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Perspectives

Poulton, Wallace and Jordan: how discoveries in *Papilio* butterflies led to a new species concept 100 years ago

Abstract A hundred years ago, in January 1904, E.B. Poulton gave an address entitled ‘What is a species?’ The resulting article, published in the *Proceedings of the Entomological Society of London*, is perhaps the first paper ever devoted entirely to a discussion of species concepts, and the first to elaborate what became known as the ‘biological species concept’. Poulton argued that species were *syngamic* (i.e. formed reproductive communities), the individual members of which were united by *synepigony* (common descent). Poulton’s species concept was informed by his knowledge of polymorphic mimicry in *Papilio* butterflies: male and female forms were members of the same species, in spite of being quite distinct morphologically, because they belonged to *syngamic* communities. It is almost certainly not a coincidence that Alfred Russel Wallace had just given Poulton a book on mimicry in December 1903. This volume contained key reprints from the 1860s including the first mimicry papers, by Henry Walter Bates, Wallace himself and Roland Trimen. All these papers deal with species concepts and speciation as well as mimicry, and the last two contain the initial discoveries about mimetic polymorphism in *Papilio*: strongly divergent female morphs must belong to the same species as non-mimetic males, because they can be observed *in copula* in nature. Poulton, together with his contemporaries Karl Jordan and Walter Rothschild, who had monographed world Papilionidae, were strongly influential on the evolutionary synthesis 40 years later. Ernst Mayr, in particular, had collected birds and butterflies for Walter Rothschild, and had visited Tring, where Jordan worked, in the 1920s. The recognition of different kinds of reproductive and geographic isolation, the classification of isolating mechanisms, the use of the term *sympatry*, and the biological species concept all trace back to Poulton’s 1904 paper. Poulton’s paper, in turn, inherits much from Wallace’s 1865 paper on Asian *Papilio* contained in the very book Wallace gave Poulton a month earlier. Wallace’s gift, and Poulton’s subsequent New Year address are thus key events in the history of species concepts, systematics and evolutionary biology.

Introduction

The term ‘biodiversity’ pays lip service to biological diversity at all levels, yet most discussions about biodiversity and its impending loss still focus on species. Recently, scientists have called for species-level taxonomy to be freely available online, and for species identification by means of ‘DNA barcodes’ (Godfray, 2002; Tautz *et al.*, 2003; Blaxter, 2003; Mallet & Willmott, 2003; Wilson, 2003).

It might seem absurd to be discussing the taxonomy and conservation of species so earnestly if the meaning of the term is not settled; yet that is exactly what we are doing. The

species has always been a source of dispute, at least since Linnaeus; but today there are probably more arguments about species than ever, as shown by the current avalanche of books and reviews on species concepts (e.g.: Claridge *et al.*, 1997; Howard & Berlocher, 1998; Wheeler & Meier, 1999; Wilson, 1999; Hey, 2001; Mallet, 2001; Cohan, 2002; Noor, 2002; Pigliucci, 2003; Sites & Marshall, 2003). It is a cliché that scientific opinions die with their authors rather than changing in the face of countervailing evidence. In today’s impasse, history might provide insight into the reasons for continual discussions about species. The kinds of questions we might ask of history are: How did we get into this pickle in the first place? How independent of pre-existing thought is each player in a debate of this kind? How novel are supposedly new ideas?

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Are superficially opposite ideas in reality facets of the same underlying principles?

Here I step back from the species debate itself to examine its roots in evolutionary biology and Darwinism. Edward Bagnall Poulton's (1904) lecture at the Entomological Society of London (now the Royal Entomological Society) and resulting publication 'What is a species?' was an early, but modern approach to species concepts. This is the centenary year of that paper. I trace the influences on Poulton's (1904) paper back to the early Darwinians, and also I show how Poulton strongly influenced posterity, particularly the 'Biological Species Concept' and the 'Evolutionary Synthesis' of genetics and speciation generally attributed to Dobzhansky (1935, 1937) and Mayr (1940, 1942). (By coincidence, 2004 is also the centenary of Ernst Mayr himself, who was born in 1904. I would like to take this opportunity to wish him many happy returns!) I am not a professional historian, and some historical links must be conjectured rather than proved, but I provide incontrovertible published evidence for some major interconnections between these ideas that seem of interest in the current debate.

Another aim of this paper is to show how lepidopterists in Britain a century ago, particularly those working on mimetic swallowtail butterflies (*Papilio*), played important but hitherto little-recognised roles in the development of modern ideas about species. I argue that Poulton, together with Karl Jordan and Walter Rothschild were at least as important as the American and German ornithologists who influenced Ernst Mayr (see Stresemann, 1975; Mayr, 1980, 1982), and as the Russian entomologists who undoubtedly were a key to Dobzhansky's views (Krementsov, 1994).

'What is a species?': Poulton's lecture

Poulton, as President of the Entomological Society of London in 1903, was required to give the annual Presidential Address. This took place on 20 January 1904. Why he decided on the topic of species 'conceptions' is not known, but it probably had something to do with a Christmas present he received from Wallace (see below). The published paper (Poulton, 1904, 1908) seems to have been read more or less *verbatim* during the address: it has lucid prose, a discursive style including many interesting if somewhat rambling digressions, and references to 'the purpose of the inquiry this evening'. [Note: for the sake of its more elaborate explanatory notes, I here refer only to pagination in Poulton (1908), a lightly edited version of the 1904 paper published in his book *Essays on Evolution*.]

Poulton first deals with the kind of criticism of Darwin (1859) with which we are now familiar (for another example, see Mayr, 1963: 12; 'Darwin failed to solve the problem indicated by the title of his work'). Poulton recalls a lecture by the 'late Professor Max Müller' in 1891, who argued that Darwin had written a great work on evolution, but that he had not solved the origin of species because the term 'species' was not defined. Poulton debunks this argument by citing Darwin's original text: '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 forms, whereas species were formerly thus connected' (Darwin, 1859: 484–485). Yet having shown that Müller's special criticism 'falls to the ground', Poulton agrees with his 'general exhortation' that we should re-examine the meanings of words, and proposes to investigate how the meaning of 'species' has changed from 'that of the years before July 1, 1858, when the Darwin-Wallace conception of Natural Selection was launched upon the world'. Here, it seems to me Poulton finesses the issue: if species need to be re-examined, the implication is that the Darwin-Wallace conception of species is inadequate.

Much later, Mayr (1942) clearly outlines the problem Poulton was in fact addressing. Darwin had used the term 'variety' loosely to include any form below the level of species, whether individual sports, local polymorphisms or geographic races. In the 1850s and 1860s, many geographic 'races' were themselves regarded as separate species, and the intergradations between them were interpreted as evidence for speciation as a result of gradual evolution. 'This complacent attitude . . . reigned supreme until the new biological species concept began to replace it' (Mayr, 1942: 113). By the turn of the century these races were being united, as subspecies, into 'polytypic' species. Forms were not considered specifically distinct unless their distributions overlapped without intergradation. 'Then it was suddenly realized by the more progressive systematists that those species between which they had found intergradation were their own creations, and not biological units' (Mayr, 1942: 113–114). Darwin had been making speciation too easy for natural selection by using a 'splitter's' concept; by 1900 'the more progressive taxonomists' were becoming 'lumpers.' (A 'splitter' is a taxonomist who 'cultivates the habit of discrimination to excess'; a 'lumper' is a taxonomist for whom 'Any two moths which are of approximately the same size and color are declared to belong to the same species . . . We are certain to have 'splitters' and 'lumpers' in the camps of science until time is no more'; see Holland, 1903: 112–113).

Furthermore, because a justification for the new polytypic or 'biological' species concept had been that it was the 'true' species concept, many believed by 1900 that Darwin's theory of natural selection could not explain the origins of these larger groups of races or 'true' species. 'As the new polytypic species concept began to assert itself, a certain pessimism seemed to be associated with it. It seemed as if each of the polytypic species (*Rassenkreise*) was as clearcut and as separated from other species by bridgeless gaps as if it had come into being by a separate act of creation. And this is exactly the conclusion drawn by men such as Kleinschmidt or Goldschmidt. They claim that all the evidence for intergradation between species in the past was actually based on cases of infraspecific variation, and, in all honesty, it must be admitted that this claim is largely justified' (Mayr, 1942: 114).

By the time Poulton was writing, and until the Evolutionary Synthesis of the 1930s and 1940s, there arose general scepticism about the importance of natural selection. Adaptation via inheritance of acquired characters seemed to explain gradual racial variation, and the new Mendelian geneticists

believed that the large gaps between species (gaps that were now obligatory if the forms were to be viewed as species) originated suddenly by means of radical mutations. Thus Darwinism was on the wane among both taxonomists and geneticists. During these bleak times for evolutionary thought, Poulton was one of the few still defending Darwin's views, especially via studies of mimicry in butterflies. He would have been keen to avoid undermining any facet of Darwinism. I believe this is why Poulton stops short of criticising of Darwin's species concept directly.

Poulton continues with a digression about the timeliness of the topic of species given the just-published correspondence of Darwin and Huxley for the understanding of the problem. This historical material is used frequently and in lengthy quotations throughout the paper. He then launches into the argument that his own speciality, the Lepidoptera, are 'pre-eminently fitted to supply examples for a discussion on species'. He quotes Bates (1863: Vol. II, p. 346) that on the wings of butterflies 'Nature writes, as on a tablet, the story of the modifications of species'. Then, in a long section, Poulton contrasts the 'conception of species' introduced by John Ray, Linnaeus, and Cuvier, with that of Darwin. The first is epitomised by Linnaeus: 'Species tot sunt, quot diversas formas ab initio produxit Infinitum Ens, quae formae, secundum generationis inditas leges produxere plures, at sibi semper similes': species are distinguishable or diagnosable forms ('diversae formae'), which were from the beginning ('ab initio') created by God, reproducing themselves forever in like form ('semper similes'). Poulton argues that Linnaeus' emphasis on fixed, created species, although perhaps vitally important for the introduction of a universal nomenclature, eventually ushered in evolutionary theory by promoting a false dogma that could be readily disproved by the evidence (see also Mayr, 1963: 13, who agrees with this analysis). By Darwin's time (Poulton here quotes letters from Darwin about his struggles with species-level taxonomy of barnacles) the difficulty of deciding what were species and what were not could no longer be brushed under the carpet as a minor detail; it was a central problem with the idea of unchanging species.

At the end of this section, Poulton lays down four definitions of 'the various groupings of individual animals and plants' important for his own conception of species.

1. 'Groups . . . defined by the Linnaean method of *Diagnosis* may conveniently be termed *Syndiagnostic*'.
2. 'Forms which freely interbreed together may conveniently be called *Syngamic*. Free interbreeding under natural conditions may be termed *Syngamy*; its cessation or absence, *Asyngamy* (equivalent to the *Amixia* of Weismann).'
3. 'Forms . . . descended from common ancestors . . . may be called *Synepigononic* [from *ἐπιγονος*, descendant]. Breeding from common parents or from a common parthenogenetic or self-fertilizing parent may be spoken of as *Epigony* or the production of *Epigononic* evidence.'
4. 'Forms found together in certain geographical areas may be called *Sympatric*. The occurrence of forms together may be termed *Sympatry*, and the discontinuous distribution of forms *Asympatry*'.

Diagnostic species concepts include the Linnaean morphological conception, as well as the more recent phenetic concept and also certain recent 'phylogenetic' species concepts that depend on fixed, diagnostic differences. Poulton shows that diagnostic definitions have the problem that geographic races, as well as polymorphic forms of mimetic *Papilio* butterflies, would be split into separate species if diagnosis alone were used. 'In immense numbers of cases it will be shown that the component individuals of a species do not form an unbroken series, but one that is sharply broken at one or more points. At each of these breaks the older systematist made a new species, which the modern systematist has rejected, because in his day the more fundamental criteria have been inferred.' (Interestingly, today the splitters are again at work and diagnostic species concepts are causing increasing numbers of geographic replacement series to become re-elevated to species rank). 'When the test of Diagnosis necessarily fails . . . the appeal is made to Syngamy and Epigony.' *Asyngamy* is none other, of course, than reproductive isolation (in particular, prezygotic isolation), while *epigony* refers to descent and phylogeny, and in particular monophyly.

Using different terms, Poulton therefore covers the gamut of possible species concepts in use today. Finally, Poulton introduces an extremely important concept into the speciation literature: he distinguishes *sympatric* groups of individuals that overlap in space from those that are geographically isolated (*asympatric*, now called *allopatric*; cf. Mayr, 1942: 148–149).

Poulton was fond of coining terms from Greek roots. In *The Colours of Animals* (1890) he had introduced the terms *aposematic* (signalling away) for warning colour, and *epigamic* for secondary sexual coloration, both of which survive in current literature. He apparently consulted others whose knowledge of Greek was perhaps greater than his own; for example 'Mr. Arthur Sidgwick' (Poulton, 1908: 61). Poulton was deeply disappointed to discover that *syngamy* had been used as a term in a different sense in the very same year, 1904, of his address: in an exasperated note in the book version of *What is a species?* (1908: 61), Poulton records how 'my friend, Professor Marcus Hartog' had also used the word *syngamy* simply to mean fertilization. In support of his own population-level term, Poulton argues that his own 1904 publication had about a month's priority over Hartog's! Nonetheless, *syngamy* did not survive in Poulton's sense, and of the four terms introduced here, only *sympatry* is generally used today.

The core of Poulton's argument that species are syngamic and synepigononic then appears in a section entitled 'Introduction to the Discussion 'What is a Species?'' on pp. 63–65 (1908). (Given we are already nearly 20 pages into the article, we can imagine the audience at this stage beginning to fidget as it wondered when the introduction would end, and Poulton would finally pose and then answer his question.) 'Syngamy and Epigony are but two sides of the same phenomenon – Reproduction. Although occasional union between individuals of distinct species may occur in nature, sometimes leading to the production of hybrid offspring, this is not the 'free interbreeding under natural conditions' which I have called Syngamy. Syngamy, thus defined, implies the production of normal offspring capable of continuing the

species – implies Epigony . . . Both Syngamy and Epigony can be established by indirect evidence based on a sufficient number of accurate observations upon the habits and modes of occurrence of individuals. The criterion of Syngamy of course fails in the case of parthenogenetic and self-fertilizing species. In such cases . . . we are compelled to fall back on Epigony.’

Poulton sides with Darwin’s argument (1859: Chapter VIII, Hybridism) that sterility is not a good species definition, because it is likely a by-product of speciation rather than its cause. ‘It will be argued that the true interspecific barrier is not sterility but Asyngamy – the cessation of interbreeding – but that the first will inevitably follow, sooner or later, as the incidental consequence of the second.’

At this point, Poulton argues for the reality of species, underpinned by biological considerations, compared with lower or higher taxa. This was another of Poulton’s innovations that was to find much favour with subsequent biologists. ‘The conclusions set forth above, if hereafter established, lead to a belief in the reality of species. Unlike and apart from genera, families and other groups employed in . . . classification, individuals stand out as objective realities. But equally real, though far less evident, are the societies into which individuals are bound together in space and time by Syngamy and Epigony’. Darwin’s own view couldn’t have contrasted more strongly: acknowledging evolution compels us ‘to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience’ (Darwin, 1859: 485). Poulton consciously overthrows Darwin’s view in favour of the one generally adopted during the evolutionary synthesis: that the species is the only ‘real’ taxon or truly natural grouping of individuals in nature (Dobzhansky, 1935, 1937; Mayr, 1940, 1942, and subsequently). Species are endowed with the unique biological ‘essence’ of reproductive continuity within species and reproductive discontinuity among species. (See also the discussion of species reality on pp. 448–449.)

After this, Poulton demonstrates how his syngamy/epigony definition works in practice, and how it rectifies ‘The failure of Diagnosis as the sole test of Species’. Often, morphological diagnosis may provide a provisional identification of the species taxon, but exceptions are widespread. Individuals may also show diagnostic differences in a number of ways unrelated to species boundaries:

- (a) *Dimorphism, Polymorphism*. Poulton uses as examples the various African forms of the butterfly *Danaus chrysippus*, and the Batesian mimetic female morphs of *Papilio dardanus*. When Roland Trimen (1869) established that these were probably members of the same species as yellow male swallowtails called *Papilio merope*, because they mated together, the creationist W.C. Hewitson expressed horror: ‘. . . I am quite incapable to believe that . . . *P. merope* . . . indulges a whole harem of females, differing as widely from it as any other species in the genus.’ These ideas were but ‘the childish guesses of the Darwinian school’ (Hewitson in Poulton, 1908: 57).
- (b) *Seasonal Dimorphism*. The European map butterfly, now known as *Araschnia levana*, which has strongly divergent

spring and late summer forms, is a good example of seasonal dimorphism. Poulton does not mention this example (cf. Wallace, 1865: 9), but cites the cases of many African butterflies that have highly divergent dry and wet season forms.

- (c) *Individual Modification*. By this, Poulton means what we would today call phenotypic plasticity, as well as quantitative genetic variation; he gives the example of woody plants pruned by wind in exposed coastal areas.
- (d) *Geographical Races or Sub-Species*. Poulton argues that such forms, provided they are syngamic (i.e. form a reproductive community) at their boundaries, are really members of the same species, but that this will not necessarily last. These races are ‘. . . as it were, trembling on the edge of disruption, ever ready, by the development of pronounced preferential mating or by the accumulated incidental effects of [geographic] isolation prolonged beyond a certain point, to break up into distinct and separate species’.
- (e) *Results of Artificial Selection*. Why do we not consider domestic breeds with fixed differences in morphology to be different species? Poulton argues it is because they remain ‘syngamic’ or reproductively compatible with other members of the same parental species.

Poulton then reviews the nature and modes of origin of a series of species characteristics, today often called ‘isolating mechanisms’ (cf. Dobzhansky, 1937: chapter VIII).

Interspecific sterility is a characteristic of many species, but it also often arises between individuals within a species, as in self-incompatibility in plants. As we have already seen, Poulton sides with Darwin, and argues that sterility is not a good test of species status; instead, sterility will result as ‘an incidental consequence of Asyngamy’.

Asyngamy itself (which apparently is not intended to include sterility or ‘postzygotic isolating mechanisms’) can be due to:

Asympatry. If populations are geographically isolated, they will not be able to form a “syngamic community”.

Mechanical incompatibility. For example, related species in the Lepidoptera often differ strongly in genitalic morphology. Morphological differences in genitalia were at this time becoming important in the systematics of Lepidoptera, and probably have some mechanical effect on the possibility of copulation. However, genitalic morphology does not necessarily function as a ‘lock-and-key’ mechanism, and genitalic differences between species are probably not often adaptive (Jordan, 1896).

Preferential mating. Here Poulton refers to Bates’ (1862) assertion that different forms of South American and African butterflies mate non-randomly, and that this led to the origin of new species (see below). He also refers to similar evidence in a personal communication (28 December, 1903) from the African butterfly expert Roland Trimen.

The breaking of a syngamic chain. Poulton argues that *Danaus chrysippus* (to which he applies the name *Limnas chrysippus*) is ‘perhaps the commonest butterfly in the world, forms a probably continuous syngamic chain stretching from the Cape of Good Hope at least as far as Southern China’. He asks whether the

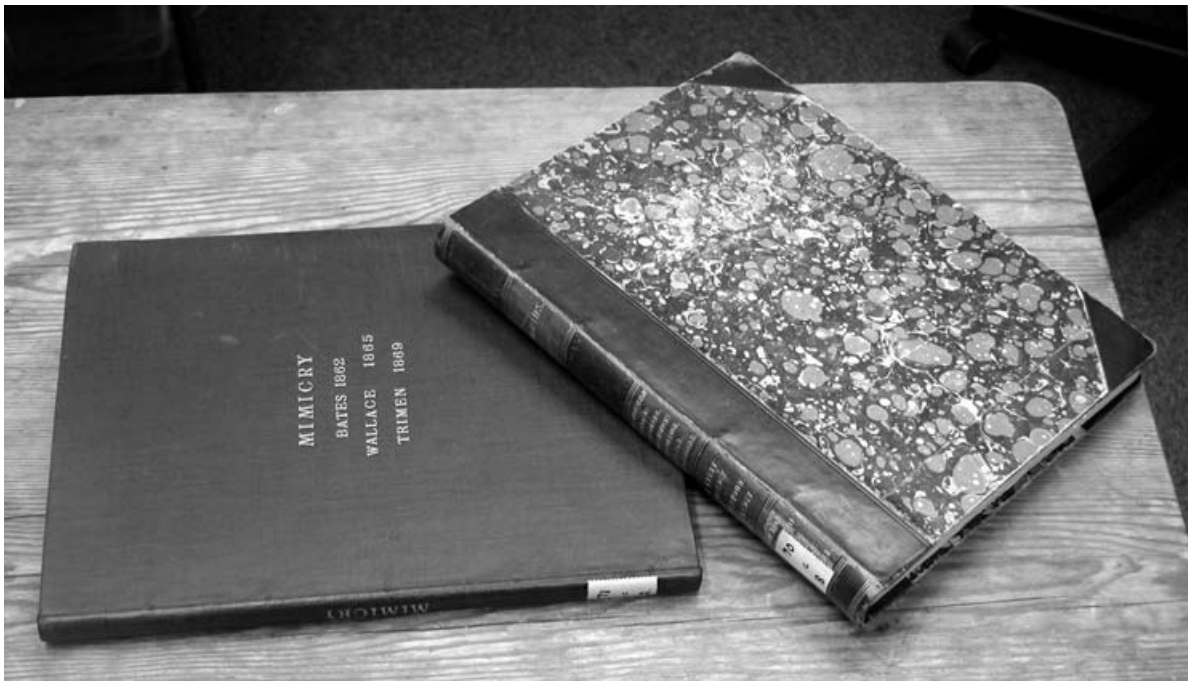


Figure 1 Wallace's 1903 gift to Poulton (right). The book is sumptuously bound in a marbled board cover. The title 'Butterflies' and details about the contents are in gold tooling on a leather spine. The Bates (1862), Wallace (1865) and Trimen (1869) papers on mimicry include hand-tinted plates; each butterfly illustration in the plates of Bates and Trimen is annotated with a Latin name in Wallace's hand. Poulton was apparently so impressed with his present that he collected up further reprints of the three key mimicry papers and had them bound in copies of a book entitled 'Mimicry' for private distribution (left). The original book given by Wallace to Poulton and a number of copies of Poulton's three-reprint collection are now in the library of The Hope Department of Entomology, University of Oxford, where Poulton was Hope Professor for almost his entire scientific career (Smith, 1986).

butterflies from Hong Kong or Macao would freely interbreed with those from Africa. 'We do not know; but it is an experiment well worth trying.' Later, Mayr (1940, 1942), citing work by Rensch and Stegmann in the 1930s, was to give convincing examples of this effect: for example, forms of the herring gull *Larus argentatus* and the lesser black-backed gull *Larus fuscus* can be interpreted as a circumpolar 'ring species'. The ends of this chain of forms are reproductively isolated where they overlap in W. Europe.

The final part of Poulton's paper speculates on a possible relationship between sterility between species and 'certain adaptations for cross-fertilization' in plants, now called self-incompatibility. Poulton calls for the establishment of tropical field-stations so that species incompatibilities might be studied in greater detail, especially in the tropical species that demonstrate reproductive isolation and the origins of species so well.

Poulton's paper then finishes somewhat abruptly without a clear conclusion or summary. Instead, Poulton ends as he begins, with a quotation from Darwin (1859; in single quotation marks): 'It has been a pleasure to me that the central idea which I have endeavoured to bring before you should be represented... by means of 'the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications'.'

Wallace's gift to Poulton

The lecture in January 1904 took place just after Poulton had received a gift from A.R. Wallace in December 1903

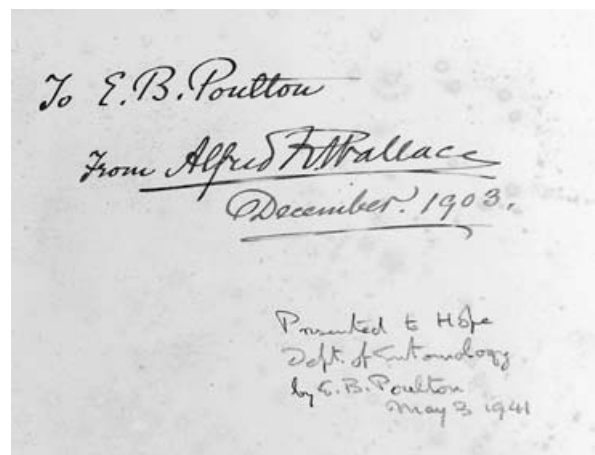


Figure 2 The inscription, in Wallace's hand, on the front endpaper of the gift volume, and a record of the donation to the Hope Library (in pencil, in the hand of former Hope Professor G.D. Hale Carpenter, Poulton's successor).

(Figs 1–3). The gift was a bound collection of three major reprints on mimicry in butterflies from Transactions of the Linnean Society (Bates, 1862; Wallace, 1865; Trimen, 1869), two pre-Darwinian papers on affinity (i.e. 'homology') and analogy by William Kirby (1822) and Josiah O. Westwood (1837), and several other related publications including two by Poulton himself.

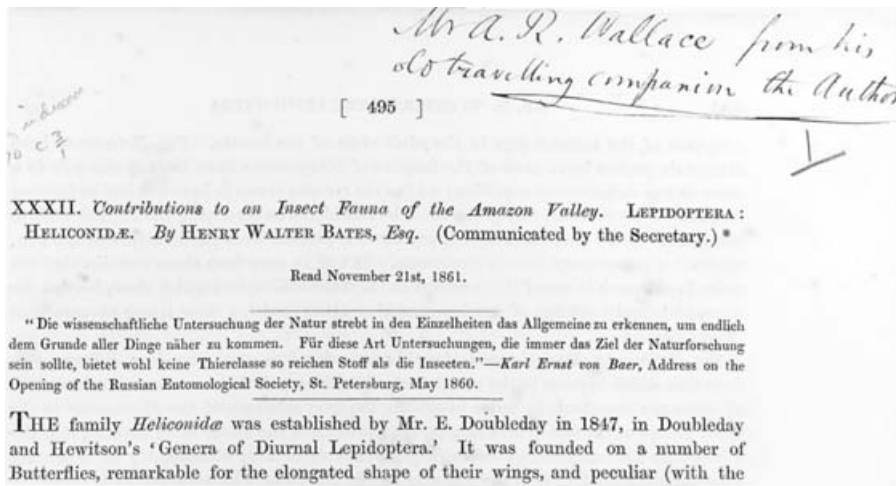


Figure 3 Bates' (1862) paper, the first in the gift volume, is apparently the very copy that Bates himself gave to Wallace, as shown by this inscription.

The dust had not settled after the publication of 'On the Origin of Species' at the time Bates (1862) and Wallace (1865) published their important papers on mimicry. These two papers are the first Darwinian discussions of mimicry; neither is merely a story about intraspecific adaptation, as might be expected from current treatments of mimicry in evolutionary texts. These papers combined discussions of natural selection, systematic monography of tropical butterflies, and, most importantly, speciation (see also Kimler, 1983). With Trimen's paper (1869), all three were investigations into species concepts, and of the power of natural selection to effect the origin of species, topics highly relevant to Poulton's (1904) lecture.

Bates on mimicry. Bates' (1862) paper has already been mentioned under Poulton's heading *Preferential mating*. The evidence, in Bates' words, is as follows: 'On observing individuals *in copula*, I almost always found the pair to be precisely the same in colours and markings' (Bates, 1862: 500). 'When the persecution of a local form of our [mimetic] *Leptalis* is close or long-continued, the indeterminate [i.e. non-mimetic] variations naturally become extinct; nothing then remains in that locality but the one exact counterfeit, whose exactness . . . is henceforward kept up to the mark by the insect pairing necessarily with its exact counterpart, or breeding *in and in*' (Bates, 1862: 513). Later, in the systematic section of the paper concerned with the ithomiine genus *Mechanitis*, Bates elaborated further: 'It is an advantage to a form to have a sphere of life different from its allies: when two sister forms keep themselves distinct in a locality, it is a sign they have acquired sufficient difference to fill two separate spheres; if they paired together, they would soon become one again' (Bates, 1862: 531, footnote). It must be said that Bates never provided the documentary evidence for his idea that sister taxa with divergent mimetic patterns tend to mate assortatively, in spite of Darwin's repeated entreaties for more details, as noted by Poulton (1908: 86). As far as I know, the idea that selection for mimicry might have incidental effects on preferential mating lay more or less dormant until Chris Jiggins showed that colour

patterns were used in mate recognition, as well as in mimicry, in sister species of *Heliconius* (Jiggins *et al.*, 2001). Jiggins' work was carried out at the Smithsonian Tropical Research Institute in Panama, exactly the sort of 'tropical biological station' recommended by Poulton (1908: 89–90) as a branch of one of 'our chief museums' for the study of species incompatibilities.

Bates (1862: 514) also details his own species concept. Related forms of *Mechanitis* living together, but not intergrading, were separate species. 'The new species cannot be proved to be established as such, unless it be found in company with a sister form which has had a similar origin, and maintaining itself perfectly distinct from it. Cases of two extreme varieties of a species being thus brought into contact by redistribution or migration, and not amalgamating, will be found to be numerous'. Thus, the means of speciation was preferential mating, while the definition of species depended on the lack of morphological amalgamation.

Wallace on mimicry and speciation in papilionid butterflies. Even more important, for Poulton, was Wallace's own paper 'On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of the Malayan region'. In twenty-first century jargon, the title for Wallace's (1865) paper would read something like 'Indonesian Papilionidae as a model system for the study of speciation and biogeography'. At least three major topics in this work were important for Poulton's (1904) thesis:

(1) *Intraspecific and interspecific variation.* 'What is commonly called variation consists of several distinct phenomena which have been too often confounded. I shall proceed to consider these under the heads of – 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' perhaps would

be the modern equivalent]; 5th, races or subspecies; and 6th, true species' (Wallace, 1865: 5–14). As far as I know, this is the first attempt by a Darwinian 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 Poulton, and later Mayr (1942) to discuss the species problem in greater detail. The similarity between Wallace's list and Poulton's own list (*Dimorphism, Polymorphism* and so on, see above) seems too coincidental; the first is almost certainly a forerunner of the second. There are also a few differences: *Seasonal dimorphism* was not treated under a separate heading by Wallace, but is mentioned with reference to *Araschnia levana* (Wallace, 1865: 9) under the heading *Polymorphism or dimorphism*.

(2) *Species definition*. An absence of intermixing or reproductive isolation is a very old idea about species, dating from long before Darwin (see Mayr, 1982; Gittenberger, 1995): Darwin's (1859) chapter 'Hybridism' was in fact an attack on the idea that intersterility was a useful definition of species. Wallace (1865: 12) touches on this idea here: '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.'

However, Wallace immediately sees problems inherent in this clear statement of what later became Poulton's asyngamic species, and Mayr's biological species concept: '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).

Exactly what Wallace means by 'founded on an assumption of the very question . . .' now seems obscure. I believe he is attempting to avoid tautology: reproductive isolation, in Wallace's view, cannot be used both as a *definition* of species and as a *cause* of speciation in evolutionary discussions (see also above for Bates' 1862 distinction between preferential mating and its result: two separate species which do not amalgamate morphologically).

Instead, Wallace uses a pragmatic, Darwinian version of the standard morphological 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? '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 admits that 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 often necessary in this situation and in any case this kind of arbitrariness isn't quite as fatal to the understanding of speciation as Mayr would have us believe.

(3) *Female-limited mimetic polymorphisms in Papilio butterflies*. Female-limited forms of *Papilio dardanus* form a key component of Poulton's argument for asyngamy as a species definition. This African butterfly has a yellow, tailed, non-mimetic male; females may also occur in non-mimetic yellow tailed forms like the males (in the Comoros, Madagascar, Somalia and Ethiopia), or as one of several mimetic tailless forms mimicking different unpalatable species in the Acraeini and Danainae (Nymphalidae). These mimetic and non-mimetic forms have *diagnostic* differences typical of those between species, but are *syngamic* and *synepigonic* (in Poulton's terminology) because, as Trimen (1869) demonstrated, they mate together where they co-occur, and different forms emerge from the same brood of larvae.

But it was, in fact, Wallace (1865) who first collated evidence for female-limited mimicry in *Papilio*, especially for the Asian species we now call *Papilio memnon*, *P. polytes* and *P. aegeus*. This explanation relied both on *epigonic* data – individuals emerging from eggs laid by a single female – and from *syngamic* pairs *in copula*. Wallace cites his own observations as well as published work and correspondence. One interesting citation is to a paper published by Benjamin D. Walsh in 1863. Walsh was an Englishman living in Pennsylvania, and a correspondent of Darwin's. Walsh was the first to show that the black form *Papilio glaucus* was conspecific with the yellow *P. turnus*. 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 at more or less the same time argue, again, that the common interests of these two scientists are not mere coincidences, but due to a flow of information between Darwinians in different countries.

Wallace (1865: 10, 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.'

Poulton (1904) cites Wallace's (1865) paper (to be accurate, he cites the updated version in Wallace's book 'Contributions to the Theory of Natural Selection', 1875) from which he obtains Bates' 1863 quotation about the value of butterflies in evolutionary studies already mentioned. Wallace, in this 1875 edition, himself records what Poulton calls 'Roland Trimen's remarkable discoveries' (1869) on *Papilio dardanus*, also in Wallace's gift volume, and which formed such a prominent component of Poulton's 'What is a species?' address. Poulton had Wallace's gift to hand at the time of preparing his lecture, having been given it a month earlier, as well, presumably, as Wallace's 1875 book.

The similarities of Poulton's species paper to Wallace's are therefore as follows:

- Both proposed a *syngamic* species definition (although Wallace follows Darwin in rejecting reproductive isolation as a strict definition of species).
- Both use *syngamy* and *synepigony* as evidence for conspecificity of female-limited mimicry morphs of *Papilio* butterflies.
- Both document different types of geographic and non-geographic variation leading to the species level, using virtually the same terminology (e.g. Poulton's *Dimorphism*, *Polymorphism* versus Wallace's *Polymorphism or Dimorphism*; Poulton's *Geographical Races or Sub-Species* versus Wallace's *Races, or subspecies*; and *Seasonal Dimorphism* used by both).
- In addition, there are other incidental similarities, such as the use of *Rosa* and *Rubus* as cases where it will be hard to distinguish species from infraspecific variants.

Perhaps Poulton had been planning his species paper before the gift from Wallace, but it seems likely he leafed through the volume, including Wallace's own paper (1865, 1875) in December 1903 and early January 1904. We can imagine him reading the material, sipping his port over the Christmas period, maybe after the children had gone to bed. Wallace's thoughts on *Papilio* in this paper were almost certainly a major influence on Poulton's talk.

Walter Rothschild and Karl Jordan

Wallace's influence on Poulton also came partly via an intermediary. In 1893 the German Karl Jordan had been hired by the great collector Walter Rothschild to curate the insect collection at his museum in Tring, Hertfordshire. In 1894 Rothschild asked him to switch from beetles, his speciality, to swallowtail butterflies. Within a year, Jordan had completed a 300-page monograph on the Papilionidae of the Old World excluding Africa (W. Rothschild [& Jordan], 1895; see M. Rothschild, 1983). As well as many other works, eight years later Jordan had monographed the entire SpHINGIDAE of the world (W. Rothschild & Jordan, 1903, 938 pages), and

three years after that the Papilionidae of the Americas (W. Rothschild & Jordan, 1906, 341 pages). In his first major systematic monograph (1895), Jordan needed to carefully read and update the taxonomic methods Wallace (1865) had applied to the Asian swallowtails. Jordan, like Wallace (1865), argued that the different classes of 'variety' had been much confused, and classified variation below the species level into individual variations, aberrations, polymorphisms, seasonal forms, and subspecies (W. Rothschild [& Jordan], 1895: 180).

By 1903, Jordan's categories of variation below the species had been reorganised into just three: individual variety (including aberrations and polymorphisms), generatory [seasonal] variety, and geographical variety or subspecies (W. Rothschild & Jordan 1903: xlili). An important innovation in Lepidoptera systematics due to Jordan, which survives to this day, was the idea that 'polytypic' species can consist of a number of distinct geographic races, which intergrade where they meet. Jordan proposed that geographic races or subspecies were to be denoted using a trinomial (e.g. *Papilio eurypylus axion* [now in the genus *Graphium*]), without the 'var.' or 'ab.' prefix used for all other local varieties and seasonal forms. The story of the 'polytypic species' revolution has been frequently told (Stresemann, 1975; Mayr, 1942, 1980, 1982). Essentially the idea arose in the latter part of the nineteenth century in Germany and the USA, and was spreading to other parts of the world by 1900 (Walter Rothschild, Ernst Hartert & Karl Jordan in the UK, for example); the revolution was more or less complete worldwide by the 1920s. The Director of the Tring museum at this time, Ernst Hartert, was also the only other curator, in this case of Rothschild's vast bird collection. Thus, Jordan would have encountered the revolution in ornithological systematics first hand. He adopted it wholeheartedly, and indeed improved on it, with Rothschild's evident approval, for the butterflies and moths.

Jordan was regarded as the 'clever' curator by the Rothschilds (in Walter Rothschild's words, 'We have terrific arguments, but the fellow is always right'; see M. Rothschild, 1983). During this period Jordan also published papers of a purely philosophical nature. Indeed, Jordan's 'mechanical selection' paper (1896) was prominently cited by Poulton (1904, see above); it vented Jordan's views on speciation and species concepts, as well as being the first major paper about genitalic morphology. At this time, genital armature was becoming an increasingly important source of taxonomic characters in the Lepidoptera; it was the DNA of its day. Jordan's early, somewhat legalistic species definition (1896: 437) appealed both to diagnostic and to epigonic principles: 'A species is a group of individuals which is differentiated from all other contemporary groups by one or more characters, and of which the descendants which are fully qualified for propagation form again under all conditions of life one or more groups of individuals differentiated from the descendants of all other groups by one or more characters.' Jordan (1896: 441–442), like Poulton (1904), also argued that 'there is a . . . real distinction between the terms 'species' and 'variety' . . . It is non-fusion of the branches [of a phylogenetic tree] that maintains species distinctness'.

As President of the Entomological Society of London, which Jordan and W. Rothschild attended frequently, and

as an expert on Papilionidae, Poulton was well aware of advances in the systematics of Papilionidae and of Jordan's more philosophical work on systematics, species and subspecies concepts, variation below the species level, and genitalic armature as a taxonomic tool. Poulton communicated with Jordan in December 1903 and January 1904, asking his advice on species and requesting his presence at the Entomological Society for the species discussions (Johnson, 2003: Chapter 4; Kristin Johnson, pers. comm.). Poulton's article is liberally sprinkled with references to Jordan's work (Poulton, 1904). Furthermore, Jordan himself was undoubtedly influenced by Poulton's paper, which he, as a fellow *Papilio* expert, would have read carefully. A year later, Jordan's (1905) article on species and varietal taxonomy promoted the idea of geographic speciation. He cited Poulton (1904) frequently, used many examples from the Papilionidae and Sphingidae he had monographed with Rothschild, as well as the *Papilio dardanus* example in Poulton (1904). Jordan again contrasted geographic racial variation with local variation and seasonal forms, and proposed that species can be defined morphologically, even though this morphological differentiation was due to the actual biological differences between species: reproductive isolation via physiological or mechanical differentiation. Jordan argued that geographic races are the forerunners of new species, that is, in Poulton's terms, that *asyngamy* would evolve as a result of *asympatry*. Finally, his updated species definition added Poulton's idea of *syngamy* to the *syndiagnosis* and *synepigony* he had himself advocated in 1896: 'The criterion for the species concept is therefore threefold, and every single point is testable: a species has certain morphological traits (is *syndiagnostic*), produces no offspring like individuals of other species (*synepigonic*) and does not blend with other species' (i.e. there is a barrier to gene flow) (Jordan, 1905: 159).

At the time Jordan was writing, creationists, Lamarckians, saltationists, mutationists and supporters of orthogenesis, as well as Darwinians, were all putting forward competing explanations of species (Mayr, 1982; Kimler, 1983; Johnson, 2003). In his taxonomic work, Jordan therefore advocated a universal method of defining species based on morphology, while averring that interbreeding and evolution (*syngamy* and *synepigony*) underlay this morphological distinctness (W. Rothschild & Jordan, 1906: 431). Arguably, we ourselves might do well to adopt a set of theory-neutral species criteria to solve the current controversy, at least with respect to taxonomy. A modern approach might employ gaps between clusters of similar genotypes, as well as gaps in morphology (Mallet, 2001). By disregarding Jordan's warning, and arguing for species concepts based on the underlying 'reality' of species, we follow Poulton, Dobzhansky and Mayr in exposing our taxonomy to instability whenever disagreements surface about the true nature of species reality. (Another argument is that theory-laden species definitions interfere with evolutionary discussion. As a trivial example, we are on difficult logical ground when we argue with creationists about the origins of species, if we insist that species are defined by monophyly or other concept which requires species to have evolved.) Experts seem likely to differ about the 'true' func-

tional or phylogenetic nature of species into the foreseeable future, so that the exact taxonomic level of the species boundary will continue to fluctuate while we insist on the incorporation of evolutionary theory into definitions of taxonomic categories.

The influence of Poulton and Jordan on Dobzhansky and Mayr

There can be no doubt that Mayr, who had been in Tring with Rothschild, Hartert and Jordan, and worked as Rothschild's collector in New Guinea and the Solomon Islands in 1928–1930 (M. Rothschild, 1983), was influenced by these prime movers of the revolution in evolutionary systematics. Rothschild's collections of butterflies and birds were and still are the largest ever amassed by a single collector. As we have seen, a major nomenclatural result of this revolution was the idea that species could consist of a number of distinct geographic races, named as trinomial subspecies, and which intergraded at their boundaries. Ernst Mayr visited Tring, and was funded by Rothschild on his collecting trip to New Guinea (M. Rothschild, 1983; Johnson, pers. comm.). On his return in the late 1920s, Mayr had been mooted by W. Rothschild as a possible successor to Hartert on the latter's retirement as curator of the birds (M. Rothschild, 1983). Instead, Mayr became, in 1930, the curator of birds at the American Museum of Natural History in New York. When Rothschild needed to raise cash to pay off a kiss-and-tell blackmailer in 1932, he sold his massive bird collection, by a coincidence, to the very same museum. Mayr was given the job of integrating the Rothschild birds with the existing collections in New York. Thus Mayr had been closely in touch with the systematic methods and species-level taxonomy of Karl Jordan, W. Rothschild and Ernst Hartert long period before 1940, when he first wrote about species concepts himself.

The biological species concept of the Evolutionary Synthesis, as elaborated by Mayr (1940, 1942) combined the taxonomy of polytypic species with an evolutionary emphasis on reproductive communities; it extended Poulton's *syngamy* argument to Jordan's concept of multiple subspecies connected geographically. However, Mayr's adoption of the terms 'reproductive isolation' and 'isolating mechanism' was clearly influenced chiefly by Dobzhansky; his 'Genetics and the Origin of Species' (1937) was in the same Columbia University Press series as Mayr's 'Systematics and the Origin of Species' (1942).

Krementsov (1994) argues convincingly that Dobzhansky himself would have been strongly influenced by the Russian entomology community to which he belonged before leaving for the USA and becoming a *Drosophila* geneticist. Dobzhansky had worked on evolution and speciation of coccinellid beetles. He was well aware of the debate on the nature of species started by Semenov-Tian-Shansky (1910), and cites it as a source for his own ideas; indeed Krementsov argues that there was a strong tradition in Russian entomological circles to study speciation as a result of incapacity to interbreed. Semenov-Tian-Shansky classified types of

reproductive isolation, including seasonal or chronological isolation, psycho-physiological or sexual isolation, and mechanical isolation (cf. Poulton's classification above). According to Krementsov, Semenov-Tian-Shansky (1910) was building on earlier ideas by Wilhelm Petersen, a Russian lepidopterist who had debated speciation at length with Karl Jordan. While Jordan argued that reproductive isolation was normally a non-selected by-product of geographic isolation, Petersen preferred an adaptive, physiological mode of speciation. Although their opinions differed, it is clear that these entomologists, who frequently communicated in German, were in strong international contact at this time. Thus, if Dobzhansky was strongly influenced by the Russian entomologists (and Krementsov (1994) makes a good case), it is almost certainly true that Jordan and Poulton were among the major influences on these Russian entomologists in their turn.

Conclusion

Mayr's (1942) book became the state-of-the-art review of speciation for the next 20 years, and in later editions (1963, 1970) for at least a further 30 years after that. The 1942 work summarised a large and international literature of animal systematics and evolution, and is still well worth reading today. When I met Ernst Mayr on 5 November 1999 at his home near Cambridge, MA, I asked him whether he had planned a strategy for this famous 1942 work. He replied that, quite to the contrary, he had just written down what he thought was the perceived wisdom of all right-minded systematists at that time. He didn't intend the book to mark the beginning of a new era. Originally, the book was commissioned jointly from Mayr and a botanist, Edgar Anderson. Mayr wrote his part on the zoology, but Edgar Anderson became ill, and the botanical sections were never completed. Mayr tidied up and submitted the zoological manuscript on its own; this explains the lack of any mention in the title to the fact that the book covered animal speciation only.

Species as reproductive communities became the firmly established 'biological species concept' starting with Mayr (1942). Mayr classified isolating mechanisms in much the same way as Wallace, Poulton, Semenov-Tian-Shansky and Dobzhansky had done earlier. As well as adding the population genetics insights from Dobzhansky's work, Mayr was able to draw on his wide experience among the systematists in Europe and the USA. He further classified the different forms of non-geographic variation and particularly geographic variation (using the terms 'individual variation', 'polymorphism', 'seasonal variation', 'subspecies, or geographic races') in almost exactly the same way that Wallace, Poulton, and particularly Jordan had done. Mayr cites Poulton (1904) for the invention of the term 'sympatry' and Poulton (1904) and Jordan (1896, 1905) for their early stabs at the biological species concept. There are sections in Mayr's work that reveal he read Poulton (1904) extremely closely; for instance, as already mentioned, Mayr (1963: 13) agrees with Poulton that Linnaeus' emphasis on species fixity had sowed the seeds of evolutionary theory. These many detailed similarities, as well

as Mayr's Tring experiences, argue for a close link between the ideas of Poulton, Jordan and Mayr. Dobzhansky and Mayr could draw on new findings in genetics (a topic which Poulton never mastered – Kimler, 1983) to examine speciation in some detail, which explains in part why the synthesis had to wait until about 1940. Furthermore, there is a clarity and 'magisterial' quality in the styles of Dobzhansky and Mayr, quite different from the long-winded and sometimes rambling (although always amusing) prose of Jordan and Poulton 40 years earlier. Thus Mayr and Dobzhansky, rather than Poulton or Jordan, became seen as the architects of the evolutionary synthesis as applied to speciation.

I am not suggesting that Mayr or Dobzhansky purloined ideas. I have already mentioned how Mayr (1942) cited Poulton; he also refers frequently to Poulton (1904) and Jordan (1905) in a published reminiscence about the influences on the Evolutionary Synthesis (Mayr, 1980). I do, however, believe that Poulton and Jordan should be more widely recognised for their contributions. Yet in a sense these two entomologists achieved a greater success than merely having their work cited by a few other scientists for a few years; their ideas contributed so strongly to common knowledge about species held by 'right-minded systematists' that they formed the basis for the Modern Synthesis. Both Poulton (1938) and Jordan (1938) seemed pleased that their viewpoints had finally prevailed during a meeting at the Linnean Society called to discuss speciation just after the publication of Dobzhansky's book. The papers on species concepts by Poulton and Jordan of 100 years ago, a topic begun originally by A.R. Wallace, were a crucial and much under-estimated foundation for subsequent work both on species concepts, and on the taxonomic treatment of subspecies compared with other varieties in zoology. If this influence of lepidopterists in Britain is accepted, perhaps the reader may also agree that Wallace's Christmas gift to Poulton, 100 years ago, was a key event in the history of biology.

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I learnt of the gift from Wallace to Poulton because a copy of Poulton's 'Mimicry' book (Fig. 1, left) is in the library of my former PhD supervisor, Lawrence E. Gilbert Jr., at the University of Texas at Austin. Gilbert had been a scholar at the University of Oxford immediately before his own Ph.D., and while there had visited the Hope Department library. Gilbert had copied every hand-written annotation from the original Wallace gift volume (Fig. 1, right) into his own copy of the Poulton collection. I am grateful to George McGavin of the Hope Department for a pleasant lunch in Jesus College under the watchful eye and huge eyebrows of E.B. Poulton (his portrait hung on the wall), and especially for rescuing Wallace's volume from the Hope library just before the current Hope librarian went on a two-week holiday. The former Hope librarian, Audrey Z. Smith, provided details of her knowledge of Poulton (see also Smith, 1986). I thank Ernst Mayr for his hospitality in 1999, and for the gift of a new facsimile edition of his 1942 book. I am also grateful to Kerry Shaw for facilitating the visit to Mayr's home. I thank Steve Stearns for generously translating passages from Jordan's (1905) paper. Kristin

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