits and structure, so as to be enabled to seize on many and widely different places in the economy of nature, *there will be a constant tendency in natural selection to preserve the most divergent offspring of any one species.* Hence during a long-continued course of modification, the slight differences, characteristic of varieties of the same species, tend to be augmented into the greater differences characteristic of species of the same genus. New and improved varieties will inevitably supplant and exterminate the older, less improved and intermediate varieties; and thus species are rendered to a large extent defined and distinct objects.”

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## Sexual selection



- “when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by 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. A hornless stag or spurless cock would have a poor chance of leaving offspring.”

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## The virtues of sex

- “I have collected so large a body of facts, showing, in accordance with the almost universal belief of breeders, that with animals and plants a cross between different varieties, or between individuals of the same variety but of another strain, gives vigour and fertility to the offspring; and on the other hand, that *close* interbreeding diminishes vigour and fertility; that these facts alone incline me to believe that it is a general law of nature (utterly ignorant though we be of the meaning of the law) that no organic being self-fertilises itself for an eternity of generations; but that a cross with another individual is occasionally perhaps at very long intervals -- indispensable.”

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## Repudiating Essentialism: Species

- “From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.” [*Origin*, p. 52]
- “. . . I believe species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links . . .” [*Origin*, p. 177]
- “Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known . . . to be connected at the present day by intermediate gradations, whereas species were formerly thus connected. . . [W]e shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.” [*Origin*, p. 485]

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## A new basis for taxonomy

- “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.”

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## One origin for all species

“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. We see this even in so trifling a circumstance as that the same poison often similarly affects plants and animals; or that the poison secreted by the gall-fly produces monstrous growths on the wild rose or oak-tree. 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.”

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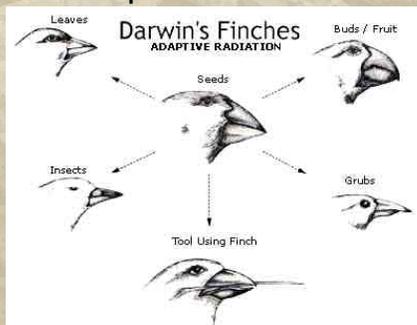
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## Adaptive radiation



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## Difficulties

- why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms?
- (how) 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 instincts be acquired and modified through natural selection?
- how can we account for species, when crossed, being sterile and producing sterile offspring, whereas, when varieties are crossed, their fertility is unimpaired?

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## Lack of transitional forms

- Extinction
- But environments are continuous
  - Plays with geological isolation during species formation
  - Dependencies on other species create gaps
  - Intermediates in small numbers are likely to go extinct
- Why no fossils from them?
  - Imperfection of the fossil record

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## On the imperfection of the geological record

- “Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps, is the most obvious and gravest objection which can be urged against my theory. The explanation lies, as I believe, in the extreme imperfection of the geological record.”

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## Creation of new forms

- “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.”

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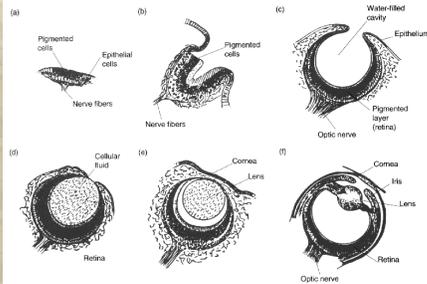
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## Evolution of the eye

**Figure 13.2** Stages in the evolution of the eye, illustrated by species of molluscs. (a) A simple spot of pigmented cells. (b) Folded region of pigmented cells, which increases the number of sensitive cells per unit area. (c) The hole camera eye, as is found in Nautilus. (d) Eye cavity filled with cellular fluid rather than water. (e) The eye is protected by adding a transparent cover of skin, and part of the cellular fluid has differentiated into a lens. (f) Full, complex eye, as found in octopus and squid. Reprinted, by permission of the publisher, from Strickberger (1990).




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## Eye and telescope

- “It is scarcely possible to avoid comparing the eye to a telescope. We know that this instrument has been perfected by the long-continued efforts of the highest human intellects; and we naturally infer that the eye has been formed by a somewhat analogous process. . . . If we must compare the eye to an optical instrument, we ought in imagination to take a thick layer of transparent tissue, with a nerve sensitive to light beneath, and then suppose every part of this layer to be continually changing slowly in density, so as to separate into layers of different densities and thicknesses, placed at different distances from each other, and with the surfaces of each layer slowly changing in form. Further we must suppose that there is a power always intently watching each slight accidental alteration in the transparent layers; and carefully selecting each alteration which, under varied circumstances, may in any way, or in any degree, tend to produce a distincter image. We must suppose each new state of the instrument to be multiplied by the million; and each to be preserved till a better be produced, and then the old ones to be destroyed.”

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## Electric organs

- “Generally when the same organ appears in several members of the same class, especially if in members having very different habits of life, we may attribute its presence to inheritance from a common ancestor; and its absence in some of the members to its loss through disuse or natural selection. But if the electric organs had been inherited from one ancient progenitor thus provided, we might have expected that all electric fishes would have been specially related to each other.”
- “In all these cases of two very distinct species furnished with apparently the same anomalous organ, it should be observed that, although the general appearance and function of the organ may be the same, yet some fundamental difference can generally be detected.”



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## Not all functional traits are adaptations

- “A trailing bamboo in the Malay Archipelago climbs the loftiest trees by the aid of exquisitely constructed hooks clustered around the ends of the branches, and this contrivance, no doubt, is of the highest service to the plant; but as we see nearly similar hooks on many trees which are not climbers the hooks on the bamboo may have arisen from unknown laws of growth, and have been subsequently taken advantage of by the plant undergoing further modification and becoming a climber.”
- Adaptive traits may be due to factors other than natural selection

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## Natural selection not optimizing

- “Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence. And we see that this is the degree of perfection attained under nature. The endemic productions of New Zealand, for instance, are perfect one compared with another; but they are now rapidly yielding before the advancing legions of plants and animals introduced from Europe. Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature. . . . Can we consider the sting of the wasp or of the bee as perfect, which, when used against many attacking animals, cannot be withdrawn, owing to the backward serratures, and so inevitably causes the death of the insect by tearing out its viscera?”

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## Not optimizing



Natural selection does not grant organisms what they "need".

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## Not optimizing - 2

- "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 supplanted by the naturalised productions from another land. 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."

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## Grandeur of evolution

- "Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely the production of the higher animals, directly follows. There is a grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved." (last paragraph of *Origin*)

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