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Introduction

To reprint edition of:

WALLACE, A.R. 1865.

On the Phenomena of Variation and Geographical Distribution as

illustrated by the Papilionidae of the Malayan Region.

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In the early days of Darwinian evolutionary theory, natural selection was viewed by Darwinists as the main cause of the origin of new species. This view is again coming into fashion, after a rather long hiatus for most of the 20th C. As is well known, the theory of natural selection first occurred to Alfred Russel Wallace of the theory of natural selection, during a bout of malaria on the island of Ternate, and his letter of 1858 on this topic to Charles Darwin, was published by the Linnean Society alongside Darwin's own ideas. The idea of natural selection brought the theory of evolution into its modern, scientific age.

After returning from his travels to the "Malay Archipelago" (as the islands of SE Asia were then known), Wallace addressed himself to scientific understanding of his and Darwin's (1859) theories of evolution via natural selection. In today's jargon, the title of Wallace's (1865) paper on Asian swallowtail butterflies, reproduced in this volume, would read something like "The Southeast Asian Papilionidae as a model system for the evolution of local varieties, geographic races, and species." This paper was read in 1864 at the Linnean Society. Wallace (1870) later emphasised the "model system" aspects of the work when he re-published the current paper as "The Malayan Papilionidae or Swallow-tailed Butterflies, as Illustrative of the Theory of Natural Selection."

Many evolutionists existed previous to 1858, but were primarily followers of Jean-Baptiste Pierre Antoine de Monet, Chevalier de Lamarck (usually known simply as Lamarck). One example of an evolutionist of this persuasion was the anonymous author of "The Vestiges of Creation" (later revealed to be Robert Chambers). Wallace read this work before embarking on his first tropical voyage with Henry Walter Bates. Another was Robert Grant, who had met and probably taught Darwin in Edinburgh, and who later became the first Professor of Zoology and Comparative Anatomy at my own institution on Gower Street, the newly-founded and rebellious University of London– now University College London. Lamarck and his disciples clearly understood the evolutionary nature of species, but were unable to suggest any very convincing mechanism. Lamarck thought that evolution was constantly driven onwards and upwards via a kind of ladder of creation, with the supposedly more complex mammals, especially humans, at the top. A primary mechanism for evolutionary change was the yearning or "need" ("besoin") for progress, driven in part by the inheritance of acquired characteristics. In this view, a giraffe's requirement for a longer neck to pull down ever higher branches would result in stretching of the neck, and the resulting longer neck was inheritable by its offspring. Darwin consulted widely with breeders of animals and plants, and had to conclude (apparently almost reluctantly), that the commonsense idea of inheritance of acquired characteristics was correct (Darwin 1859, 1875). In contrast, Wallace was convinced more by the purity of the idea of natural selection than by the abundance of erroneous data that clouded Darwin's beliefs; Wallace steadfastly denied any importance to Lamarckism throughout his life. As it turned out, Wallace was right to be suspicious, since the inheritance of acquired parental adaptations does not occur for genetic traits. Inheritance of acquired characteristics can work, in a sense, for the transmission of human culture, but our knowledge of DNA and genetics indicates that such a mechanism is virtually impossible for physical characteristics, and essentially never contributes to evolution in nature.

Natural selection, in contrast, provides a completely inanimate and naturalistic theory for evolution, which requires neither guidance by a deity, nor the teleological goal of "progress" suggested by Lamarck. This purely mechanistic view created some initial problems for the theory's complete acceptance, and indeed still does. However, in the long run, it also eventually led to a wide acceptance of the Darwin-Wallace evolutionary ideas by allowing evolution to be self-contained and assumption-free. Wallace's 1865 paper should be seen very much on this historical background. For Wallace, the important ultimate goal for this very long paper was to address the problem of species and the role of natural selection in their origin. This goal of understanding the evolution of species had indeed been central to the original plans he had made with Henry Walter Bates xx years earlier, when they planned their first trip to the Amazon together (my life? Bates?).

Bates' paper on mimicry in South American butterflies as a forerunner

Wallace's treatise on SE Asian swallowtail butterflies consists of a careful systematic revision of the Papilionidae, together with an extensive introductory section in which he details the importance of the data to understanding local and geographic variation and the origin of species. It followed and seems closely modelled on the similar paper in the same journal by Henry Walter Bates (1862) on the "Heliconidae" (heliconiine, danaine and ithomiine butterflies) of the Amazon basin.

Bates' paper, like Wallace's, consisted of a systematic revision, as well as a long introductory section about natural selection and the origin of species. Bates (1862), like Wallace, used a rather unprepossessing title: "Contributions to an Insect Fauna of the Amazon Valley," which greatly disguises the importance of the paper. Today, this paper is chiefly recognized as the first to provide an evolutionary theory of mimicry which relied entirely on natural selection, a result admired by Darwin himself, who also expressed frustration at its burial in a long systematic paper with a cryptic title (Darwin 1863). Bates describes in particular how the colours of certain butterflies allied to the cabbage white butterflies, which he called "Leptalides" (now Pieridae: Dismorphiinae), copied local members of the "Danaoid Heliconidae" (now Danainae: Ithomiini) and "Acraeoid Heliconidae" (now Heliconiinae: Heliconiini). Wallace immediately understood and enthusiastically adopted Bates' theory of mimicry, which forms a major component of Wallace's paper. It seems to have been generally known before Bates' paper that certain palatable flies, beetles and moths were mimics of stinging wasps, although mimicry had hitherto never been explained as a result of natural selection. Bates's insights were far better documented than earlier ideas, and come from several special features he was the first to recognize in the Ithomiini, Heliconiini and Dismorphiinae system.

The first feature that Bates understood from his butterflies (as did Wallace) was the importance of geographic distribution in natural selection. Bates had not recognized mimicry in the butterflies he had collected before returning to London. As he began to pin out his specimens, he describes how he suddenly noticed not just that nearly identical colour patterns were found in multiple unrelated species from the same area, but that the colour patterns of all these species or lineages would themselves switch every few hundred miles. This was as true for the multiple species of models in the Danaini and Ithomiini as for the copies or "mimics" in the Heliconiini and Dismorphiinae. Anyone who has captured Ithomiini or Heliconiini knows that most are clearly defended by pungent and noxious-seeming smells, and from this and their great abundance in the field Bates assumed they were protected from birds and other predators. Although he provided only anecdotal evidence based on observations of birds in the wild, later work has shown that Bates was absolutely correct (e.g. Brower et al. 1963, Chai 1986). Bates recognized that dismorphiine mimics were probably palatable, and today, where a palatable species parasitises the colour pattern of an unpalatable, protected species, we call the phenomenon Batesian mimicry in his honour. Bates also recognized that some rarer, unpalatable species, such as in the genus *Heliconius*, also mimicked Ithomiini, with exactly the same geographic pattern of switching colours. He argued (correctly) that the rare Heliconiini were protected by commoner Ithomiini, although he failed to understand why mimicry among pairs of extremely abundant species such as those in the genus *Melinaea* and *Mechanitis* could be favoured by natural selection.

Today, mimicry between pairs of unpalatable species is known as Müllerian mimicry, after Fritz Müller (1879), who provided a mathematical justification of why mimicry between poisonous species was favoured, and of how the benefits to each mimetic partner were split according to the inverse square of their relative abundance. It is clear that Bates had discovered Müllerian mimicry already. However, this is not to belittle in any way the tremendous achievement of Müller, who was the first to clearly understand its mechanistic and mathematical basis (Joron & Mallet 1998; Mallet & Joron 1999), but also who apparently produced the first mathematically reasoned theoretical argument in evolutionary biology.

Regardless of the type of mimicry, the feature that Bates had understood most clearly, and which most convincingly implicated natural selection, was parallel geographic switching of mimicry "rings" of Ithomiini, Heliconiini and their mimics across the Amazon basin. With dozens of species and lineages involved, and dozens of geographic switches, this geographic insight was the best evidence produced yet (and perhaps ever!) for the power of natural selection to affect variation in the wild. Wallace, as we shall see, completely agreed with Bates' deductions, and showed that both mimicry and geography had significant evolutionary effects elsewhere in the tropics.

The second major deduction of Bates concerned causes for the origins of species. Bates argued that natural selection for mimicry was the cause of geographic variation, but also that geographic variation led ultimately to the evolution of new species. After geographic variation had given rise to new forms, they might ultimately disperse until they overlapped in the same region, whereupon one outcome is that they could coexist but remain separate. If the different forms did not intercross, the result would be the coexistence of two species. Bates seems to have believed that selection on mimicry could in some way influence mating behaviour; he wasn't very specific on mechanisms, but his 1862 paper suggests that he found examples in the genus *Mechanitis* of closely related forms with different colour patterns not mating together; his travel book (1863) also suggests that he found similar examples in co-existing *Heliconius* forms. I believe that in some cases the poorly understood systematics of these groups had confused him, and that he in fact had found examples of good *Mechanitis* species that coexisted, or of *Heliconius melpomene* or *Heliconius erato* with red and black postman patterns coexisting with other species of heliconiines such as *Neruda aoede*, *Heliconius elevatus*, and *Heliconius demeter*. (This is no criticism of Bates, because we are still finding new, cryptic species in this group today.)

Darwin (1863) urged Bates to provide more detail for his findings that colour varieties of these mimetic butterflies became reproductively isolated, but as far as I know, Bates never did so. Instead, his later work concentrated on chiefly on beetles and managing the Royal Geographical Society. As a postscript, we now know that Bates' idea was correct in broad outline: there are examples of closely related *Heliconius* species that differ in mimicry ring; these are able to remain separate species in part because their mating behaviour depends strongly on the colour pattern (Jiggins et al. 2001).

In any case, in 1865, Wallace admired and frequently cited Bates' butterfly paper, and he was able to greatly amplify its results, as well as add new proofs of natural selection for mimicry, as well as the geographical nature of species in his Papilionidae paper.

Wallace's contribution

Wallace's 1865 paper has been misunderstood, I believe, largely because of its complexity, discursiveness, and length (71 quarto pages including a complete systematic revision and descriptions of around 20 new species, and additionally, 8 plates of engravings, which were laboriously hand-tinted in published versions), and partly because Wallace himself later underemphasised what I believe are some of the major contributions of the paper. Wallace republished abridged versions of the evolutionary introduction to his paper in various forms, first in 1864 in "The Reader", and later as Chapter IV of his book "Contributions to the Theory of Natural Selection" (1870).

Wallace's argument for the Papilionidae as the most advanced butterflies

Wallace starts out by arguing that butterflies provide an excellent group for testing theories of evolution, and then discusses whether Papilionidae are most advanced. There seems to have been some friendly banter amongst Darwinists about which was the top group of butterflies. Bates (1862) started the ball rolling by arguing that the "heliconids" (i.e. Ithomiini and Heliconiini) were most advanced, because, in company with the rest of the Nymphalidae, of the extreme reduction of their forelegs. Most Lepidoptera have three pairs of fully functional legs, but there is progressive diminution of the size of the forelegs in certain butterflies, particularly the Lycaenidae, Riodinidae, and Nymphalidae, in the latter of which the Ithomiini and Heliconiini belong. Wallace rejects Bates's argument on the grounds that degeneration of organs cannot be used to measure advancement. In contrast, Wallace argues that the 4-branched median wing vein, and Y-shaped "osmeterium" thoracic organ in papilionid caterpillars are true signs of advancement in the Papilionidae, indicative of novel additional traits or organs not present in other groups. A few years later, Trimen (1869) rejected Wallace's arguments, arguing that the Danaini are in fact the most advanced. However, Wallace (1870) re-issued his 1865 paper, and in a revised section, rebutted Trimen's arguments one by one. Trimen had argued that the reduction of limbs was indeed an advance because this led the butterflies to be more "aerial." Wallace (1870) argued that the argument that the most aerial were most advanced would also mean that swifts and frigate birds were more advanced than passerines; however "no ornithologist has ever so classified them." Instead Wallace argued that one of three groups of birds with highly developed feet – falcons, parrots, or thrushes and crows – had greater claim to be the most advanced. Wallace (1870) again argued for the Papilionidae as top butterflies.

In retrospect this argument is more amusing than informative: today, evolutionary biologists agree that since all extant groups have evolved and been tested by natural selection for exactly the same period of time, there is no objective way in which we can decide which groups are more "advanced." Nonetheless, the Papilionidae are often the group of butterflies treated first in typical books, even today (e.g. Scott 1986, Larsen 1991, Tolman & Lewington 1997), so perhaps Wallace's argument had some effect. On the other hand, R.I. Vane-Wright informs me (pers. comm.), that another reason for including the Papilionidae at the head of the butterflies may be that they are the most ancient lineage in the Papilionoidea. In essence, this is to argue the reverse: that the swallowtails are most 'primitive.'

Papilionidae and the evolution of new species

An important evolutionary part of the paper now begins. Here Wallace outlines his view of species, and the various kinds of variation at the subspecific level. "What is commonly called variation consists of several distinct phenomena which have too often been confused". Today's evolutionary biologists rarely read Victorian texts and tend to believe that Darwin and the Darwinists of the 1850s and 1860s were confused about species, and that this led to a very incomplete theory of speciation (Mayr 1982, Coyne & Orr 2004). Darwin discussed what he meant by species, of course, but he did not carefully describe variation at the subspecific level, especially when dealing with geographically distant populations. Most people can recognize species when they coexist (i.e. in "sympatry"), but the eternal problem in taxonomy is how to treat differentiated forms that occur in different areas (i.e. in "allopatry"), since the test of coexistence is not available. Modern commentators such as Ernst Mayr (1982) or Jerry A. Coyne and H. Allen Orr (2004) have claimed that Darwin (1859) did not understand the nature of species, and didn't answer the question posed by the title of his book.

I believe that Wallace's paper very much rebuts the notion that Darwinists had a poor understanding of the nature of species. Wallace gives a long discussion of geographic and non-geographic variation, and carefully distinguishes species from geographic races and local varieties or forms. He distinguishes: 1st, simple variability [equivalent to quantitative variation]; 2nd, polymorphism or dimorphism [discrete forms separated by morphological gaps, which nonetheless belong to the same species]; 3rd, local forms or varieties [clinal variation]; 4th, coexisting varieties ... a somewhat doubtful case [reserved for coexisting forms which differ in very few constant characters, but which seem to be separate species; 'sibling species' or 'ecological races' perhaps would be the modern equivalent]; 5th, [geographic] races or subspecies; and 6th, true species" (Wallace, 1865: 5-14). As far as I know, this is the first attempt by a Darwinist to enumerate and classify the geographical and non-geographical "varieties" that Darwin argued were the forerunners of species: the lack of a detailed discussion by Darwin is exactly what prompted Mayr (1942, 1963, 1982) and followers to accuse Darwinists of having failed to produce an adequate species definition. In fact, I believe that Darwin, as well as Darwinists such as Wallace and Bates, understood the nature of species very well, even in modern terms (Mallet 2004, and in prep., Biol. J. Linn. Soc.). Darwin himself, in what he always intended only as a brief "abstract" (1859) did not discuss species definitions in great detail. As a result, this 1865 paper of Wallace's is perhaps the best statement of the party line by an early Darwinist of what was meant by species in the new evolutionary age, and of how local and geographic variation within species was to be distinguished from that at the species level. Wallace's (1865) discussion is an important forerunner of similar discussions of geographic and non-geographic variation by E.B. Poulton and Karl Jordan, which themselves formed major influences on Mayr and others (see Mallet 2004). The main point of Wallace's argument is to show that it is hard to distinguish species from geographic subspecies, unless they overlap and show few intermediates.

Wallace, like Darwin, agrees that species are typically reproductively isolated but is inclined to reject a simple-minded application of the idea of reproductive isolation as a definition of species, on the grounds that reproductive isolation is a cause of speciation, so cannot also serve as a criterion: "Species are merely those strongly marked races or local forms which, when in contact, do not intermix, and when inhabiting distinct areas are generally regarded to have had a separate origin, and to be incapable of producing a fertile hybrid offspring. But as the test of hybridity cannot be applied in one case in ten thousand, and even if it could be applied, would prove nothing, since it is founded on an assumption of the very question to be decided – and as the test of origin is in every case inapplicable – and as, further, the test of non-intermixture is useless, except in those rare cases where the most closely allied species are found inhabiting the same area, it will be evident that we have no means whatever of distinguishing so-called 'true species' from the several modes of variation here pointed out, and into which they so often pass by an insensible gradation" (Wallace 1865: 12). Perhaps if this argument together with Darwin's arguments against "hybridism" being used as a hard-and-fast definition of species had been generally accepted, we could have seen a smooth transition from Darwinian thought to today's genetics-based understanding of evolution. However, it was not to be, and there are now many fruitless arguments about species definitions that are helping to distract attention from other more pressing problems in taxonomy, biodiversity and conservation (Coyne & Orr 2004; Isaac et al. 2004).

The extraordinary sex-limited polymorphisms of butterflies such as *Papilio memnon* and *Papilio polytes* were of major importance in leading Wallace to his view of sympatric species, and he seems to have been among the first to discuss their importance in print. Wallace (1865) was the first to collate evidence for female-limited polymorphism and mimicry in *Papilio*, especially for the Asian species we now call *Papilio memnon*, *P. polytes* and *P. aegeus*. This explanation relied on detailed morphological comparisons, unification of pairs of "species" where only males were known with others only known as females (e.g. *P. polytes*, *P. 'pammon'*), breeding data -- individuals emerging from eggs laid by a single female -- and from observations of pairs *in copula*. Wallace cites his own observations as well as published work and correspondence. A revealing citation is to a paper published by Benjamin D. Walsh in 1863. Walsh was an Englishman living in Pennsylvania, and yet another correspondent of Darwin's. Walsh was the first to show that the black form *Papilio glaucus* was conspecific with the yellow *P. turnus* in the Proceedings of the Entomological Society of Philadelphia. Later in the same year Walsh, in the same journal, proposed his own species concept based on interbreeding (Walsh, 1863: 220; see also Berlocher & Feder, 2002); the common topics of Walsh's and Wallace's papers in these few years after the publication of 'The Origin' argue, again, that the consensus of these scientists were not coincidental, but due to a constant flow of information between

Darwinists tackling similar problems, not just within the UK, but also internationally.

Wallace (1865: 10-11, footnote) imagines the situation if *Papilio*-like genetics were found among humans: "The phenomena of dimorphism and polymorphism may be well illustrated by supposing that a blue-eyed, flaxen haired Saxon man had two wives, one a black-haired, red-skinned Indian squaw, the other a woolly-headed, sooty-skinned negress -- and that instead of the children being mulattoes of brown or dusky tints, ... all the boys should be pure Saxon boys like their father, while the girls should altogether resemble their mothers. ... Yet the phenomena ... in the insect world are still more extraordinary; for each mother is capable not only of producing male offspring like the father, and female like herself, but also of producing other females exactly like her fellow-wife, and altogether differing from herself."

While I think Wallace's view that interbreeding, sympatric forms were members of the same species is today quite uncontroversial, he also tackles the much more difficult problem of which allopatric forms to call species, and which to call geographic races. Wallace employs a pragmatic definition of species, i.e.: "the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations" (Darwin, 1859: 484). But what to do about the forms isolated on different islands in the Malay Archipelago, where intermediate gradations could not occur because of the absence of a land connection? "The rule ... that I have endeavoured to adopt is, that when the difference between two forms inhabiting separate areas seems quite constant, when it can be defined in words, and when it is not confined to a single peculiarity only, I have considered such forms to be species. When, however, the individuals of each locality vary among themselves, so as to cause the differences between the two forms to become inconsiderable ... I class one of the forms as a variety of the other" (Wallace, 1865: 4).

Wallace touches here on a problem that has bedevilled application of the biological species concept since its inception. Mayr (1963: 29-30) highlights "the importance of a non-arbitrary definition of species", but also agrees that, in practice, some arbitrariness is unavoidable for forms that are not in geographic contact: "It cannot be denied that an objective delimitation of species in a multidimensional system [i.e. over large expanses of space or time] is an impossibility" (Mayr, 1963: 13). A solution like Wallace's is a practical necessity in this situation and it seems to me that this need to make a decision about allopatric forms isn't as fatal to the understanding of speciation as Mayr and his followers have claimed.

Examining the actual ranks that Wallace uses in his revision suggests that he tended to split species up geographically more than today's butterfly systematists would tend to do, especially in very brightly coloured and geographically variable groups. Wallace argues that the Malayan region is richer in Papilionidae than any other tropical region on the planet. However, "this superior richness is partly real and partly apparent. The breaking up of a district into small isolated portions, as in an archipelago, seems highly favourable to the segregation and perpetuation of local peculiarities in certain groups ... From this point of view, therefore, the superior number of Malayan species may be considered as apparent only. Its true superiority is shown, on the other hand, by the possession of three genera and twenty groups of *Papilio* against a single genus and eight groups in South America, and also the much greater size of the Malayan species" (pp. 27-28). Today, there are considered to be 10 genera of Papilionidae in the neotropics, as compared to S.E. Asia, considered to have around 10 genera among the taxa treated by Wallace here. Furthermore, "much greater size" doesn't seem such a major claim on superiority as it may have seemed to Wallace. We are left with the idea that perhaps most of the greater diversity of Malay Archipelago is "apparent." (N.B. A recent study has shown that the most diverse area of the world for Papilionidae was in a border region of NE India; see Haüser et al. 1995). In part, Wallace's inflation of S.E. Asian species diversity stems from the species concept he adopted. He often recognized disjunct forms on different islands as closely related members of the same lineages, but nonetheless classified them as separate species "when the difference between two forms inhabiting separate areas seems quite constant, when it can be defined in words, and when it is not confined to a single peculiarity only." Thus, he classified as separate species what are now considered three different island forms of the 'gloss swallowtail,' *Papilio ulysses*, on the grounds of strong morphological differences. For the New Guinea form *penelope* Wallace (= *Papilio ulysses autolycus* Felder), he argues: "As all the other forms closely allied to *P. Ulysses* have received names (*Telemachus*, Montr., *Chaudoiri*, Feld., *Telegonus*, Feld., and *Ulyssinus*, Westw.), I have also given one to this form peculiar to New Guinea and the Papuan Islands, the distinctive characters of which, though very slight, seem sufficiently constant" (p. 44). Similarly, several of the forms recognized as species by Wallace among the showy birdwing butterflies (*Ornithoptera*), are today regarded as subspecies.

Wallace could have recognized such obvious "replacement forms" as subspecies. However, in the 1860s, there was no International Commission of Zoological Nomenclature, and no recognized rules distinguishing clearly demarcated subspecies from local sports and variants – all were subsumed within the term "variety." So Wallace felt that as varieties, these clearly differentiated forms would not gain much publicity: in order to make sure that they were recognized as distinct, he felt he had to classify them as species. "Varieties ... continually get overlooked; in lists of species they are often altogether unrecorded; and thus we are in danger of neglecting the interesting phenomena of variation and distribution which they represent. I think it advisable, therefore, to name all such forms [i.e. as separate species]; and those who will not accept them as species may consider them as subspecies or races" (p. 12). Wallace is here admitting to taxonomic inflation, but in a good cause: in order to make sure that the forms are recognized as being on the speciation spectrum, even if future authors do not recognize them as full species (as is today the case). He does this quite openly, according to his criteria, given above, and also in order to draw other systematists' attention to the distinctness of the local form that he names as a separate species. In the late 19th C. and early 20th C., this problem of recognition of well-marked subspecific forms was formalized with the introduction of the trinomial Linnaean nomenclature, whereby subspecies could receive formal names, and indeed one of the major works to formalize this system was that by Rothschild [& Jordan] (1895) on the Papilionidae.

Overall, we can assess Wallace's work as follows. He well understood the spectrum of divergence between varieties and species, and after his extensive travels, the Papilionidae provided him with ample material to understand geographical variation and geographical speciation. From the evidence just presented, he clearly understood that he was inflating the importance of certain related forms found on different islands as separate species, but he frankly admitted the arbitrariness of his approach. His approach is in fact rather similar to the diagnostic delimitation of species as practiced by followers of Joel Cracraft (1989), an approach which has led to a great deal of recent taxonomic inflation among the vertebrates (Isaac et al. 2004), and which is also beginning to affect butterfly nomenclature (e.g. Tolman & Lewington 1997).

But although Wallace can perhaps be criticized with hindsight as a splitter of geographically identifiable subspecies into species, as a pioneer he surely has some right to make a few mistakes. He was, after all, the very first to make a detailed study on the topic of species delimitation and geographic variation in a post-1859 context. Reading the text carefully, I am continually impressed by how enlightened he appears, even compared to some of today's taxonomists. We should not forget that he wasn't working with 2007 knowledge, he was in fact the original developer of the ideas that later came to be used in Papilionidae and other butterflies, particular by Walter Rothschild, Karl Jordan and others. In fact, Wallace's 1865 and Bates's 1862 papers together were the first stabs at species delimitation that clearly acknowledged an evolutionary framework (see also Mallet 2004).

Parallel evolution

The final topic I would like to cover is the topic that, perhaps for Wallace, was the most important goal, and that was to collate geographic evidence for natural selection, and its involvement in speciation. This evidence is covered in two sections, entitled "Variation as specially influenced by Locality" (pp. 14-19), and "Mimicry" (pp. 19-22).

In the former section, Wallace notices some patterns which are rather baffling, and which have still not been explained, to my knowledge. "I find that larger or smaller districts, or even single islands, give a special character to the majority of their Papilionidae. For instance: 1. The species of the Indian region (Sumatra, Java, and Borneo) are almost invariably smaller than the allied species inhabiting Celebes and the Moluccas; 2. The species of New Guinea and Australia are also, though in a less degree, smaller than the nearest species or varieties of the Moluccas; 3. In the Moluccas themselves, the species of Amboyna are the largest; 4. The species of Celebes equal or even surpass those of Amboyna; 5. The species and varieties of Celebes possess a striking character in the form of the anterior wings, different from that of the allied species and varieties of all the surrounding islands; 6. Tailed species in India or the Indian region become tailless as they spread eastward through the archipelago" (p. 14). The "striking character of the anterior wings" mentioned was that the forewing is often more falcate (i.e. forked), and/or that the costa (i.e. the forewing anterior margin) is more abruptly curved. Wallace cites some 16 Celebes [i.e. today's Sulawesi] species in 9 groups of *Papilio* with these characters enhanced, as compared with allied species from surrounding islands, and figures the curvatures of the wings in line drawings of 6 pairs of species in Plate 8. He also argues that the same is true for some 10 species of Pieridae and some other examples from the Nymphalidae.

"The facts now brought forward seem to me to be of the highest interest" (p. 17), but what could be the explanation? The only papilionids which do not show this Celebes effect are the *Aristolochia*-feeding group now included in the Troidini, and which are frequently the objects of mimicry by *Papilio*. Wallace correctly assumes that the troidines are protected from predators, "probably in a peculiar odour or taste". In contrast, the other *Papilio* do not get such protection, and Wallace argues: "the arched costa and falcate form of wing [found in the *Papilio* of Celebes] is generally proposed to give increased powers of flight, or, as seems to me more probable, greater facility in making sudden turnings, and thus baffling a pursuer. ... It would thus appear as if there must be (or once have been) in the island of Celebes, some peculiar enemy to these larger-sized butterflies which does not exist, or is less abundant than in the surrounding islands" (p. 18). In spite of his travels, Wallace cannot come up with such an enemy, although he toys with ideas that it could be a bird or one of the larger dragonflies.

Plate 8 clearly shows the curved character of the Celebes wings, and their relative sizes. As far as I know, this rather puzzling effect of parallel evolution seems to be correct, and has never been investigated with modern methods (Vane-Wright & de Jong 2003). Rather than the average size, Wallace used the largest specimens from each island to make these claims, presumably to avoid the problem that a few adults in most butterfly populations are dwarfed by starvation as larvae when they eat up their whole foodplant; but still, a proper statistical analysis is therefore required. In retrospect, I wonder whether the larger size of the Celebes butterflies are the cause of the more abruptly curved costa and the more falcate wing tip; it would be easy to imagine the latter happening as a correlated effect of the extra growth on Celebes and Amboyna. In any case, even the size alone would provide powerful evidence of parallel evolution on Celebes. Dwarfism and gigantism on islands vs. mainlands has long been recognized in vertebrates, and is the subject of much debate even today (e.g. Case 1978, Lomolino 2005, Raia & Meiri 2005), and so a reinvestigation of the Celebes phenomenon in the Papilionidae would be of extreme interest. The Papilionidae and butterflies in general could provide much more powerful evidence of parallel evolution because of the much higher degree of replication in this group than in mammals, birds or reptiles.

Assuming Wallace's analysis is correct, he is way ahead of his time in pointing to this kind of parallel evolution as strong evidence for natural selection. If many different lineages independently evolve in a single direction, this is the best comparative evidence that natural selection, rather than random factors, is involved in producing the result. Today, parallel speciation is one of the strongest arguments for speciation by ecological causes (Schluter & Nagel 1995); the argument is precisely the same as that used by Bates and Wallace.

The second topic which provides evidence for local natural selection and parallel evolution is of course mimicry. We have already mentioned Wallace's evidence that Batesian mimicry explained the multiple female forms of species such as *Papilio memnon*, *Papilio polytes* and others. These female forms all mimicked protected members of the *Aristolochia*-feeding Troidini (at that time included within the genus *Papilio*). Wallace also recognized mimicry between palatable Papilionidae and unpalatable Danainae: that *Papilio*(= *Chilasa*) *paradoxa* and relatives mimicked a variety of *Euploea*, that *Papilio* (= *Graphium*) *thule* mimicked members of the genus '*Danaus*' (= *Parantica* and *Ideopsis*), and that *Papilio* (=

Graphium) *idaeoides* and others mimicked *Hestia* (= *Idea*) spp. Finally, he was also clear that a local form, *Papilio* (*aegeus*) *pandion* mimicked the protected *Drusilla* (=*Taenaris*) *bioculat*[*us*] in the Morphinae. He discusses why mimicry in some pairs of species should so often favour the female. According to Wallace, it is explained partly by Darwin's hypothesis of sexual selection – the male pattern seems more conservative in this group, and may be explained as a result of conservative female preference – and partly due to different habits of the males and females. Males are not so laden with eggs, and can therefore evade predators better, and so do not 'require' mimicry. All of these cases demonstrated that the Papilionidae of the region "have undergone an amount of special adaptive modification rarely equalled among the more highly organized animals" (p. 22). Once again, the extraordinary parallel geographic variation in mimicry between unpalatable model species and all of their mimics in the Papilionidae is an extremely strong argument for natural selection.

Conclusion

This work is perhaps the pinnacle of Wallace's achievement in science. In it, he describes more species than in any of his other systematic works. He lays out the detailed groundwork for today's theories of species and speciation, and carefully distinguishes between geographic and non-geographic varieties (or races) and species. And he produces some of the best replicated evidence for the power of natural selection to affect, not just single species, but whole groups of species at a time in terms of size, wing shape, and mimicry.

Wallace's paper also clearly demonstrates that Darwinists in the decade following the publication of 'the Origin' had a clear understanding of the nature of species;

it is difficult to sustain the frequent modern criticism (e.g. Mayr 1982, Coyne & Orr 2004) that Darwin and his followers misunderstood species, and that a better understanding had to wait until the mid 20th Century. Quite to the contrary: today's evolutionary view of species stem in part from this paper, via Poulton, Rothschild and Jordan, who all worked on the Papilionidae and had to carefully read Wallace's work (Mallet 2004). In addition, Wallace was a much more engaging writer than either Darwin or Bates: the paper is still a delight to read, and it is spiced with many extraordinary phenomena that bear further examination with today's modern tools of science, such as genetics and statistics.

References (ignore! this list of author-date pairs is for deletion)

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(Wallace 1870)

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(Wallace 1864)

(Trimen 1869)

(Scott 1986)

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(Mallet 2004; Mayr 1942)

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