Charles Darwin and Alfred Russel Wallace

On the Tendency of Species to Form Varieties, and on the Perpetuation of Varieties and Species by Natural Means of Selection

1858

Reissued with a Preface and Commentary
By Michael T. Ghiselin
California Academy of Sciences

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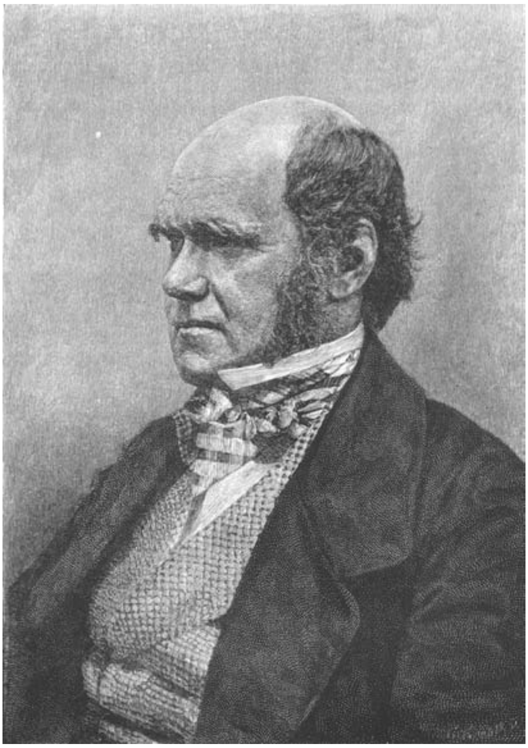
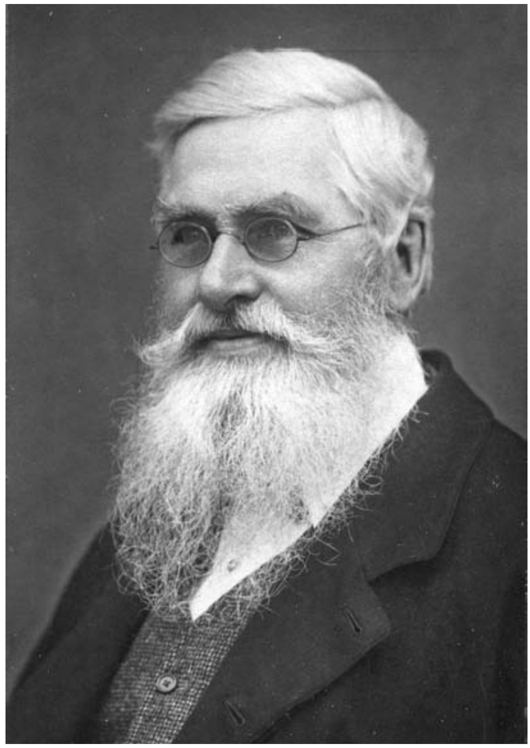
Preface

The Darwinian revolution is widely considered the most important event in the entire history of the human intellect. But when did it begin? The revolution that gave the thirteen American colonies their independence from Great Britain might be said to have started when organized armed conflict broke out at the battles of Lexington and Concord in 1775. The decisive break, however, occurred with the *Declaration of Independence* on July 4, 1776. By analogy, we might say that Darwinian revolution began on July 1, 1858, with the reading of a joint communication by Charles Darwin and Alfred Russel Wallace before the Linnean Society of London. That was, so to speak, the opening shot. Of course it was the publication, on November 24, 1859, of Darwin's book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* that really got the struggle going. It took about ten years for Darwin and his followers to convince most of the scientific community that evolution is a fact, and another hundred or so for natural selection to be generally recognized as the main, though not exclusive, cause of it. Of course, it was not just a revolution in science for it affected so many aspects of human life and culture. And it is no exaggeration to say that the Darwinian revolution is still going on.

The joint publication established Darwin and Wallace as co-discoverers of the principle of natural selection. The circumstances surrounding this event were most unusual, and the fact that Darwin and Wallace were both happy with the arrangement says a great deal about the character of the two scientists. Darwin's two parts are quite different from that of Wallace. The first was an excerpt of a draft of a book that he had written in 1844. It was intended to show that he had discovered natural selection many years previously. The second was taken from a letter to Asa Gray of Harvard University dated September 5, 1857. It was intended to show, among other things, that although Darwin had not yet published on natural selection, he had discussed it privately with his colleagues, and that he was in fact writing a book about it.



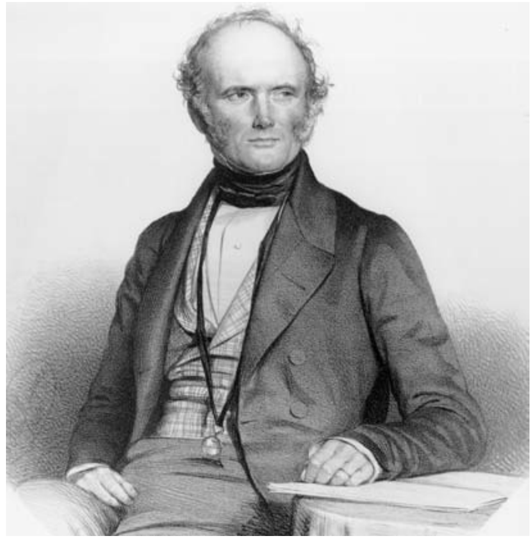
Charles Darwin, ca.1854



Alfred Russel Wallace

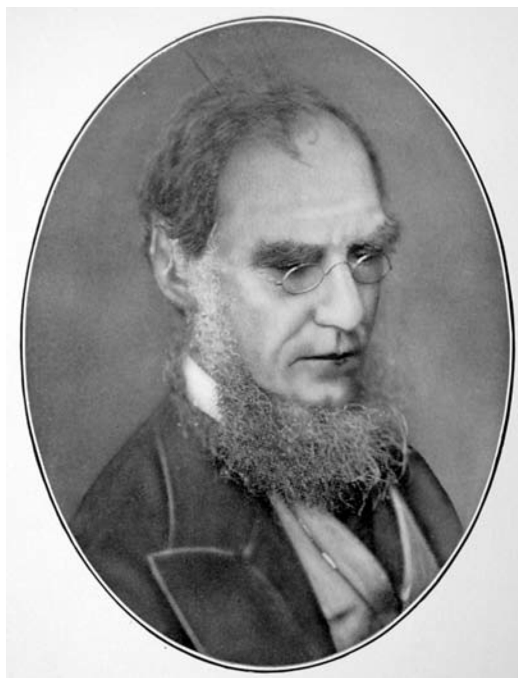
Asa Gray

Wallace's contribution reads like a preliminary note on an idea that had recently occurred to him. Evidently he was not sure whether it was ready for publication, and his reason for sending it to Darwin was to ask his older, and much esteemed, colleague what he thought of it. Nonetheless it provides a very clear exposition of the principle of natural selection. Wallace also explains how his ideas are superior to those of Lamarck, and how natural selection might explain adaptation and the diversification of life through time.



Charles Lyell

The manuscript was read to the Linnaean Society on July 1, 1858, and the printed version was distributed in August of the same year. In retrospect, we can easily appreciate the importance of the ideas that it contains. The original audience and readers were in a quite different situation than we are. Many would have found it difficult to understand, and the larger implications were not obvious. Both Darwin and Wallace explain the struggle for existence that results as a consequence of competition for limited resources. And both use the analogy of the artificial selection, in which breeders of domesticated animals and plants select the kind of organism they prefer as breeding stock, with natural selection, in which the conditions of existence have the same basic effect. Readers of the paper at the time it was published would not have objected to the proposition that selection, whether artificial or natural, might produce a limited amount of change, giving rise to breeds and perhaps varieties within species. Whether selection is sufficient to account for the origin of new species, let alone the descent of all organisms from a single common ancestor,



Joseph Dalton Hooker

would obviously have met with much more resistance. So, until the *Origin of Species* was published, natural selection evoked little more than curiosity upon the part of the scientific community. People knew that Darwin was writing a book. They awaited its publication with interest. But they did not anticipate what Wallace called "a new science," much less its philosophical implications.

TEXT

On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection. By Charles Darwin, Esq., F.R.S., F.L.S., & F.G.S., and Alfred Wallace, Esq. Communicated by Sir Charles Lyell, F.R.S., F.L.S., and J. D. Hooker, Esq., M.D., V.P.R.S., F.L.S., &c.

[Read July 1st, 1858.]

London, June 30th, 1858.

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

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

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

1. Extracts from a M.S. work on Species*, by Mr. Darwin, which was sketched in 1839, and copied in 1844, when the copy was read by Dr. Hooker, and its contents afterwards communicated to Sir Charles Lyell.{1} The first Part is devoted to "The Variation of Organic Beings under Domestication and in their Natural State;" and the second chapter of that Part, from which we propose to read to the Society the extracts referred to, is headed, "On the Variation of Organic Beings in a state of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and true Species."

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

{1} These dates are inaccurate and misleading. Darwin wrote a rough outline, traditionally called the "Sketch" in 1842 and expanded it into a book called the "Essay" in 1844. (M.T.G.)

2. An abstract of a private letter addressed to Professor Asa Gray, of Boston, U.S., in October 1857, by Mr. Darwin, in which /45-46/ he repeats his views, and which shows that these remained unaltered from 1839 to 1857.{2}

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

We have the honour to be yours very obediently,

Charles Lyell.
Jos. D. Hooker.

J. J. Bennett, Esq.,
Secretary of the Linnean Society.

I. *Extract from an unpublished Work on Species, by* C. DARWIN, Esq., *consisting of a portion of a Chapter entitled, "On the Variation of Organic Beings in a state of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and true Species."*

De Candolle, in an eloquent passage, has declared that all nature is at war, one organism with another, or with external nature. /46-47/ Seeing the contented

{2} Again this claim is misleading. Although many of Darwin's ideas go back as far as 1838, the principle of divergence of character was discovered around 1852. (M.T.G.)

face of nature, this may at first well be doubted; but reflection will inevitably prove it to be true. The war, however, is not constant, but recurrent in a slight degree at short periods, and more severely at occasional more distant periods; and hence its effects are easily overlooked. It is the doctrine of Malthus applied in most cases with tenfold force. As in every climate there are seasons, for each of its inhabitants, of greater and less abundance, so all annually breed; and the moral restraint which in some small degree checks the increase of mankind is entirely lost. Even slow-breeding mankind has doubled in twenty-five years; and if he could increase his food with greater ease, he would double in less time. But for animals without artificial means, the amount of food for each species must, *on an average*, be constant, whereas the increase of all organisms tends to be geometrical, and in a vast majority of cases at an enormous ratio. Suppose in a certain spot there are eight pairs of birds, and that *only* four pairs of them annually (including double hatches) rear only four young, and that these go on rearing their young at the same rate, then at the end of seven years (a short life, excluding violent deaths, for any bird) there will be 2048 birds, instead of the original sixteen. As this increase is quite impossible, we must conclude either that birds do not rear nearly half their young, or that the average life of a bird is, from accident, not nearly seven years. Both checks probably concur. The same kind of calculation applied to all plants and animals affords results more or less striking, but in very few instances more striking than in man.

Augustine Pyrame de Candolle

Thomas Robert Malthus

Many practical illustrations of this rapid tendency to increase are on record, among which, during peculiar seasons, are the extraordinary numbers of certain animals; for instance, during the years 1826 to 1828, in La Plata, when from drought some millions of cattle perished, the whole country actually *swarmed* with mice. Now I think it cannot be doubted that during the breeding-season all the mice (with the exception of a few males or females in excess) ordinarily pair, and therefore that this astounding increase during three years must be attributed to a greater number than usual surviving the first year, and then breeding, and so on till the third year, when their numbers were brought down to their usual limits on the return of wet weather. Where man has introduced plants and animals into a new and favourable country, there are many accounts in how surprisingly few years the whole country has become stocked with them. This increase would /47-48/ necessarily stop as soon as the country was fully stocked; and yet we have every reason to believe, from what is known of wild animals, that *all* would pair in the spring. In the majority of cases it is most difficult to imagine where the checks fall—though generally, no doubt, on the seeds, eggs, and young; but when we remember how impossible, even in mankind (so much better known than any other animal), it is to infer from repeated casual observations what the average duration of life is, or to discover the different percentage of deaths to births in different countries, we ought to feel no surprise at our being unable to discover where the check falls in any animal or plant. It should always be remembered, that in most cases the checks are recurrent yearly in a small, regular degree, and in an extreme degree during unusually cold, hot, dry, or wet years, according to the constitution of the being in question. Lighten any check in the least degree, and the geometrical powers of increase in every organism will almost instantly increase the average number of the favoured species. Nature may be compared to a surface on which rest ten thousand sharp wedges touching each other and driven inwards by incessant blows. Fully to realize these views much reflection is requisite. Malthus on man should be studied; and all such cases as those of the mice in La Plata, of the cattle and horses when first turned out in South America, of the birds by our calculations &c., should be well considered. Reflect on the enormous multiplying power *inherent and annually in action* in all animals; reflect on the countless seeds scattered by a hundred ingenious contrivances, year after year, over the whole face of the land; and yet we have every reason to suppose that the average percentage of each of the inhabitants of a country usually remains constant. Finally, let it be borne in mind that this average number of individuals (the external conditions remaining the same) in each country is kept up by recurrent struggles against other species or against external nature (as on the borders of the Arctic regions, where the cold checks life), and that ordinarily each individual of every species holds its place, either by its own struggle and capacity of acquiring nourishment in some period of its life, from the egg upwards; or by the struggle of its parents (in short-lived organisms, when the main check occurs at longer intervals) with other individuals of the *same* or *different* species.

But let the external conditions of a country alter. If in a small degree, the relative proportions of the inhabitants will in most cases simply be slightly changed; but let the number of /48-49/ inhabitants be small, as on an island, and free access to it from other countries be circumscribed, and let the change of conditions continue progressing (forming new stations), in such a case the original inhabitants must cease to be as perfectly adapted to the changed conditions as they were originally. It has been shown in a former part of this work, that such changes of external conditions would, from their acting on the reproductive system, probably cause the organization of those beings which were most affected to become, as under domestication, plastic. Now, can it be doubted, from the struggle each individual has to obtain subsistence, that any minute variation in structure, habits, or instincts, adapting that individual better to the new conditions, would tell upon its vigour and health? In the struggle it would have a better *chance* of surviving; and those of its offspring which inherited the variation, be it ever so slight, would also have a better *chance*. Yearly more are bred than can survive; the smallest grain in the balance, in the long run, must tell on which death shall fall, and which shall survive. Let this work of selection on the one hand, and death on the other, go on for a thousand generations, who will pretend to affirm that it would produce no effect, when we remember what, in a few years, Bakewell effected in cattle, and Western in sheep, by this identical principle of selection?

To give an imaginary example from changes in progress on an island:— let the organization of a canine animal which preyed chiefly on rabbits, but sometimes on hares, become slightly plastic; let these same changes cause the number of rabbits very slowly to decrease, and the number of hares to increase; the effect of this would be that the fox or dog would be driven to try to catch more hares: his organization, however, being slightly plastic, those individuals with the lightest forms, longest limbs, and best eyesight, let the difference be ever so small, would be slightly favoured, and would tend to live longer, and to survive during that time of the year when food was scarcest; they would also rear more young, which would tend to inherit these slight peculiarities. The less fleet ones would be rigidly destroyed. I can see no more reason to doubt that these causes in a thousand generations would produce a marked effect, and adapt the form of the fox or dog to the catching of hares instead of rabbits, than that greyhounds can be improved by selection and careful breeding. So would it be with plants under similar circumstances. If the number of individuals of a species with plumed seeds could be increased by greater powers of dissemination within its own area /49-50/ (that is, if the check to increase fell chiefly on the seeds), those seeds which were provided with ever so little more down, would in the long run be most disseminated; hence a greater number of seeds thus formed would germinate, and would tend to produce plants inheriting the slightly better-adapted down*.

Besides this natural means of selection, by which those individuals are preserved, whether in their egg, or larval, or mature state, which are best adapted to the place they fill in nature, there is a second agency at work in most unisexual

* I can see no more difficulty in this, than in the planter improving his varieties of the cotton plant.—C.D. 1858.

animals, tending to produce the same effect, namely, the struggle of the males for the females. These struggles are generally decided by the law of battle, but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship, as in the dancing rock-thrush of Guiana. The most vigorous and healthy males, implying perfect adaptation, must generally gain the victory in their contests. This kind of selection, however, is less rigorous than the other; it does not require the death of the less successful, but gives them fewer descendants. The struggle falls, moreover, at a time of year when food is generally abundant, and perhaps the effect chiefly produced would be the modification of the secondary sexual characters, which are not related to the power of obtaining food, or to defence from enemies, but to fighting with or rivalling other males. The result of this struggle amongst the males may be compared in some respects to that produced by those agriculturalists who pay less attention to the careful selection of all their young animals, and more to the occasional use of a choice mate.

II. *Abstract of a Letter from* C. DARWIN, Esq., to Prof. ASA GRAY, *Boston, U.S., dated Down, September* 5*th*, 1857.

1. It is wonderful what the principle of selection by man, that is the picking out of individuals with any desired quality, and breeding from them, and again picking out, can do. Even breeders have been astounded at their own results. They can act on differences inappreciable to an uneducated eye. Selection has been *methodically* followed in *Europe* for only the last half century; but it was occasionally, and even in some degree methodically, followed in the most ancient times. There must have been also a kind of unconscious selection from a remote period, namely in /50-51/ the preservation of the individual animals (without any thought of their offspring) most useful to each race of man in his particular circumstances. The "roguing," as nurserymen call the destroying of varieties which depart from their type, is a kind of selection. I am convinced that intentional and occasional selection has been the main agent in the production of our domestic races; but however this may be, its great power of modification has been indisputably shown in later times. Selection acts only by the accumulation of slight or greater variations, caused by external conditions, or by the mere fact that in generation the child is not absolutely similar to its parent. Man, by this power of accumulating variations, adapts living beings to his wants — may be said to make the wool of one sheep good for carpets, of another for cloth, &c.

2. Now suppose there were a being who did not judge by mere external appearances, but who could study the whole internal organization, who was never capricious, and should go on selecting for one object during millions of generations;

who will say what he might not effect? In nature we have some *slight* variation occasionally in all parts; and I think it can be shown that changed conditions of existence is the main cause of the child not exactly resembling its parents; and in nature geology shows us what changes have taken place, and are taking place. We have almost unlimited time; no one but a practical geologist can fully appreciate this. Think of the Glacial period, during the whole of which the same species at least of shells have existed; there must have been during this period millions on millions of generations.

3. I think it can be shown that there is such an unerring power at work in *Natural Selection* (the title of my book), which selects exclusively for the good of each organic being. The elder De Candolle, W. Herbert, and Lyell have written excellently on the struggle for life; but even they have not written strongly enough. Reflect that every being (even the elephant) breeds at such a rate, that in a few years, or at most a few centuries, the surface of the earth would not hold the progeny of one pair. I have found it hard constantly to bear in mind that the increase of every single species is checked during some part of its life, or during some shortly recurrent generation. Only a few of those annually born can live to propagate their kind. What a trifling difference must often determine which shall survive, and which perish!

4. Now take the case of a country undergoing some change. This will tend to cause some of its inhabitants to vary slightly — /51-52/ not but that I believe most beings vary at all times enough for selection to act on them. Some of its inhabitants will be exterminated; and the remainder will be exposed to the mutual action of a different set of inhabitants, which I believe to be far more important to the life of each being than mere climate. Considering the infinitely various methods which living beings follow to obtain food by struggling with other organisms, to escape danger at various times of life, to have their eggs or seeds disseminated, &c. &c., I cannot doubt that during millions of generations individuals of a species will be occasionally born with some slight variation, profitable to some part of their economy. Such individuals will have a better chance of surviving, and of propagating their new and slightly different structure; and the modification may be slowly increased by the accumulative action of natural selection to any profitable extent. The variety thus formed will either coexist with, or, more commonly, will exterminate its parent form. An organic being, like the woodpecker or misseltoe, may thus come to be adapted to a score of contingences [*sic*] — natural selection accumulating those slight variations in all parts of its structure, which are in any way useful to it during any part of its life.

5. Multiform difficulties will occur to every one, with respect to this theory. Many can, I think, be satisfactorily answered. *Natura non facit saltum* answers

some of the most obvious. The slowness of the change, and only a very few individuals undergoing change at any one time, answers others. The extreme imperfection of our geological records answers others.

6. Another principle, which may be called the principle of divergence, plays, I believe, an important part in the origin of species. The same spot will support more life if occupied by very diverse forms. We see this in the many generic forms in a square yard of turf, and in the plants or insects on any little uniform islet, belonging almost invariably to as many genera and families as species. We can understand the meaning of this fact amongst the higher animals, whose habits we understand. We know that it has been experimentally shown that a plot of land will yield a greater weight if sown with several species and genera of grasses, than if sown with only two or three species. Now, every organic being, by propagating so rapidly, may be said to be striving its utmost to increase in numbers. So it will be with the offspring of any species after it has become diversified into varieties, or subspecies, or true species. And it follows, I think, from the foregoing facts, that the varying offspring of each species will try /52-53/ (only few will succeed) to seize on as many and as diverse places in the economy of nature as possible. Each new variety or species, when formed, will generally take the place of, and thus exterminate its less well-fitted parent. This I believe to be the origin of the classification and affinities of organic beings at all times; for organic beings always *seem* to branch and sub-branch like the limbs of a tree from a common trunk, the flourishing and diverging twigs destroying the less vigorous — the dead and lost branches rudely representing extinct genera and families.

This sketch is *most* imperfect; but in so short a space I cannot make it better. Your imagination must fill up very wide blanks.

C. DARWIN.

III. *On the Tendency of Varieties to depart indefinitely from the Original Type.* By ALFRED RUSSEL WALLACE.

One of the strongest arguments which have been adduced to prove the original and permanent distinctness of species is, that *varieties* produced in a state of domesticity are more or less unstable, and often have a tendency, if left to themselves, to return to the normal form of the parent species; and this instability is considered to be a distinctive peculiarity of all varieties, even of those occurring among wild animals in a state of nature, and to constitute a provision for preserving unchanged the originally created distinct species.

In the absence or scarcity of facts and observations as to *varieties* occurring among wild animals, this argument has had great weight with naturalists, and has led to a very general and somewhat prejudiced belief in the stability of species.

Equally general, however, is the belief in what are called "permanent or true varieties,"—races of animals which continually propagate their like, but which differ so slightly (although constantly) from some other race, that the one is considered to be a *variety* of the other. Which is the *variety* and which is the original *species*, there is generally no means of determining, except in those rare cases in which the one race has been known to produce an offspring unlike itself and resembling the other. This, however, would seem quite incompatible with the "permanent invariability of species," but the difficulty is overcome by assuming that such varieties have strict limits, and can never again vary further from the original type, although they may return to it, which, from the /53-54/ analogy of domesticated animals, is considered to be highly probable, if not certainly proved.

It will be observed that this argument rests entirely on the assumption, that *varieties* occurring in a state of nature are in all respects analogous to or even identical with those of domestic animals, and are governed by the same laws as regards their permanence or further variation. But it is the object of the present paper to show that this assumption is altogether false, that there is a general principle in nature which will cause many *varieties* to survive the parent species, and to give rise to successive variations departing further and further from the original type, and which also produces, in domesticated animals, the tendency of varieties to return to the parent form.

The life of wild animals is a struggle for existence. The full exertion of all their faculties and all their energies is required to preserve their own existence and provide for that of their infant offspring. The possibility of procuring food during the least favourable seasons, and of escaping the attacks of their most dangerous enemies, are the primary conditions which determine the existence both of individuals and of entire species. These conditions will also determine the population of a species; and by a careful consideration of all the circumstances we may be enabled to comprehend, and in some degree to explain, what at first sight seems inexplicable — the excessive abundance of some species, while others closely allied to them are very rare.

The general proportion that must obtain between certain groups of animals is readily seen. Large animals cannot be so abundant as small ones; the carnivora must be less numerous than the herbivora; eagles and lions can never be so plentiful as pigeons and antelopes; the wild asses of the Tartarian deserts cannot equal in numbers the horses of the more luxuriant prairies and pampas of America. The greater or less fecundity of an animal is often considered to be one of the chief causes of its abundance or scarcity; but a consideration of the facts will show us that it really has little or nothing to do with the matter. Even the least prolific of animals would increase rapidly if unchecked, whereas it is evident that the animal population of the globe must be stationary, or perhaps, through the influence of man, decreasing. Fluctuations there may be; but permanent increase, except in restricted localities, is almost impossible. For example, our own observation must convince us that birds do not go on increasing every year in a geometrical ratio, as they would do, where there not /54-55/ some powerful check to their natural increase. Very few birds produce less than two young ones each year, while many have six, eight, or ten; four will certainly be below the average; and if we suppose that each pair produce young only four times in their life, that will also be below the average, supposing them not to die either by violence or want of food. Yet at this rate how tremendous would be the increase in a few years from a single pair! A simple calculation will show that in fifteen years each pair of birds would have increased to nearly ten millions! whereas we have no reason to believe that the number of the birds of any country increases at all in fifteen or in one hundred and fifty years. With such powers of increase the population must have reached its limits, and have become stationary, in a very few years after the origin of each species. It is evident, therefore, that each year an immense number of birds must perish — as many in fact as are born; and as on the lowest calculation the progeny are each year twice as numerous as their parents, it follows that, whatever the average number of individuals existing in any given country, *twice that number must perish annually*,— a striking result, but one which seems at least highly probable, and is perhaps under rather than over the truth. It would therefore appear that, as far as the continuance of the species and the keeping up the average number of individuals are concerned, large broods are superfluous. On the average all above *one* become food for hawks and kites, wild cats and weasels, or perish of cold and hunger as winter comes on. This is strikingly proved by the case of particular species; for we find that their abundance in individuals bears no relation whatever to their fertility in producing offspring. Perhaps the most remarkable instance of an immense bird population is that of the passenger pigeon of the United States, which lays only one, or at most two eggs, and is said to rear generally but one young one. Why is this bird so extraordinarily abundant, while others producing two or three times as many young are much less plentiful? The explanation is not difficult. The food most congenial to this species, and on which it thrives best, is abundantly distributed over a very extensive region, offering such differences of soil and climate, that in one part or another of the area the supply never fails. The bird is capable of a very rapid and long-continued flight, so that it can pass without fatigue over the whole of the district it inhabits, and as soon as the supply of food begins to fail in one place is able to discover a fresh feeding-ground. This example strikingly shows us that the procuring a constant supply /55-56/ of wholesome food is almost the sole condition requisite for ensuring the rapid increase of a given species, since neither the limited fecundity, nor the unrestrained attacks of birds of prey and of man are here sufficient to check it. In no other birds are these peculiar circumstances so strikingly combined. Either their food is more liable to failure, or they have not sufficient power of wing to search for it over an extensive area, or during some season of the year it becomes very scarce, and less wholesome substitutes have to be found; and thus, though more fertile in offspring, they can never increase beyond the supply of food in the least favourable seasons. Many birds can only exist by migrating, when their food becomes scarce, to regions possessing a milder, or at least a different climate, though, as these migrating birds are seldom excessively abundant, it is evident that the countries they visit are still deficient in a constant and abundant supply of wholesome food. Those whose organization does not permit them to migrate when their food becomes periodically scarce, can never attain a large population. This is probably the reason why woodpeckers are scarce with us, while in the tropics they are among the most abundant of solitary birds. Thus the house sparrow is more abundant than the redbreast, because its food is more constant and plentiful,— seeds of grasses being preserved during the winter, and our farm-yards and stubble-fields furnishing an almost inexhaustible supply. Why, as a general rule, are aquatic, and especially sea birds, very numerous in individuals? Not because they are more prolific than the others, generally the contrary; but because their food never fails, the sea-shores and river-banks daily swarming with a fresh supply of small mollusca and crustacea. Exactly the same laws will apply to mammals. Wild cats are prolific and have few enemies; why then are they never as abundant as rabbits? The only intelligible answer is, that their supply of food is more precarious. It appears evident, therefore, that so long as a country remains physically unchanged, the numbers of its animal population cannot materially increase. If one species does so, some others requiring the same kind of food must diminish in proportion. The numbers that die annually must be immense; and as the individual existence of each animal depends upon itself, those that die must be the weakest — the very young, the aged, and the diseased, — while those that prolong their existence can only be the most perfect in health and vigour — those who are best able to obtain food regularly, and avoid their numerous enemies. It is, as we commenced by remarking, "a struggle for existence," in /56-57/ which the weakest and least perfectly organized must always succumb.

Now it is clear that what takes place among the individuals of a species must also occur among the several allied species of a group, — viz. that those which are best adapted to obtain a regular supply of food, and to defend themselves against the attacks of their enemies and the vicissitudes of the seasons, must necessarily obtain and preserve a superiority in population; while those species which from some defect of power or organization are the least capable of counteracting the vicissitudes of food, [*sic*] supply, &c., must diminish in numbers, and, in extreme cases, become altogether extinct. Between these extremes the species will present various degrees of capacity for ensuring the means of preserving life; and it is thus we account for the abundance or rarity of species. Our ignorance will generally prevent us from accurately tracing the effects to their causes; but could we become perfectly acquainted with the organization and habits of the various species of animals, and could we measure the capacity of each for performing the different acts necessary to its safety and existence under all the varying circumstances by which it is surrounded, we might be able even to calculate the proportionate abundance of individuals which is the necessary result.

If now we have succeeded in establishing these two points — 1st, *that the animal population of a country is generally stationary, being kept down by a periodical deficiency of food, and other checks*; and, 2nd, *that the comparative abundance or scarcity of the individuals of the several species is entirely due to their organization and resulting habits, which, rendering it more difficult to procure a regular supply of food and to provide for their personal safety in some cases than in others, can only be balanced by a difference in the population which have to exist in a given area* — we shall be in a condition to proceed to the consideration of *varieties*, to which the preceding remarks have a direct and very important application.

Most or perhaps all the variations from the typical form of a species must have some definite effect, however slight, on the habits or capacities of the individuals. Even a change of colour might, by rendering them more or less distinguishable, affect their safety; a greater or less development of hair might modify their habits. More important changes, such as an increase in the power or dimensions of the limbs or any of the external organs, would more or less affect their mode of procuring food or the range /57-58/ of country which they inhabit. It is also evident that most changes would affect, either favourably or adversely, the powers of prolonging existence. An antelope with shorter or weaker legs must necessarily suffer more from the attacks of the feline carnivora; the passenger pigeon with less powerful wings would sooner or later be affected in its powers of procuring a regular supply of food; and in both cases the result must necessarily be a diminution of the population of the modified species. If, on the other hand, any species should produce a variety having slightly increased powers of preserving existence, that variety must inevitably in time acquire a superiority in numbers. These results must follow as surely as old age, intemperance, or scarcity of food produce an increased mortality. In both cases there may be many individual exceptions; but on the average the rule will invariably be found to hold good. All varieties will therefore fall into two classes — those which under the same conditions would never reach the population of the parent species, and those which would in time obtain and keep a numerical superiority. Now, let some alteration of physical conditions occur in the district — a long period of drought, a destruction of vegetation by locusts, the irruption of some new carnivorous animal seeking "pastures new" — any change in fact tending to render existence more difficult to the species in question, and tasking its utmost powers to avoid complete extermination; it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organized variety would suffer first, and, were the pressure severe, must soon become extinct. The same causes continuing in action, the parent species would next suffer, would gradually diminish in numbers, and with a recurrence of similar unfavourable conditions might also become extinct. The superior variety would then alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species and variety.

The *variety* would now have replaced the *species*, of which it would be a more perfectly developed and more highly organized form. It would be in all respects better adapted to secure its safety, and to prolong its individual existence and that of the race. Such a variety *could not* return to the original form; for that form is an inferior one, and could never compete with it for existence. Granted, therefore, a "tendency" to reproduce the original type of the species, still the variety must ever remain preponderant in numbers, and under adverse physical conditions *again alone survive*. /58-59/ But this new, improved, and populous race might itself, in course of time, give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must, by the same general law, in their turn become predominant. Here, then, we have *progression and continued divergence* deduced from the general laws which regulate the existence of animals in a state of nature, and from the undisputed fact that varieties do frequently occur. It is not, however, contended that this result would be invariable; a change of physical conditions in the district might at times materially modify it, rendering the race which had been the most capable of supporting existence under the former conditions now the least so, and even causing the extinction of the newer and, for a time, superior race, while the old or parent species and its first inferior varieties continue to flourish. Variations in unimportant parts might also occur, having no perceptible effect on the life-preserving powers; and the varieties so furnished might run a course parallel with the parent species, either giving rise to further variations or returning to the former type. All we argue for is, that certain varieties have a tendency to maintain their existence longer than the original species, and this tendency must make itself felt;

for though the doctrine of chances or averages can never be trusted to on a limited scale, yet, if applied to high numbers, the results come nearer to what theory demands, and, as we approach to an infinity of examples, become strictly accurate. Now the scale on which nature works is so vast — the numbers of individuals and periods of time with which she deals approach so near to infinity, that any cause, however slight, and however liable to be veiled and counteracted by accidental circumstances, must in the end produce its full legitimate results.

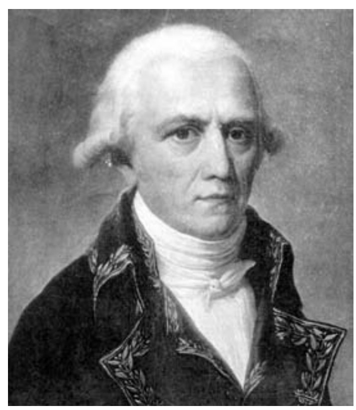
Let us now turn to domesticated animals, and inquire how varieties produced among them are affected by the principles here enunciated. The essential difference in the condition of wild and domestic animals is this, — that among the former, their well-being and very existence depend upon the full exercise and healthy condition of all their senses and physical powers, whereas, among the latter, these are only partially exercised, and in some cases are absolutely unused. A wild animal has to search, and often to labour, for every mouthful of food—to exercise sight, hearing, and smell in seeking it, and in avoiding dangers, in procuring shelter from the inclemency of the seasons, and in providing for the subsistence and safety of its offspring. There is no muscle of /59-60/ its body that is not called into daily and hourly activity; there is no sense or faculty that is not strengthened by continual exercise. The domestic animal, on the other hand, has food provided for it, is sheltered, and often confined, to guard it against the vicissitudes of the seasons, is carefully secured from the attacks of its natural enemies, and seldom even rears its young without human assistance. Half of its senses and faculties are quite useless; and the other half are but occasionally called into feeble exercise, while even its muscular system is only irregularly called into action.

Now when a variety of such an animal occurs, having increased power or capacity in any organ or sense, such increase is totally useless, is never called into action, and may even exist without the animal ever becoming aware of it. In the wild animal, on the contrary, all its faculties and powers being brought into full action for the necessities of existence, any increase becomes immediately available, is strengthened by exercise, and must even slightly modify the food, the habits, and the whole economy of the race. It creates as it were a new animal, one of superior powers, and which will necessarily increase in numbers and outlive those inferior to it.

Again, in the domesticated animal all variations have an equal chance of continuance; and those which would decidedly render a wild animal unable to compete with its fellows and continue its existence are no disadvantage whatever in a state of domesticity. Our quickly fattening pigs, short-legged sheep, pouter pigeons, and poodle dogs could never have come into existence in a state of nature, because the very first step towards such inferior forms would have led to the rapid extinction of the race; still less could they now exist in competition with their wild allies. The great speed but slight endurance of the race horse, the unwieldy strength of the ploughman's team, would both be useless in a state of nature. If turned wild on the pampas, such animals would probably soon become extinct, or under favourable circumstances might each lose those extreme qualities which would never be called into action, and in a few generations would revert to a common type, which must be that in which the various powers and faculties are so proportioned to each other as to be best adapted to produce food and secure safety, — that in which by the full exercise of every part of his organization the animal can alone continue to live. Domestic varieties, when turned wild, *must* return to something near the type of the original stock, *or become altogether extinct*. /60-61/

We see, then, that no inferences as to varieties in a state of nature can be deduced from the observation of those occurring among domesticated animals. The two are so much opposed to each other in every circumstance of their existence, that what applies to the one is almost sure not to apply to the other. Domestic animals are abnormal, irregular, artificial; they are subject to varieties which never occur and never can occur in a state of nature: their very existence depends altogether on human care; so far are many of them removed from that just proportion of faculties, that true balance of organization, by means of which alone an animal left to its own resources can preserve its existence and continue its race.

The hypothesis of Lamarck — that progressive changes in species have been produced by the attempts of animals to increase the development of their own organs, and thus modify their structure and habits — has been repeatedly and easily refuted by all writers on the subject of varieties and species, and it seems to have been considered that when this was done the whole question has been finally settled; but the view here developed renders such an hypothesis quite unnecessary, by showing that similar results must be produced by the action of principles constantly at work in nature. The powerful retractile talons of the falcon- and cat-tribes have not been produced or increased by the volition of those animals; but among the different varieties which occurred in the earlier and less highly organized forms of these groups, *those always survived longest which had the greatest facilities for seizing their prey*. Neither did the giraffe acquire its long neck by desiring to reach the foliage of the more lofty shrubs, and constantly stretching its neck for the purpose, but because any varieties which occurred among its antitypes with a longer neck than usual *at once secured a fresh range of*



Jean-Baptiste Lamarck

pasture over the same ground as their shorter-necked companions, and on the first scarcity of food were thereby enabled to outlive them. Even the peculiar colours of many animals, especially insects, so closely resembling the soil or the leaves or the trunks on which they habitually reside, are explained on the same principle; for though in the course of ages varieties of many tints may have occurred, *yet those races having colours best adapted to concealment from their enemies would inevitably survive the longest*. We have also here an acting cause to account for that balance so often observed in nature, — a deficiency in one set of organs always being compensated by an increased development of some others — powerful wings accompanying weak /61-62/ feet, or great velocity making up for the absence of defensive weapons; for it has been shown that all varieties in which an unbalanced deficiency occurred could not long continue their existence. The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude, because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure soon to follow. An origin such as is here advocated will also agree with the peculiar character of the modifications of form and structure which obtain in organized beings — the many lines of divergence from a central type, the increasing efficiency and power of a particular organ through a succession of allied species, and the remarkable persistence of unimportant parts, such as colour, texture of plumage and hair, form of horns or crests, through a series of species differing considerably in more essential characters. It also furnishes us with a reason for that "more specialized structure" which Professor Owen states to be a characteristic of recent compared with extinct forms, and which would evidently be the result of the progressive modification of any organ applied to a special purpose in the animal economy.

We believe we have now shown that there is a tendency in nature to the continued progression of certain classes of *varieties* further and further from the original type — a progression to which there appears no reason to assign any definite limits — and that the same principle which produces this result in a state of nature will also explain why domestic varieties have a tendency to revert to the original type. This progression, by minute steps, in various directions, but always checked and balanced by the necessary conditions, subject to which alone existence can be preserved, may, it is believed, be followed out so as to agree with all the phenomena presented by organized beings, their extinction and succession in past ages, and all the extraordinary modifications of form, instinct, and habits which they exhibit.

Ternate, February, 1858

Commentary

Charles Darwin was born at Shrewsbury on February 12, 1809. His father was a wealthy physician and his mother was the daughter of a manufacturer, Josiah Wedgwood. He, therefore, had independent means, which allowed him to pursue his scientific interests without having to earn a living. After a couple of years of medical school, he went to Cambridge University to prepare for a career as a clergyman. He had, however, developed a taste for the natural sciences and became the unofficial naturalist on a surveying expedition that took him around the world (1831-1836). During the voyage he read Charles Lyell's *Principles of Geology*, and he made some important discoveries about geology. As a result, he became both a protégé of Lyell, and one of his main supporters. He also studied the minerals, plants and animals, and collected a vast quantity of natural history specimens. As a consequence, he made many observations on the geographical distribution of organisms, especially those of islands.

After he returned to England Darwin realized that the geographical distribution of animals and the relationships some of the fossils that he found in South America to living animals were evidence for evolution. He began to search for a mechanism that could account for it, speculating as he read about a wide range of topics. In late September of 1838, he read a book on political economy, [Thomas] Robert Malthus' *An Essay on the Principle of Population*. Malthus argued that human populations grow rapidly as long as food is abundant. Although the food supply can be increased, that increase is not sufficient to maintain a high level of population growth indefinitely. Ultimately food will become scarce, standards of living will fall, and population numbers will stabilize. He said that population increases geometrically, whereas resources are augmented arithmetically. The mathematics was not a crucial part of Malthus's argument. Malthus and others had noted that when population numbers are decreased owing to a plague, there follows a period in which people bear and raise more offspring so that the population tends to return to its former levels and stabilize. Likewise, when new land is opened up to cultivation, as in North America, the abundant food supply leads to a higher reproductive rate. Darwin realized that any advantage that an individual organism might have in avoiding enemies and utilizing the available resources relative to other organisms of the same species would mean that it would leave relatively more offspring. Whatever properties that gave the organism that advantage would tend to be passed on to the next generation, transforming the species. Evolution would result from reproductive competition between organisms of the same species. Darwin already was well aware of the fact that breeders of domesticated animals and plants were able to effect changes by "selecting" the organisms with the desired traits and using them as breeding stock. He now understood that something similar to what happens under artificial conditions would result because of the scarcity of resources under natural conditions. The environment would take the place of the breeder. Darwin now had a plausible mechanism for evolution, and one that was similar to a familiar process.

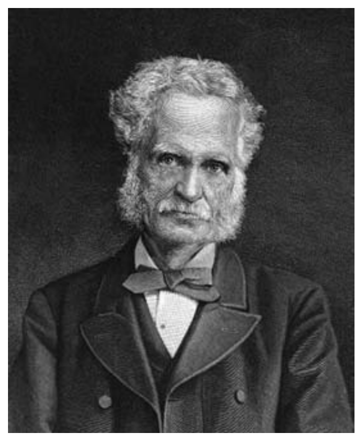
Darwin speculated a great deal and gradually elaborated the theory of evolution by natural selection that was published in *The Origin of Species*. But twenty years elapsed between that event and his reading of Malthus. Various reasons have been given for the delay. The most obvious and straight forward is that he needed to publish the results of his geological research. His work was much delayed by illness, no doubt exacerbated by anxiety. In retrospect we can find many hints of Darwin's evolutionism in his earlier publications. Among these was his semi-popular account of his travels, a book which has appeared under various titles, the most appropriate of which is the *Journal of Researches*. It appeared in two editions. The first, published in 1839, was written when Darwin was already an evolutionist, but before he had read Malthus. The second was prepared in 1845 and contains a great deal of material that is relevant to Darwin's ideas about natural selection and the competitive natural economy. It even includes a discussion of the Malthusian notion of geometrical population increase. Prior to that time, however, Darwin had begun to prepare a book on his theory. A "Sketch" of this theory was produced in 1842. This was basically a working outline with notes and memoranda. A much longer "Essay" was completed in 1844. It is from this manuscript that the excerpt in the Darwin-Wallace paper was taken. Darwin realized that it would take a considerable amount of time and work to get the manuscript into a form in which it could be published. He feared that he might die before completing it. Therefore he made arrangement for its posthumous publication. Having become a good friend of the botanist Joseph Hooker, Darwin thought he might be a suitable editor, and in 1847 he sent Hooker a copy.

In 1848, Darwin began to do some zoological work. The result was that he wrote a monograph on barnacles well over a thousand pages long. That delayed serious work on his book on evolution until around September of 1854. Although only implicitly so, the barnacle monograph was in fact Darwin's first book on evolution. It made him a very eminent zoologist who could speak with authority on a vast range of biological matters and he found the research very instructive. One discovery that he made while doing the barnacle research was what he called "the principle of divergence of character." As he saw it, the various groups in the natural system of classification are lineages connected by common ancestry. They become increasingly diversified with the passage of time because it is advantageous for the organisms to seize upon different places in the economy of nature, or, as we would now say, to occupy a variety of niches. This notion was basic to

Darwin's evolutionary ecology. Darwin began to organize his notes on evolutionary topics and did a considerable amount of experimental and comparative research.

Meanwhile Alfred Russel Wallace was thinking along somewhat similar lines. Born in 1828, Wallace came from a family of very modest means. Largely self-educated, he early on became an amateur naturalist. In his readings he encountered some of the pre-Darwinian evolutionary, or proto-evolutionary, literature. The topic was not considered intellectually respectable at the time. Indeed it was considered socially and politically reprehensible. Wallace, who had very much a mind of his own, was favorably disposed to it nonetheless. Around the time that the second edition of Darwin's *Journal of Researches* was published, which Wallace read, he also read Malthus' essay on population. It seems likely that Wallace gained some hints about Darwin's views from his readings.

Wallace became the friend of another amateur naturalist who later became a famous evolutionist, Henry Walter Bates. Together they decided to undertake an expedition to the Amazon in the hope of finding evidence that might bear upon the larger evolutionary questions. Their plan was to collect natural history specimens and sell some of them to dealers as a means of financing the expedition. In this they were successful, but some of Wallace's collections were destroyed by a fire at sea on the way back to England in 1852. Undaunted, Wallace embarked upon a similar research and collecting trip to the Malay Archipelago, reaching Singapore in April, 1854. In spite of great hardship, he explored a vast area and collected a remarkable number of specimens. Wallace's biogeographical studies led him to the same conclusions that Darwin's had. In 1855, he published a paper entitled "On the law which has regulated the introduction of new species." His point was that whenever a new species appears, it does so close (both in space and time) to a closely-related and previously-existing species. The implication would be that one species has given rise to another.



Henry Walter Bates

Wallace's paper attracted the attention of Lyell as well as Darwin. During a visit to Darwin's home in 1856, Lyell asked about Darwin's theory, and Darwin explained it. Realizing that Wallace was working along the same lines, Lyell urged Darwin to publish. So Darwin began to write a long book, to be entitled *Natural Selection*, in which he would expound his theory at great length, and in minute detail. That same year, Darwin began to correspond with the Harvard botanist Asa

Gray, in the hope of obtaining some information about plants that he wanted. In that letter, Darwin revealed that he was working on evolutionary theory. In May of 1857, Darwin also wrote to Wallace, informing him that he had a species theory. And, in September (or October), he again wrote to Gray, explaining natural selection. That letter provided part of the joint publication. In December, Darwin once more wrote to Wallace, commenting on another of Wallace's papers. In his letter, Darwin said that he was working on a book about his theory, but that it would be some time before it would be ready for publication.

In February 1858, perhaps quite soon after Darwin's letter had reached him, Wallace, while suffering from a bout of malaria, discovered natural selection. He wrote a manuscript explaining the idea and sent it to Darwin with a covering letter asking for his opinion and saying that if he felt that it was of any value to send it on to Lyell. Darwin had been making slow but steady progress on *Natural Selection* and was astonished when Wallace's manuscript arrived on June 18. He immediately got in touch with Hooker and Lyell, who arranged for the joint publication that was read before the Linnaean Society on July 1. Although their covering letter is dated June 30, the arrangement must have occurred somewhat earlier. In effect, everything was set up in about a week's time. Very little is known about what actually went on. Darwin himself was not much involved, for he was at his home in the country, and was distracted by such events as the death of his youngest child. Darwin was much upset about the whole affair. He went on vacation for a few weeks, but on July 20 he began to write what he called an "abstract" of *Natural Selection*.

Wallace could not have been aware of what was going on at the time, and Darwin was really worried as to how Wallace would react. Would he feel that he had been treated unfairly? But, in due course, Wallace was informed of what had taken place, and on October 6 he wrote a letter to Hooker saying that he approved of the joint publication.

Meanwhile, Darwin began a new manuscript of a shorter book, still intending to publish the long one that he had been working on when Wallace's manuscript arrived. Although the official date of publication of this "abstract," *The Origin of Species,* was November 24, 1859, the entire edition was sold at the publishers' trade sale on November 22. Some prepublication copies were available somewhat earlier, and of course Wallace was among the recipients. Wallace was profoundly impressed. In a letter to Bates dated December 24, 1860 he evaluates the book as follows:

> I do not know how or to whom to express fully my admiration of Darwin's book. To him it would seem flattery, to others self-praise; but I do honestly believe that with however much patience I had worked up and experimented on the subject, I could never have

> approached the completeness of his book—its vast accumulation of evidence, its overwhelming argument, and its admirable tone and spirit. I really feel thankful that it has not been left to me to give the theory to the public. Mr. Darwin has created a new science and a new philosophy, and I believe that never has such a complete illustration of a new branch of knowledge been due to the labours and researches of a single man. Never have such vast masses of widely scattered and hitherto disconnected facts been combined into a system, and brought to bear upon the establishment of such a grand and new and simple philosophy!

Wallace returned to London on April 1, 1862, and he and Darwin met soon after Darwin arrived by train the next day, probably at the home of Darwin's older brother, Erasmus Alvey Darwin. Wallace became one of Darwin's most effective supporters. Darwin, conversely, went out of the way to give Wallace full credit as co-discoverer of natural selection. They often disagreed about various topics both scientific and philosophical, but their discussions were always cordial. Their main area of disagreement had to do with human evolution. Wallace denied that natural selection could explain human mentality. With that one exception, however, Wallace attributed more to natural selection than Darwin did. Wallace was rather eccentric and openly endorsed spiritualism. That created something of a strain with Darwin, and more than that with Hooker and some other scientists. Although he was able to earn money by writing and lecturing, Wallace was never able to obtain suitable employment. In addition, he was inept at handling his financial affairs. Darwin arranged for a government pension for him. Wallace was a prolific contributor to the literature on evolutionary biology. Perhaps his most important contributions were to biogeography. His *Island Life* and *Geograpical Distribution of Animals* are both classics. Darwin had, in effect, opted out of working on biogeography and left the topic largely to Wallace.

Since Wallace gracefully went along with the arrangement for joint publication, the issue of whether Wallace was treated fairly or not is academic. He knew that Darwin had a theory and had many hints of what it was. The discovery was not as "independent" of Darwin as one might think. His manuscript was circulated for comments by Darwin and Lyell and not submitted for publication. If it had been published separately, it likely would not have attracted much attention anyhow. On the other hand, the joint publication made Wallace a famous man. He was welcomed into scientific circles. His books and papers, both scholarly and popular, were much esteemed and widely read. And, quite unwittingly, he got Darwin to write a much shorter book and a better one, and to present it to the world much sooner than he had intended.

Chronology

1809
12 February, Charles Darwin born

1823
8 January, Alfred Russel Wallace born

1828
January, Darwin began studies at Cambridge

1831
27 December, Darwin left England on voyage around the world

1832
28 February, Darwin arrived in South America

1836
2 October, Darwin arrived in England

1837
7-12 March, Darwin became an evolutionist

1838
28 September-2 October, Darwin read Malthus's *Essay on the Principle of Population* and discovered natural selection

1839
1 June, Darwin's Journal of Researches published

1842 Darwin wrote a "Sketch" of his evolutionary thory

1844
11 January, Darwin wrote to Joseph Hooker, revealing his evolutionary views
5 July, Darwin completed his Essay on evolution

1844-1846
Wallace, a school teacher at Leicester, read Malthus's *Essay on the Principle of Population* and Darwin's *Journal of Researches* (probably the second edition)

1845
5 April, Darwin finished preparation of the second edition of his *Journal of Researches*

1847
7 January, Hooker received a copy of Darwin's 1844 Essay

1848
26 May, Wallace and Bates reached the Amazon
1 October, Darwin began to work on barnacles

1852
12 July, Wallace departed for England, arriving 1 October

1854
20 April, Wallace arrived in Singapore
9 September, having completed his work on barnacles, Darwin began to write a book on species

1855
September, Wallace's paper "On the law which has regulated the introduction of new species" published

1856
13-16 April, during a visit to Darwin, Charles Lyell asked about Wallace's paper of 1855; Darwin told him about natural selection; Lyell urged him to publish
14 May, Darwin began to work on manuscript of Natural Selection and continued to do so until Wallace's manuscript arrived in 1858
20 July, Darwin, in a letter to Asa Gray, reveals his evolutionary views

1857
1 May, in a letter to Wallace, in which Darwin comments on Wallace's 1855 paper, he remarks that he has a species theory
20 July, Darwin wrote an openly evolutionary letter to Gray
5 September, Darwin sends a letter to Gray with an enclosure explaining natural selection
27 September, Wallace responded to Darwin's letter of 1 May
29 November, Darwin clarifies his evolutionary ideas in a letter to Gray
22 December, responding to Wallace's letter of 27 September, Darwin comments on Wallace's paper and says that he has plans for a book

1858
February, Wallace discovered natural selection
18 June, Wallace's manuscript on natural selection reached Darwin, who wrote to Lyell
28 June, Darwin's infant son, Charles Waring Darwin, died
1 July, the joint paper was read to the Linnaean Society; it was published in August
6 October, in a letter to Hooker, Wallace expresses approval of joint publication

1859
24 November, *The Origin of Species* published

1860
24 December, Wallace wrote Bates, praising *The Origin of Species*

1862
20 February, Wallace left Singapore, arriving in London April 1

1882
19 April, Darwin died

1913
7 November, Wallace died

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