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Haldane's view of natural selection

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Abstract. Among many things, J. B. S. Haldane is known for demonstrating how the principle of natural selection can be used to build a mathematical, and in particular quantitative, theory of evolution. However, to the end, he remained open to the idea of other evolutionary mechanisms. In his late writings, he repeatedly drew attention to situations in which natural selection did not operate, was hemmed in by constraints, or worked in a surprising manner. In this respect Haldane stands out among the architects of the Modern Synthesis.

Keywords. evolution; modern synthesis; alternatives to natural selection.

Introduction

J. B. S. Haldane was among the leading contributors to the clarification of the evolutionary process that emerged in the first half of the 20th century, variously referred to as the neo-Darwinian Synthesis, Evolutionary Synthesis or Modern Synthesis. He also pioneered the study of enzyme catalysis and initiated the union of biochemistry and genetics. The title page of his 1932 book (Haldane 1932a/1990), which identifies him as Professor of Physiology, Reader in Biochemistry and Head of Genetical Department—in three different institutions—, gives an indication of his versatility, not to speak of energy. He was a peerless communicator, known equally for his technical and popular writings (see Clark 1984 for a full-length biography of Haldane; Nanjundiah 1992 contains a brief description of his life and science). Haldane was a great believer in the importance of explaining science in ordinary language without compromising on accuracy. More than once an original contribution to biology was made by him in a newspaper article or essay meant for the general public. For instance, his first analysis of the Origin of Life problem was in *The Rationalist Annual* (Haldane 1929. At times, Haldane's idea remained submerged in a newspaper or periodical until someone else came up with it independently; on this occasion A. I. Oparin had anticipated him). Writing for the public, he was compelled to get across the gist of what he wanted to convey as simply and directly as possible. As his most famous student put it, '… he [had] a genius for taking a complex biological problem and simplifying it to the stage at which it could be posed in mathematical form, without at the same time distorting it out of recognition. It was this same gift for simplifying without distortion which he used in his essays, and in his weekly articles in *The Daily Worker*' (Maynard Smith 1965). Haldane's justification for the effort was that '…the public has a right to know what is going on inside the laboratories, for some of which it pays' (Haldane 1940, Preface, p. 7). The writings were informative, entertaining and provocative, often with an aim to arouse interest by startling the reader. According to his colleague Pirie, only Haldane could write two articles with the titles 'Why I am a materialist' and 'I am not a materialist' without being inconsistent (Pirie 1992). No wonder Haldane characterized both himself and his work as *S.D.T.C.* ('somewhat difficult to classify'; Jayakar 1966).

During the last seven years of his life, which were spent in India, he carried on working at the same intensity as before. If anything, the range of issues he tackled had widened. They included general science, natural history, logic, Indian philosophy, religion, statistics, evolutionary theory and mathematical genetics (Rao 2013, 2015). Haldane was extraordinarily nondogmatic in scientific matters, and the present article illustrates this with examples from his late nontechnical writings. In them, he argued forcefully in favour of unorthodox ways in which evolution could act, ways that downplayed the importance of the means to evolutionary change most associated with the names of Darwin and Wallace, namely natural selection.

The sufficiency of natural selection for explaining evolution has been, and remains to this day, contested on several grounds. In the years after Darwin's death in 1882 many thought that natural selection was either unnecessary or entirely off the mark and the feeling intensified after Mendel's laws were rediscovered in 1900 (Mayr 1982). What opinion did Haldane, one of the chief architects of post-Darwinian evolutionary theory, hold? It is uncontested that Haldane worked out the mathematical consequences of natural selection in detail and demonstrated that theory and observation matched; typically, he did so with numbers ('A satisfactory theory of natural selection must be quantitative'; Haldane 1924). The late writings show that at the same time, he kept advocating the importance of looking into explanations for evolution that differed from neo-Darwinian orthodoxy, at times radically.

We start by situating what is to come within the twin contexts of the migration to India and the development of the Modern Synthesis. Next we take up Haldane's late thoughts on evolution as expressed in nontechnical pieces, three of which were published after the move. Towards the end we reiterate that his views were consistent, not just with what he had said earlier, but in part also with Darwin, and point out that they remain relevant even today.

Haldane in India

Haldane and his wife Helen Spurway emigrated from Great Britain to India on July 1957 and took up Indian citizenship in 1961. There were many reasons behind the move. On Haldane's part, they included unhappiness with the foreign policy of the then British government, what he thought were promises regarding offers of positions at the John Innes Institution and University College London being broken repeatedly, and a fondness for India that he had long had, a feeling that Spurway came to share (Rao 2015). Haldane died in Bhubaneswar, Orissa, on 1 December 1964. In between he was Research Professor at the Indian Statistical Institute (ISI), Calcutta, left ISI to establish a short-lived Council for Scientific and Industrial Research (CSIR) unit, also in Calcutta, and finally, in July 1962, established a Genetics and Biometry Laboratory in Bhubaneswar.

While remaining engaged on his own research, he was closely involved in the work of his Indian students and colleagues, especially in the areas of human genetics, quantitative biology and evolutionary theory. He assisted in efforts to strengthen research in the biological sciences in universities and laboratories in several places in India. His belief in the importance of building scientific relations and encouraging collaborations across countries was such that he went to the extent of financing a World Health Organisation project from his own pocket (the project was aimed at identifying genetic predispositions for resistance to malaria and involved field work in south India by the Italian geneticist Marcello Siniscalco; see Rao 2013). Haldane thought that the tropics were ideal for the study of evolution, and that India was one place where it was possible to carry out high-quality research in biology with simple and inexpensive equipment. The lack of sophisticated instruments was no bar to doing interesting science; if anything it offered many advantages, the main one being the wealth of information that could be gathered by careful observations on the rich plant and animal life all around. As he put it more than once, '…plenty of things can be done here that can't be done in London or Long Island' (Haldane to Demerec 1958). To help that belief to be realised, he stressed the importance of using statistics as much in the design of experiments as in the analysis of data—not a common attitude among biologists even now.

During the seven years in India, Haldane wrote technical papers in several areas, among them the origin of life—a subject whose elevation to the status of a scientific question owed as much to him as to A. I. Oparin (see the accompanying piece by Tirard 2017)—, genetics, evolutionary theory and mathematical aspects of natural selection. Shortly before his death, in the course of rebutting Ernst Mayr's attack on the achievements of population geneticists, he gave a brilliant exposition of the role of mathematical modelling in biology (Haldane 1964, discussed in Rao and Nanjundiah 2010/2011). In addition to that, Haldane remained attentive to the importance of communicating to the general public. He continued to write for newspapers and spoke on the radio, on topics as wide ranging as science, religion, astronomy, philosophy and problems with the Indian education system. Overall there were about 150 articles from the stay in India, 50-plus scientific papers including some with Jayakar that took up Haldane's old interest in natural selection as a force for conservation rather than change, by showing that selection intensities that varied in space or time (e.g. across generations) could result in balanced polymorphisms (e.g. Haldane and Jayakar 1963) and 50-odd short pieces that appeared in *The Hindu* newspaper. Throughout his last years, Haldane kept reassessing the causes of evolution (which was also the title of his famous book).

The Modern Synthesis

A broad consensus regarding the means through which biological evolution operated had developed by the 1950s (Mayr and Provine 1980/1998). Following the title of a book by Julian Huxley (Huxley 1942) it has come to be called the Modern Synthesis, and also the Evolutionary Synthesis or the neo-Darwinian Synthesis. Investigations in many fields contributed to it. They included Mendelian genetics, cytology, population genetics, studies of genetic and chromosomal variations in nature, natural history, systematics and palaeontology (it is generally agreed that biochemistry and embryology began to get incorporated much later). The Synthesis showed that Mendelian genetics was consistent with the principle of natural selection as formulated by Darwin and Wallace and as a result, there was widespread agreement that evolution by natural selection was the correct way to understand most features of living organisms. But disagreements persisted on when, and to what extent, one had to take seriously the possibility that evolution could take place without the action of natural selection. Depending on the phenomenon to be explained, major changes resulting from systemic mutation, chance factors, the locked-in nature of developmental processes and population structure were all put forward as plausible candidates (a situation which persists).

Haldane's thoughts on evolution are of particular interest in this context. He began a series of papers on the mathematical theory of natural and artificial selection in 1924. Some years thereafter he took the opportunity afforded by an invitation to give a series of lectures to develop a personal perspective on the evolutionary process; it was published as *The causes of evolution* (Haldane 1932a/1990). Along with natural selection, the book mentions other routes to evolutionary change including mutations with major consequences and chance (drift). As early as 1932, Haldane did not view Darwinian natural selection as an all-encompassing hypothesis for evolution. In the book he said (pp. 138–139) 'But if we come to the conclusion that natural selection is probably the main cause of change in a population, we certainly need not go back completely to Darwin's point of view. In the first place, we have every reason to believe that new species may arise quite suddenly, sometimes by hybridization, sometimes perhaps by other means. Such species do not arise, as Darwin thought, by natural selection.' As the later writings show, he retained this attitude till the end. If anything, he seems to have become more convinced than ever that natural selection was not the sole reason for evolutionary change.

Haldane's late views on natural selection

For illustrative purposes we concentrate on four pieces, *Natural selection* (Haldane 1955a), *The present position of Darwinism* (Haldane 1958), *The theory of natural selection today* (Haldane 1960) and *Natural selection* (Haldane 1959). They are based, respectively, on talks given at a meeting in Calcutta held in honour of the 70th birthday of D. M. Bose (a pioneer of research in cosmic ray in physics), at the 45th session of the Indian Science Congress in Madras and at the 'Centenary and Bicentenary Congress of Biology in commemoration of the works of Darwin, Wallace and Linnaeus' held at Singapore; and on a paper written for a volume also brought out to mark the 100th anniversary of publication of *The origin of species.*

In these writings Haldane refers to natural selection as one of a group of theories about our distant past along with geology and cosmology. Thanks to palaeontology, many facts of evolution have been as well established as those of historical geology or those of cosmology, if not better. Now that it is a century old, 'Darwin's theory of natural selection, like any other century-old scientific theory, cannot be accepted as it stands. … It is instructive to ask what are the most important facts discovered in the last century which, had he known them, would have induced Darwin to formulate his theory differently' (Haldane 1958). Even though an admirer of Darwin, he cautions scientists against believing in everything Darwin had said. Among the many new discoveries made in the 100 years since Darwin presented his paper to the scientific world, Haldane stresses the importance of some: the particulate nature of inheritance; the distinction between phenotype and genotype; the realization that selection can maintain diversity, not only cause change; the feature known as allopolyploidy; and limitations imposed on natural selection by development. We will take up the last three, specifically the contentions that (i) Natural selection is more an agent for conservation than innovation; thus it does not function in the manner that Darwin and Wallace believed it did; (ii) sometimes major changes in evolution can take place abruptly, without the intervention of natural selection; and (iii) the scope of natural selection is constrained by the nature of the developmental system. Haldane's summary description of natural selection provides the backdrop: 'Heredity could be defined statistically as a positive correlation between characters in a group of ancestors and their descendents, which is not due to a positive correlation between the environments of ancestors and "descendants"', and 'All species vary. But not all variations are inherited. Natural selection discourages most variations from the structures and functions normal in a species. It encourages a few variations; and if these are inherited evolution will take place' (Haldane 1960, he is uncertain whether 'inherit' is the right word to use, because it can be applied to a property and to a character equally.)

(*i*) ***Natural selection tends to foster stasis rather than change***: Unlike what was believed by those who took natural selection as a valid explanation for evolution, Haldane reminds us that much of the time natural selection is centripetal; it promotes stasis rather than change (but centrifugal selection comes into play when crosses between species result in infertile hybrids). In other words, it tends to reduce the variance of a trait rather than to affect its mean. This goes against naïve expectation—at least, 'the process observed is not very like what Darwin imagined… Its main effect is to stabilize species by weeding out abnormal individuals of various kinds. In most situations only a tiny fraction of the selection which occurs has any evolutionary effect' (Haldane 1955a). One must stress that here Haldane is not arguing against natural selection (or its sufficiency), but is saying that Darwin and Wallace would not have expected it to operate so. 'We see that in these cases natural selection, so far from causing species to change their character, brings them back towards the normal if they diverge from it. In addition, it is natural selection which plays a large part in conserving the differences between species…Now this is a most surprising situation. Darwin postulated natural selection to explain evolution, i.e. to say a certain kind of change. With some difficulty it has been discovered and measured, and in the best observed cases it has been found not to cause change but to oppose it' (Haldane 1958).

Mutation, migration and segregation act to keep gene frequencies stable. Recurrent mutation permits the retention of rare alleles that are deleterious when homozygous. If different allelic combinations are favoured in different regions, migration allows genetic polymorphisms to persist; and because of Mendelian segregation, alleles that lead to low fitness when homozygous are retained in stable equilibrium if the heterozygous condition leads to the highest fitness (e.g. the sickle cell and wild-type alleles in a malarial environment). Haldane alludes to two other examples of balancing selection where the genetic basis is not known: Karn and Penrose (1951) had found that new-born babies with birth weights close to the mean had a lower mortality than those at either extreme, and Cain and Sheppard (1950) observed that predation by birds was the balancing agent responsible for maintaining a polymorphism in the snail Cepea: 'During the early spring when there were few leaves, the yellow snails were killed preferentially; later on when the leaves were green, they were preferentially spared' (Haldane 1958). He mentions the distinction made by Waddington between normalizing and stabilizing selection and points out that both correspond to centripetal phenotypic selection (Haldane 1959).

(ii) ***Evolution can occur in jumps***: 'Darwin thought that evolution worked by imperceptibly small steps. Today we know that some of the steps have been fairly abrupt; and this is the main modification to which the account of evolution given a century ago must be subjected' (Haldane 1960). Haldane states that species differences between descendants of a common ancestor are striking examples of major evolutionary change. Darwin thought that varieties were incipient species, and that speciation was the outcome of gradual adaptive natural selection occurring for a long time in different lineages, until individuals from the two lines were no longer able to breed. There are indeed examples of differences among related species being correlated with several single gene differences, but in other cases chromosome-level differences are involved (he cites the work of Spurway, Lantz and Callan on newts). In general, it is difficult to establish by genetic experiments that speciation is based on the spread of different alleles in two lines. A fertile hybrid raises the question of whether the parents belonged to different species at all, and a sterile hybrid makes the experiment infructuous. Besides, as Darwin had stressed, natural selection via the accumulation of adaptive changes is necessarily a slow process. Among other reasons, this must be so because adaptations involve several genetic changes, and intense selection acting simultaneously on many loci can cause numbers to fall so drastically that the species is at risk of going extinct. Haldane draws attention to exceptional situations such as the very rapid evolution by natural selection of melanism in the normally 'peppered' moth *Biston betularia*, which he himself had worked out (Haldane 1956). He directs attention to the fact that, unusually, the switch between the two morphs appears to be correlated with change at a single genetic locus that alters the phenotype at one go without an entire developmental system being modified.

Allopolyploidy (polyploidy in which the chromosomes come from parents belonging to different taxa), which is well known in several plant groups, is alluded to repeatedly: 'We now come to a fact which would have surprised Darwin considerably, and which is perhaps the most important correction which must be made to his theory of the origin of species' (Haldane 1959). The significance of Kihara, Ono and Winge's contributions is highlighted: 'It is probable that Kihara has made the most important amendment to Darwin and Wallace's account of evolution as a historical fact' (Haldane 1960). Allopolyploidy causes chromosome combinations that result in the abrupt appearance of an entirely new species, i.e. its appearance within a single generation. This happens without any involvement of natural selection whatsoever (except, presumably, to the extent that selection would weed out inviable polyploids). 'However, such species have not arisen as the result of natural-selection, and therefore constitute a genuine exception to Darwin's conclusion' (Haldane 1959; presumably natural selection would shape the subsequent evolution of the newly arisen species).

Another way for an entirely new form to evolve rapidly, Haldane says, is via a change in timing of gene action (an early insight of his; Haldane 1932b). The possibility had come to light thanks to the work of Garstang, Bolk, de Beer and others; neither Darwin nor his followers had the least inkling that such a thing could happen. For instance, many animals go through an immature larval stage which is specialized for its own kind of life. If there is a shift in the temporal pattern of development so that reproduction occurs when some or most of the nonreproductive organs are still in the larval stage, the outcome may be the appearance of a hitherto unknown form of adult. Copepod crustaceans and the Axolotl provide examples. Haldane refers to something similar that has played an important role in human evolution. For example, a chimpanzee does not mature till about eight years compared to a human being who matures about 16 years and never develops many of the characters of adult apes, nor that of other mammalian groups. Because the embryonic character of cranial flexure has been preserved in human beings, their eyes are directed forwards. (Interestingly, the concept of heterochrony–the contemporary term—has been traced back to Haeckel; see Hall 2003.)

(iii) ***Evolution is not open-ended***: 'Can natural selection explain evolution? If Darwin thought that he could, this was perhaps because he thought that members of a species varied in all possible directions, and natural selection could favour any kind of variation. This is probably not so. Only certain kinds of heritable variations seem to be possible in any particular species' (Haldane 1960). Developmental constraints are weak in some groups and strong in others. Lantern flies (Fulgoridae) vary a great deal in the morphologies of their body parts whereas fruit flies do not: 'It is at least possible that developmental processes are less integrated in this family than in most insects, so that a mutant with a large outgrowth from its thorax is otherwise normal. This is not the case with *Drosophila,* for example' (Haldane 1958). Extreme selectionists assumed that variations in all directions were possible, which amounted to believing that the scope of natural selection was unlimited. This cannot be true, says Haldane, because all conceivable types of heritable variation are not possible. In any species, the integration of developmental processes acts as a constraint on the variation that is permitted: 'Natural selection can decide which path or paths will be taken. It cannot force a species to take a path not open to it' (Haldane 1958).

Contemporary relevance and antecedents

There is much else that Haldane cites in the pieces referred to as worthy of examination. He takes as demonstrated that grafting can lead to (genetic) hybridization and says the 'Michurinist' findings of Benoit (see Ho 2009) should be looked at carefully (Benoit contended that the injection of DNA from a donor to a host duck could induce heritable modifications of pigmentation and morphological characters). He refers to Lysenko's claim of transforming winter wheat into spring wheat, adding it 'may be important for agriculture but had little bearing on evolution' (see accompanying article by deJong-Lambert 2017). He says animals can actively choose their environments, which implies that one has to take a second look at the notion of adaptation 'to' an environment. He explains how an instinct can evolve—in small steps, through natural selection—by means of genetic assimilation, and why learning is more important when animals live in social groups of unrelated individuals (e.g. bird flocks) than in groups of relatives (e.g. honeybee workers): '…just because the birds in a flock are not brothers and sisters, a novel type of call note will not be automatically understood. Hence birds have to learn many of their call notes. The fact that an insect society is a family makes an unlearned language possible' (Haldane 1958). Here, and in his discussion of how genotypic selection differs from phenotypic selection, one is reminded of his original thinking on the role of shared genes in the evolution of 'altruistic' behaviour (Haldane 1955b). Haldane and Spurway's intense engagement with the topics of mind and behaviour in evolution deserves a separate discussion (see accompanying article by Bateson 2017).

Haldane's seeming heterodoxy with regard to evolutionary mechanisms invites four comments. First, on the whole he remained a committed selectionist, and when he put forward an alternative, he was not thinking of an evolutionary framework that could entirely supplant natural selection. Second, as stated, it was by no means a novel stance on his part, nor, one should add, were Wright, Fisher or Chetverikov unwilling to accept nonselectionist elements in their evolutionary picture, though they may not have written as much, or been as outspoken, about it as Haldane. Already in 1932—in *The causes of evolution*—he mentions speciation via allopolyploidy as a means whereby evolution can take place other than by conventional natural selection; he also discusses there the probability of gene fixation via a combination of selection and chance and the evolution of altruistic behaviour via selection at the supra-individual level. It is interesting that Haldane remained firm in his views, because his engagement with population genetics had flagged over the previous 20–30 years. Third, the relevance of nonstandard attitudes to evolution continues to be discussed—and disputed—today. Balancing selection (Charlesworth 2016), speciation occurring abruptly, or other than by the accumulation of small genetic differences and as a consequence of chromosomal mechanisms (Forsdyke 2017), hybridization through grafting (and in an extra twist, via the formation of an allopolyploid; Fuentes *et al.* 2014), organisms shaping their own environments (Scott-Phillips *et al.* 2014) and developmental constraints (Arthur 2002, Hall 2003) are all themes in the contemporary biological literature.

Fourth, and perhaps most importantly, Darwin's (and more so Wallace's) name tends to be associated with the advancement of natural selection as 'the' way in which evolution took place. But, even if one disregards Darwin's well-known Lamarckian leanings and Wallace's doubts regarding the origin of the human mind, that is simply not true. Darwin had made that clear: '…I am convinced that Natural Selection has been the main but not exclusive means of modification' (Darwin 1859, p. 6). For example, he laid great stress on the capacity of developmental constraints, in his words 'laws of growth' or 'laws of correlation', to restrict the directions in which natural selection could act. Consider, for instance, his referring to the difference between the inner and outer flowers of some plants as an example of 'the importance of the laws of correlation in modifying important structures, independently of utility and, therefore, of natural selection' (Darwin 1859, chap. V, 'Laws of variation', p. 144). Craw (1984) goes so far as to state that on many occasions Darwin thought 'laws of growth' were more important than natural selection. As for Wallace, in the famous joint publication[1] (see note at the end of the text) with Darwin he postulated a principle of balance in living organisms, 'a deficiency in one set of organs always being compensated by an increased development of some others' and compared it to the feedback (as we would say today) inherent in the working of the governor of a centrifugal engine, 'which checks and corrects any irregularities almost before they become evident' (Darwin and Wallace 1858). The implication is that in a complex system that functions near-optimally, the interactions between its components are such that they do not permit certain forms of variation in the system. There are intriguing parallels between developmental constraints, Darwin's 'laws of growth' and Galton's 'organic stability' (Gillham 2001), and we can add Wallace's 'centrifugal governor' to the list. Whether developmental constraints only close a few doors, so to speak, or can lead to genuinely explanatory hypotheses, is another matter (see Charlesworth *et al.* 1982). More recently Bonner (2013) has drawn on Darwin's views in support of the thesis that morphological variation in microorganisms is often neither advantageous nor disadvantageous and can get fixed by chance. The possibility of abrupt speciation is the one thing Darwin may have ruled out. Curiously, as early as 1909, William Bateson had proposed a model based on natural selection (!) for the evolution of reproductive barriers between temporarily isolated subpopulations of a species (cited in Bateson 2002, along with an interesting modification of the basic theme).

Summing up

It has been remarked that unlike what is true of the other founders of population genetics, Haldane's picture of evolution was not underpinned by a single dominant idea. With the name of R. A. Fisher one tends to associate panmixis and natural selection; Wright is remembered for stressing the importance of populations that are subdivided into small endogamous groups between which genes are exchanged only occasionally; Chetverikov for emphasising the significance of a large reservoir of cryptic genetic variation in nature (Adams 1980, p. 262). In this respect Haldane was the outlier. According to Crow 'He never argued for any particular hypothesis. He was open-minded to a fault' (Crow 1992). Edwards (2011) argues that the approach of Haldane and Wright were analytic, whereas that of Fisher was synthetic and so more akin to Darwin's. In the course of comparing Haldane with Fisher and Wright, Leigh declares that he did not found a system (Leigh 1990). In trying to probe why, Leigh poses the rhetorical question 'Did his sense of the mysteries of life put him off system building?', and quotes Haldane's own words that suggest as much. As we have said, Haldane stood by natural selection as the basis for adaptive evolution. But it was vital to keep checking whether natural selection was likely to explain any given evolutionary phenomenon, because 'No important event has only one cause' (Haldane 1960). He went on to draw special attention to the many circumstances in which the operation of selection is restricted. It is hemmed in by developmental constraints; even when it acts, it need not lead to change, in fact it can be an agency for preserving the status quo; and significant evolutionary change, most prominently speciation, often takes place without the intervention of natural selection at all. When it came to considering how evolution worked, he was never reluctant to question what others took for granted. The diversity of his interests, his readiness to take up unpopular causes, his opposition to authority, are all of a piece with his openness to the idea of natural selection being in peaceful coexistence, as it were, with other evolutionary pathways.

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Note

[1]Is it correct to refer to the 1858 presentation to the Linnean society of Darwin and Wallace's thoughts as a joint publication? In the page of the Darwin Online site (http://darwin-online.org.uk/content/frameset?itemID=F350&viewtype=text&pageseq=1) that deals with the presentation, the head of the printed version of the original carries the title 'On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection'. In their introductory note Lyell and Hooker refer to 'The accompanying papers' and proceed to list three. Numbers I and III are the well-known contributions of Darwin and Wallace; II is an abstracted version of Darwin's 1857 letter to Asa Grey. I carries the long title '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'. III is titled 'On the tendency of varieties to depart indefinitely from the original type. By Alfred Russel Wallace'. A comparison of the words within quotation marks indicates that the title of the whole—i.e. of the substantive part of Lyell and Hooker's communication—is quite different from the titles of parts I and III. This makes us conclude that in effect, what was presented to the Linnean Society on July 1st, 1858, was a joint paper, or at least was considered to have the status of a joint paper. If this interpretation is valid, the Darwin–Wallace paper resembles acknowledged multiauthored publications in which individuals contribute distinct parts and each part is capable of standing on its own. The famous papers of Timoféeff-Ressovsky, Zimmer and Delbrück (Timoféeff-Ressovsky *et al.* 1935), and of Luria and Delbrück (1943), come to mind. The first contains three parts that deal with distinct but overlapping themes, one under the name of each author, and a fourth under all three names. The second carries a footnote saying 'Theory by M. D., experiments by S. E. L.' Of course in one important respect the comparisons do not hold, because Darwin and Wallace were writing—if one may so describe parts I and III—the same paper, though independently and in different words. It would be interesting to see whether there are other examples (multiauthored reviews?). Incidentally, a bibliographical note by R. B. Freeman (see http://darwin-online.org.uk/EditorialIntroductions/Freeman_TendencyofVarieties.html) would appear to support our view. Freeman says 'This famous paper originally appeared in the

Journal of the Linnean Society of London, Zoology' and later, 'The Darwin–Wallace paper'. In both cases the reference to the publication is in the singular. One might add that offprints of 'the paper' were prepared as a single unit, though that is not a major point.

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