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A Comparative Analysis of the Darwin-Wallace Papers and the Development of the Concept of Natural Selection

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Summary: The classical theory of descent with modification by means of natural selection had no mother, but did have two English fathers, Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913). In 1858, the Linnean Society of London published two contributions of these naturalists and acknowledged both authors as the proponents of a novel hypothesis on the driving force of organismic evolution. In the present report the most important sections of the Darwin-Wallace papers are summarized. This close reading of both publications reveals six striking differences in emphasis: Darwin and Wallace did not propose identical ideas. The species definitions of both authors are described and the further development of the concept of natural selection in wild populations is reviewed. It is shown that the contributions of A. R. Wallace, who died 90 years ago, are more significant than usually acknowledged. I conclude that natural selection's lesser known co-discoverer should be regarded as one of the most important pioneers of evolutionary biology, whose original contributions are underestimated by most contemporary scientists.

Introduction

Ninety years ago the English naturalist Alfred Russel Wallace (1823–1913) died at Old Orchard, Broadstone, United Kingdom. In spite of the fact that Wallace published many seminal papers and books on topics such as biogeography, mimicry and anthropology, his most important contribution was the co-discovery of the principle of natural selection (Raby 2001, Shermer 2002). In February of 1858, while he suffered from an attack of malaria in the Moluccas, Wallace combined the well-known ideas of Thomas Malthus (1766–1834) on the limits of population growth and the phe-

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nomenon of biological variability to a hypothetical mechanism that may cause the occurrence of new varieties and species in natural populations. In essence, this was the concept of the "survival of the fittest" (Raby 2001). As soon as Wallace had recovered from his illness, he wrote down his ideas and sent it off to Charles Darwin (1809–1882), with whom he had begun a correspondence some years earlier. This naturalist had been entertaining very similar concepts for the past twenty years, and now a threat to his priority on this basic idea loomed. He contacted his friends, who decided to present the manuscript of Wallace, together with some unpublished fragments from Darwin's notebook, to the next meeting of the Linnean Society.

In June 1858 Charles Lyell and Joseph Hooker communicated two papers to the Linnean Society of London which related to the same subject: "the laws which affect the production of varieties, races and species" (Fig. 1). It is generally assumed that Darwin and Wallace published the same theory (Barlow 1958, Gould 2002). However, a close reading of these papers, which are cited here as separate publications (Darwin 1858, Wallace 1858), reveals several significant differences. In this contribution a detailed analysis of this basic concept of evolutionary biology is presented. In addition, the meanings of the term "species" in major books and papers of both naturalists are compared. In the second part, the elaboration of the principle of natural selection with special reference to industrial melanism and the corresponding work by Wallace (1889) is reviewed.

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.

Fig. 1. Title and first paragraph of the classical Darwin-Wallace papers, published in the Journal of the Proceedings of the Linnean Society London, Zoology, 3, 45–62, 20. Aug. 1858. (Adapted from the original publication).

Charles Darwin 1858

The contribution of Darwin consists of two separate parts, an extract from a unpublished work on species (I) and an abstract of a letter from the author to Asa Gray, dated Sept. 5th, 1857 (II). The most important sentences are summarized below. In the first part (I) of his original paper, Darwin referred to the doctrine of Robert Malthus and cited earlier naturalists that had written that "all nature is at war, one organism with another, or with external nature" (Darwin 1858, p. 46). He deduced the principle of natural selection as follows: "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. [...] this average number of individuals [...] in each country is kept up by recurrent struggles against other species or against external nature" (Darwin 1858, p. 48). The relationship between the struggle for existence and the observed variability within interbreeding groups of animals and plants was described as follows: "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; [...] 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?" (Darwin 1858, p. 49).

In addition to the principle of natural selection the author mentioned the struggle among the males in the course of sexual reproduction: "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 animals tending to produce the same effect, namely, the struggle of the males for the females" (Darwin 1858, p. 50).

In the second part (II) of his paper, the author described results from animal breeders: "It is wonderful what the principle of selection by man, that 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" (Darwin 1858, p. 50). He pointed out that the domestic animal races such as sheep and cattle are the result of artificial selection: "I am convinced that intentional and occasional selection has been the main agent in the production of our domestic races; [...] 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" (Darwin 1858, p. 51).

The influence of the environment on heritable variability (i. e., the classical concept of J. B. de Lamarck, see below) is described in this passage and repeated several times. In the next paragraph, Darwin compared domestic animals with wild species and referred to information obtained from geology: "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" (Darwin 1858, p. 51).

Then he introduced the principle of natural selection and the term "struggle for life", which was used by several earlier naturalists with a slightly different meaning: "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. [...] 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!" (Darwin 1858, p. 51).

The same train of thought was expressed in the next paragraph, where the living conditions of the organisms were taken into account: "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, etc. etc., I cannot doubt that during millions of generations individuals of a species will be occasionally born with some slight variation, profitable to some part of their economy. Such individuals will have a better chance of surviving, and of propagating their new and slightly different structure; and the modification may be slowly increased by the accumulative action of natural selection to any profitable extent. The variety thus formed will either coexist with, or, more commonly, will exterminate its parent form" (Darwin 1858, p. 52).

In the last paragraph of his paper, the author introduced the principle of divergence in the origin of species. Here, Darwin clearly distinguished between varieties, subspecies and true species: "The same spot will support more life if occupied by very diverse forms. [...] 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 sub-species, or true species. [...] 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" (Darwin 1858, pp. 52–53). In the last sentence of this page the author explicitly pointed out that this sketch is most imperfect: "Your imagination must fill up very wide blanks". Less than eighteen month later, Darwin's most influential book *On the Origin of Species by means of Natural Selection* (1859) was published.

Alfred R. Wallace 1858

In the introduction to this paper, the author wrote that domesticated animals are not analogous to those varieties that live under natural conditions. In a later part of his publication, Wallace concluded that "no inferences as to varieties in a state of nature can be deduced from the observation of those occurring among domestic 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" (Wallace 1858, p. 61).

In the second paragraph of his contribution, he pointed out that "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 appears so inexplicable – the excessive abundance of some species, while others closely allied to them are very rare" (Wallace 1858, p. 54).

Then the author introduced his observations and deductions concerning population growth in free-living animals: "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 [...]. 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, were there not some powerful check to their natural increase" (Wallace 1858, pp. 54–55). The author illustrates his conclusion by the following quantitative example: "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" (Wallace 1858, p. 55).

It should be pointed out that Wallace used the term population as a synonym for a group of interbreeding birds. Moreover, the title of Darwin's book (*Origin of Species*) occurs in this paragraph of Wallace's paper. A few sentences later the author described the principle of natural selection, but did not use this term: "[...] 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" (Wallace 1858, p. 55). This basic idea is further elaborated in the following phrase: "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 which the weakest and least perfectly organized must always succumb" (Wallace 1858, pp. 56–57).

The concepts of adaptation and differential survival of favoured individuals are described in detail: "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 [...] must diminish in numbers, and, in extreme cases, become altogether extinct" (Wallace 1858, p. 57).

After a brief summary of these observations and conclusions Wallace discussed the subject of biological variability in animal populations: "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" (Wallace 1858, p. 58).

In the next section the author concluded that the new variety would now have replaced the original species, of which it would be a 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" (Wallace 1858, p. 58).

Since this new, improved race can by itself, in the course of time, give rise to new varieties, he concluded that "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" (Wallace 1858, p. 59).

In the subsequent section, Wallace picks up his discussion of domesticated versus wild animals, a topic introduced in the first sentences of his paper: "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" (Wallace 1858, p. 59).

The concepts of J. B. de Lamarck (1744–1829), who published his basic ideas in his classical book entitled *Philosophie Zoologique* (1809), were sharply criticized by Wallace. Like most naturalists of his time, Lamarck was an adherent of the principle of an inheritance of acquired characteristics. Wallace commented on this idea as follows:

"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 [...]. "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 pasture over the same ground as their shorter-necked companions, and on the first scarcity of food were thereby enabled to outlive them" (Wallace 1858, p. 61).
Thereafter, the author discussed an example for the struggle for existence from the world of invertebrate animals: "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" (Wallace 1858, p. 61). In this sentence, he described what centuries later became one of the most cited examples of evolution by natural selection: industrial melanism in the peppered moth (Kettlewell 1965). This subject is discussed in detail below.
Finally, Wallace proposed that there may be 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 [...] 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" (Wallace 1858, p. 62).

Comparative analysis

Neither the geologist Charles Lyell and the botanist Joseph Hooker, nor Darwin himself did mention the striking differences in the logical deduction of the principle of natural selection inherent in these original papers. Moreover, in his autobiography, Darwin wrote that the essay of Wallace "contained exactly the same theory as mine" (Barlow 1958, p. 121). In most books on the history of evolutionary biology it is implicitly assumed that the Darwin-Wallace publication contains interchangeable concepts (Futuyma 1998, Gould 2002), with some notable exceptions (Bowler 1984, Ruse 1996, Junker and Hoßfeld 2001). The most important differences between the Darwin-Wallace papers can be summarized as follows:

1. Wallace emphasized the distinction between domestic and natural varieties. In fact, he regarded domestic animals as "abnormal" and pointed out that they can not be regarded as "model systems" for animals in

nature. Darwin, however, stressed the similarities between domestic and natural variants in the construction of his argument.

2. In the paper by Wallace only animals (vertebrates, insects) are cited as examples for the "struggle for existence". Darwin, on the other hand, explicitly referred to animals and plants, i. e., to mobile and sessile organisms.

3. Wallace stressed competition of animals in relation to the environment (whether living or inorganic) and between separate species: the struggle against enemies and predators is the decisive process in his paper. Darwin, on the other hand, emphasized the interspecific competition: the struggle against one's fellow-species. This aspect was described at length in his *Origin of Species* (Darwin 1859, 1872).

4. From the very beginning of his career as an evolutionist, Wallace (1858) rejected the concept proposed by Lamarck, whereas Darwin, throughout his life, adhered to the principle of the inheritance of acquired characteristics.

5. Wallace did not mention the factor time (i. e., the number of generations that must pass) until new varieties of species may occur as a result of the consistent force of natural selection. Darwin pointed out the importance of geological time intervals with respect to the origin of new species and referred to thousands (or millions) of generations.

6. Darwin introduced, in addition to the natural means of selection, a second principle: the struggle among males for females (sexual selection, described at length in the *Origin of Species*). In his original paper, Wallace did not mention this second kind of selection, which is a result of differential mating success (Andersson 1994).

Finally, it should be pointed out that the term "natural selection" was not used by Wallace, but by Darwin in several sentences. However, Wallace introduced the terms "adaptation" and "population" in a modern sense. Neither Darwin nor Wallace did mention the word "evolution", although in their later books they referred to this key term on several occasions (Darwin 1859, 1972, Barlow 1958, Wallace 1889). Both authors used the word "species" in their original 1858 papers. Their elaboration on this important topic is described in the next section.

The species concepts of Darwin and Wallace

Although Darwin and Wallace used the term "species", they did not define this key word in their first publications on this subject. Wallace (1858, p. 53) pointed out that "which is the variety and which the original spe-

cies, there is generally no means of determining". Darwin (1858) used the terms "varieties, subspecies and true species". However, no definitions were provided. In *The Origin of Species* (1859, 1872), in the first and last editions, Darwin pointed out that no good line of demarcation can be drawn between varieties and species: "in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow." (Darwin 1859, p. 57). "It is all-important to remember that naturalists have no golden rule by which to distinguish species and varieties" (Darwin 1872, p. 335). He regarded varieties as a step in the process that leads over thousands of generations to new species. Hence, the occurrence of intermediate forms between varieties and "true species" was crucial for Darwin's argument for "descent with modification", i. e., the gradual transformation of species. As pointed out by Grant (1994), Darwin did not explicitly define the terms "varieties" and "species", although some of his statements indicate that he held the widespread view of species as discrete reproductive collectives.

In his later publications, Wallace repeatedly defined the term "species"; the most important definitions are summarized below. In his monograph on papilionid butterflies of the Malay archipelago, he wrote that "Species are merely those strongly marked races or local forms which when in contact do not intermix, and when inhabiting distinct areas are generally believed to have had a separate origin, and to be capable of producing fertile offspring" (Wallace 1864, p. 32).

In 1885 Wallace was invited to give a series of lectures on "Darwinism" at the Lowell Institute, Massachusetts, USA. His oral presentations were written down and published as a book (Wallace 1889). In chapter III he characterized a species as an assemblage of individuals which are adapted to their particular conditions of life, are differentiated from other allied assemblages, reproduce their like, and usually breed together. Six years later, Wallace presented his final definition: "A species [...] is a group of living organisms, separated from all other such groups by a set of distinctive characters, having relations to the environment not identical with those of any other group of organisms, and having the power of continuously reproducing its like" (Wallace 1895, p. 441). This comprehensive and precise definition is very similar to the biological species concept, which has multiple roots (Grant 1994, Howard and Berlocher 1998). One of the founders of this modern species concept, E. Mayr, defined this key term as follows: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942, p. 120). More than four decades later, the same author published a short definition that has been adopted by the majority of contemporary evolutionists: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1988,

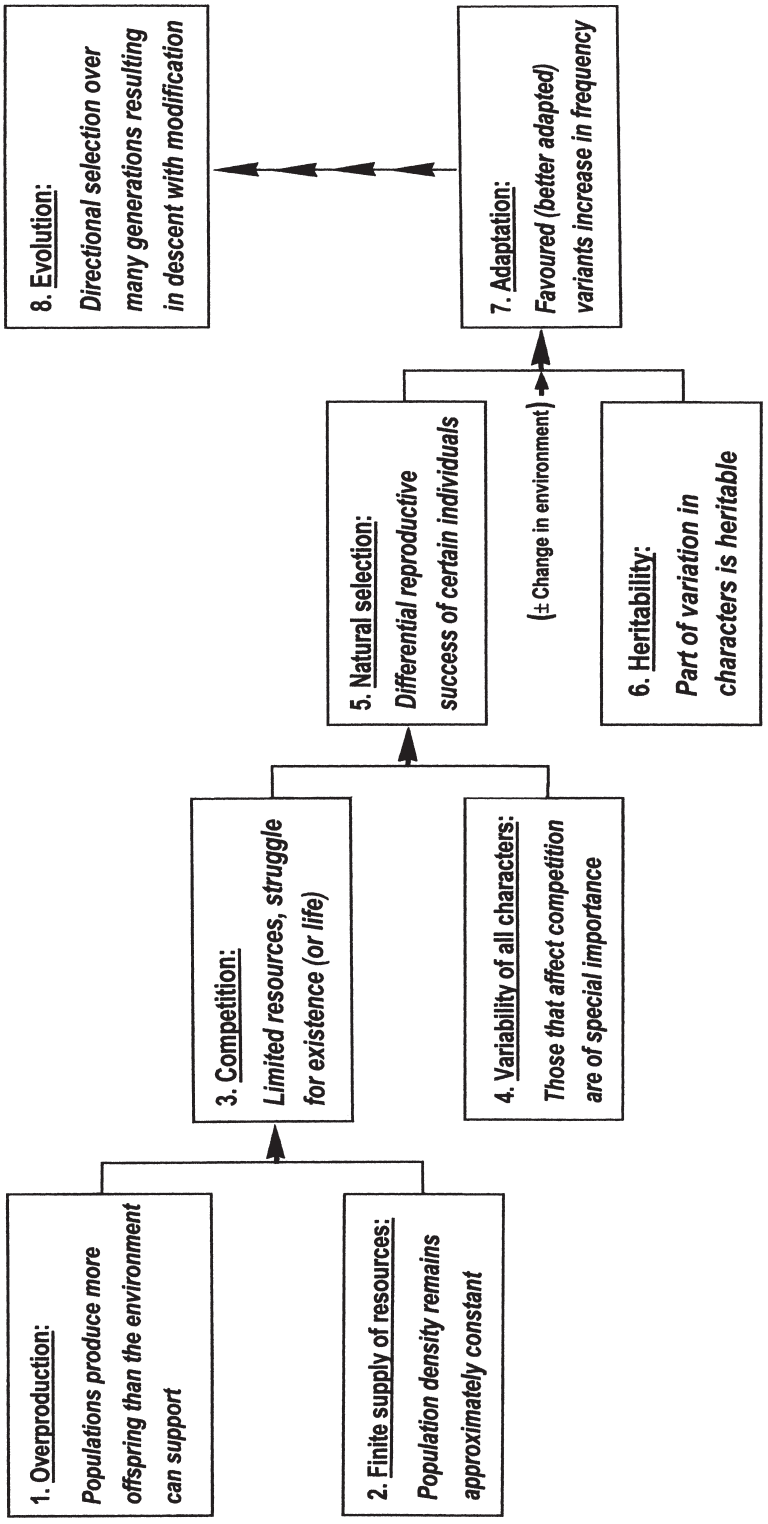

Fig. 2. Flow diagram of the basic logic leading to descent with modification (evolution). In this scheme the original Darwin-Wallace observations and conclusions are expanded by more recent concepts.

p. 318). A comparison of the species definitions of Darwin, Wallace and Mayr reveals that A. R. Wallace was one of the "fathers" of the modern biological species concept. Darwin (1859, 1872), however, did not explicitly point out how he defined this key term in his famous book entitled *On the Origin of Species*.

Natural selection: elaboration of the classical concept

Both Darwin (1859, 1872) and Wallace (1889) devoted a full chapter of their books to the principle of natural selection, which they presented under the headline "The struggle for existence". The most important definitions, quoted from the last edition of Darwin's work, are summarized below:

1. The causes of biological variability in natural populations: "Changed conditions of life are of the highest importance in causing variability, both by acting directly on the organisation, and indirectly by affecting the reproductive system" (Darwin 1872, p. 53).
2. Struggle for existence: "I use this term in a large and metaphorical sense including dependence of one being on another, and including (what is more important) not only the life of the individual, but success in leaving progeny" (Darwin 1872, p. 73).
3. Intraspecific versus interspecific competition: "(The) struggle for life (is) most severe between individuals and varieties of the same species" (Darwin 1872, p. 84).
4. The relationship between natural selection and the term fitness: "This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection or the Survival of the Fittest" (Darwin 1872, p. 88). In later editions of his 1859-book, Darwin borrowed the unfortunate phrase "survival of the fittest" (Spencer 1864, p. 444) from the philosopher and founder of Social Darwinism Herbert Spencer (1820–1903). Since survival is only one component of natural selection and the term "fitness" has a variety of meanings, this terminology led to much confusion, notably among non-biologists (Endler 1986, Kutschera 2001).
5. On the last page of his book, Darwin summarized his theory of descent with modification as follows: [. . .] "Variability from the indirect and direct action of the conditions of life, and from use and disuse: a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less improved forms" (Darwin 1872, p. 506).

These citations show that Darwin (1872) fully accepted the concept of the inheritance of acquired characteristics as a major cause for biological variability in populations; competition between individuals leads to a struggle for existence (or life) and hence to natural selection (the survival of the fittest). Since the reproductive success is emphasized, it follows that Darwin (1872) implicitly used the term fitness in our modern sense: as a synonym for 'lifetime reproductive success' (Bell 1997, Niklas 1997).

In contrast to Darwin (1859, 1872), Wallace (1889) rejected Lamarck's concept of the inheritance of acquired characteristics and readily accepted the conclusions of Weismann (1892). Like this German Zoologist, he was convinced of the power of natural selection: "We have seen that Professor Weismann's theory of the continuity of the germ-plasm and the consequent non-heredity of acquired characters, while in perfect harmony with all the well-ascertained facts of heredity and development, adds greatly to the importance of natural selection as the one invariable and ever-present factor in all organic change" (Wallace 1889, p. 444).

In the subsequent decades, hundreds of experimental studies were published that have shown that Wallace's conclusion was correct. Endler (1986) described the concept of natural selection from a modern perspective, showed that it is neither a tautology nor a metaphysical exercise, and summarized numerous examples observed in wild populations. Today we know that natural selection works by the elimination of the un-fit: 'a lack of fit' between organism and the environment reduces the lifetime reproductive success of these particular individuals within a population. As a result, certain genotypes will leave fewer offspring than those that 'fit to the environment' (i. e., are better adapted). A general scheme of the modern concept of natural selection, adapted and modified from Mayr (1988) and Bell (1997), is depicted in Fig. 2.

The causes of biological variability in natural populations were unknown to Darwin and Wallace. It was the zoologist Weismann (1892) who pointed out in several of his publications that sexual reproduction in animal populations creates with each generation new combinations of individual variation. Wallace (1889) referred to this novel idea and hence must be classified as one of the first adherents of neo-Darwinism (a term coined by G. J. Romanes in 1896, defined as "Darwinism without an inheritance of acquired characters", Mayr 1988, p. 535).

As cited above, Wallace (1858) hypothesized that insects that resemble in colour the trunks on which they reside will survive the longest, due to the concealment from predators. It follows that he was the spiritual father of the most obvious experimental proof of the Darwin-Wallace-concept: industrial melanism in the peppered moth (Fig. 3). The relatively rapid rise and fall in the frequency of mutation-based melanism in *Biston*-populations, that occurred in parallel on two continents (Europe, North America), is a compelling example for rapid microevolution in nature caused by

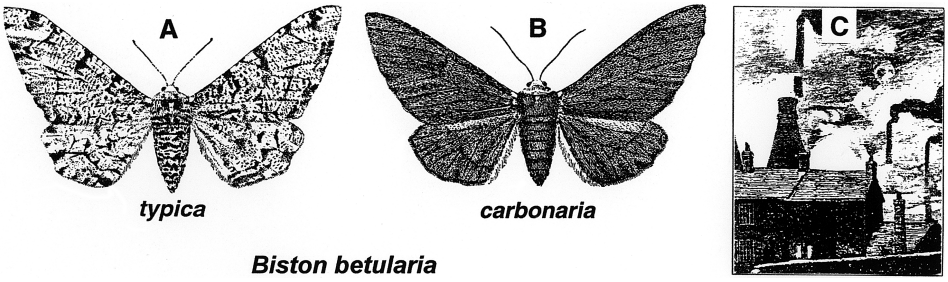

Fig. 3. Industrial melanism in populations of the peppered moth (*Biston betularia*). Before 1850, white moths peppered with black spots (typica) dominated in England (A). Between 1850 and 1920, typica was largely replaced by a black form (carbonaria) (B), produced by a single allele. Between 1950 and 1995, this trend reversed, making form (B) rare and (A) again common. The increase in black moths was attributable to air pollution (C) that accompanied the rise of heavy industry: dark moths are protected from predation by birds. (Adapted from Kettlewell 1965).

mutation and natural selection. The hypothesis that birds were selectively eating conspicuous insects in habitats modified by industrial fallout is consistent with the data (Majerus 1998, Cook 2000, Coyne 2002, Grant 2002).

It should be noted that Coyne (1998) concluded that *B. betularia* probably does not rest on tree trunks: only "two moths have been seen in such a position in more than 40 years". If this would be correct, the *Biston*-story could no longer be accepted in its original version. However, Coyne's (1998) statement is erroneous. According to the data of Majerus (1998), 26–34 % of the moths were observed to rest on tree trunks, usually several meters above ground (M. Majerus, pers. comm.). Hence, selective predation by birds is supported by evidence, as originally proposed by Kettlewell (1965).

In his famous book, Wallace (1889) devoted a comprehensive chapter to the topic 'warning coloration and mimicry with special reference to the Lepidoptera'. One of the most conspicuous day-flying moths in the Eastern tropics was the widely distributed species *Opthalmis lincea* (Agaristidae). These brightly coloured moths have developed chemical repellents that make them distasteful and saves them from predation (Müllerian mimetics). Wallace (1889, p. 246) wrote that "we may expect to find other moths which are not so protected imitating them, and this is the case". *Opthalmis lincea* (Fig. 4 A) is mimicked by the moth *Artaxa simulans* (Liparidae), which was collected during the voyage of the *Challanger* and later described as a new species (Fig. 4 B). This survival mechanism is called Batesian mimetics (Kettlewell 1965).

In summary, this historical analysis clearly shows that the experimental verfication of the concept of natural selection can be traced back to the work of A. R. Wallace.

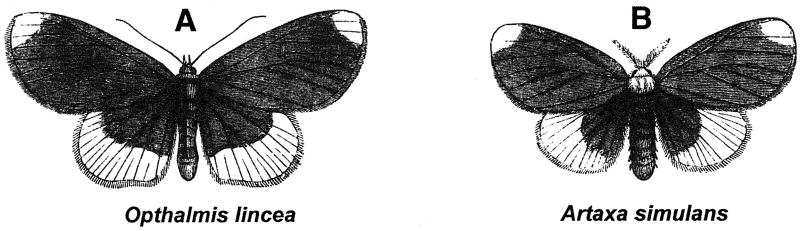

Fig. 4. Insects have evolved highly efficient survival mechanisms that were described in detail by A. R. Wallace. One common moth species (*Opthalmis lincea*) (A) contains chemical repellents to make the insects distasteful. This moth is mimicked by a second species (*Artaxa simulans*) (B). (Adapted from Wallace 1889).

Conclusions

In a talk given by Dawkins (2002), when a plaque in the Royal Academy commemorating the reading of the Darwin-Wallace papers was unveiled, this British evolutionist pointed out that the "second man in the shadow of Darwin" should no longer be neglected by historians of science. In two new biographies it was stressed that the co-discoverer of the principle of natural selection was an eminent scientist: evolutionist, naturalist, biogeographer and anthropologist (Raby 2001, Shermer 2002). In spite of this late recognition by two authors the striking differences in emphasis and content between the Darwin-Wallace papers, as outlined in this historical review, have been largely ignored (Futuyma 1998, Gould 2002).

If we take into account that Wallace (1895, 1889) defined the bio-species as a reproductive community of organisms that inhabits a distinct environment and that he rejected Lamarck's (1809) concept of the inheritance of acquired characteristics there remains only one conclusion: A. R. Wallace was "the second Darwin" who contributed substantially to the rise of the new field of evolutionary biology. This naturalist should no longer be regarded as a person second in rank compared to the much more famous Charles Darwin. As Dawkins (2002) pointed out, we should use the term 'Darwin/Wallace-mechanism of natural selection'. In addition, it is appropriate to regard Wallace as one of the founders of the Biological Species Concept and of Neo-Darwinism.

With respect to the theory of sexual selection, Darwin (1859, 1872) developed this novel concept but did not describe the function of this behaviour (for instance, the role of the male peacock's tale). As Dawkins (2002) has pointed out, it was Wallace who speculated that a male with bright coloured tail feathers is showing that he is a high-quality individual. Subsequent studies have shown that this idea is supported by experimental evidence (Møller and Alatalo 1999). Hence, with respect to the second mode of selection in nature, Wallace developed the concept originally proposed

by Darwin (1959, 1872) and did draw the correct conclusions. At old age, Wallace converted to become a spiritualist, a behaviour that took many of his collegues by surprise (Raby 2001, Shermer 2002). In spite of this unfortunate development of the late A. R. Wallace, this naturalist was one of the most original thinkers and a major pioneer of evolutionary biology.

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