# Chapter 6

In: Smith, C.R. and Beccaloni, G.W. (eds.): *Natural Selection and Beyond: The Intellectual Legacy of Alfred Russell Wallace.* Oxford University Press.

# Wallace and the Species Concept of the Early Darwinians

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## Introduction

One of the extraordinary features of modern evolutionary biology is an inability to agree on a common definition of species. This lack of agreement, together with changes in the species concepts of taxonomists, is leading to an unprecedented level of taxonomic instability. In a sense, this is perhaps less of a problem than it at first appears, since almost everyone in the debate agrees that species evolve from populations within species, and that speciation is liable to be gradual: there will thus always be intermediate stages that are hard to classify. But in some cases, disagreements spill over into human affairs and cause practical problems. This is especially true in conservation (Isaac et al. 2004; Meiri and Mace 2007).

My own involvement in this debate dates from 1995, when I saw that the roots of the controversy might lie in misinterpretations of Darwin's and the early Darwinians' concept of species of the latter part of the 19th Century (Mallet 1995). The standard view among evolutionists, which in modern form appears to originate with Ernst Mayr (1942), was that Darwin was confused about species, and that this led to an inability on his part to properly formulate a theory of speciation (Mallet 2008a). Doubting this perceived weakness in Darwinian theory, I argued (Mallet 1995) that modern genetic data was leading us in exactly the opposite direction, towards a "genotypic cluster" definition of species close to Darwin's view of species as morphological clusters of similar individuals, rather than as reproductively isolated communities as in the Mayr view. The reader of this chapter should be advised that my views have not yet been widely accepted. Nonetheless, I do not believe that appreciating the historical conclusions of this chapter depend on the reader adopting my own very pro-Darwinian view of species.

Here, I outline the contribution of Alfred Russel Wallace and that of other Darwinians to the understanding of the nature of species, and their evolution. In particular, I summarise their views about the importance of "reproductive isolation." Since 1995, I have gradually been collecting information on how early Darwinians viewed species. These readings lead me to believe that all the most important Darwinian evolutionists soon after 1859 carefully read and generally agreed with views expressed about the evolution of species in the *Origin*, often corresponded with Darwin, and appeared to close ranks on a common viewpoint. By 1889, when Darwinism was under a number of threats, Wallace reiterated his support for the Darwinian point of view on species in his book *Darwinism* (S724), which remains today probably the most complete statement of the early Darwinian position. I believe that Wallace's clearly enunciated statements negate the traditional view of the Darwinian species concept as poorly developed and inadequate for the purpose of studying evolution (Mallet 2004; Mallet 2008a).

## Wallace and Bates on the Nature of Species Circa 1845

Wallace and Henry Walter Bates (1825-1892) had corresponded on the matter of species before their joint trip to Amazon. Wallace first ran into Bates in Leicester, where the younger man sparked his interest in natural history collecting, and beetles in particular. Wallace had already been reading natural history books, but around the time he met Bates he read the anonymously-penned *Vestiges of the Natural History of Creation* (Chambers 1844), and was particularly impressed. He wrote to Bates about it (McKinney

1969). A little later, Wallace seems to have decided that the evolution of species should be his life work, and suggested to Bates that they travel together to a tropical location, in order to study natural history and the species question, financing the trip by selling specimens to collectors:

> In the autumn of 1847, Mr. A.R. Wallace, who has since acquired wide fame in connection with the Darwinian theory of Natural Selection, proposed to me a joint expedition to the river Amazons, for the purposes of exploring the Natural History of its banks; the plan being to make for ourselves a collection of objects, dispose of the duplicates in London to pay expenses, and gather facts, as Mr. Wallace expressed it in one of his letters, "towards solving the problem of the origin of species," a subject on which we had conversed and corresponded much together (Bates 1863, iii).

Writing to Bates in the Amazon several years later in January 1858 from the Malay Archipelago, Wallace discussed Darwin's interest in the origin of species question:

> I have been much gratified by a letter from Darwin, in which he says that he agrees with 'almost every word' of my paper. He is now preparing his great work on 'Species and Varieties,' for which he has been collecting materials twenty years. He may save me the trouble of writing more on my hypothesis, by proving that there is no difference in nature between the origin of species and of varieties; or he may give me trouble by arriving at another conclusion; but, at all events, his facts will be given for me to work upon. Your collections and my own will furnish most valuable material to illustrate and prove the universal application of the hypothesis (S729 1905, 1:361).

Darwin's gratifying letter had been in response to Wallace's own earlier 'Sarawak Law' paper on species (S20 1855): the exchange of letters took place just before Wallace's famous bout of fever on the island of Gilolo, in which he suddenly had the revelation of natural selection (Raby 2001). As is now well known, this led to a quick letter and paper dashed off to Darwin explaining his theory, and the ultimate joint publication of both Wallace's and Darwin's ideas on natural selection (Darwin and Wallace 1858).

## Darwin's View of Species in *The Origin*

Elsewhere, I have documented in great detail Darwin's (1859) view of species, and have also attempted to refute the idea that Darwin was confused about species (Mallet 2008c), as is commonly believed even today. In brief, Darwin strongly believed that species came to be well-defined after a long evolutionary period of divergent evolution:

> To sum up, I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links...
>
> …if my theory be true, numberless intermediate varieties, linking most closely all the species of the same group together, must assuredly have existed; but the very process of natural selection constantly tends…to exterminate the parent-forms and the intermediate links (Darwin 1859, 177, 179).

Species thus differed from varieties only in that varieties were still connected together, whereas species did not blend into one another, but were separated by gaps in the distribution of morphologies. At the same time, he argued that species were not "real" in the sense that they did not differ "essentially" from varieties and geographic forms below the species level. The rank at which we define the word "species" is up to us.

> …it will be seen that I look upon the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.
>
> In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species (Darwin 1859, 52, 485).

He recognized that because of the continuous nature of evolution, and the lack of an appropriate essence of species, there would always be difficulties in defining species in the early stages of divergence.

> But cases of great difficulty, which I will not here enumerate, sometimes occur in deciding whether or not to rank one form as a variety of another…Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow (Darwin 1859, 47).

Although "essentially" and "essence" are words that can be used in colloquial English in a somewhat imprecise way, it seems to me clear that Darwin was using these words advisedly; he was evidently referring to species essentialism in a strict, Aristotelian sense, and rejecting it. He knew exactly what he meant by species (summed up in the word "gaps"), but he specifically argued that there is no single "essence" of species true in all cases; in particular he argued in great detail in his chapter "Hybridism" against the idea that species were always isolated by hybrid inviability or sterility. In so doing, he rejected an older "reproductive isolation" notion of species dating back to Ray and Buffon. This view must have been as commonly accepted in his day, and earlier, as it was from the 1940s onwards. Although he did not deny that many species were intersterile, Darwin (1859) in his chapter "Hybridism" strongly argued against sterility of hybrids between forms as a *sine qua non* of species status. The major arguments he used were: that some pairs of species occurring together were largely interfertile; that populations of plants within species were often intersterile; that fertility of hybrids between a particular pair of species varied depending on the populations used in the crosses; and that infertility in one direction of cross (*e.g.* male of species A x female of species B) was accompanied by fertility in the other (male of B x female of A). Darwin argued that post-mating reproductive isolation arose largely as a by-product of changes after separation of the two species, rather than being itself a useful definition of species.

## Henry Walter Bates's View of Species

Bates is today most famous for his natural selection-based theory of mimicry, whereby the colour pattern of one species converges for predator defence on the colour pattern of another that is defended against predators. Curiously, Wallace had already written to Darwin about the same phenomenon of mimicry in butterflies:

> P.S. "Natural Selection" explains almost everything in Nature, but there is one class of phenomena I cannot bring under it,--the repetition of the forms & colours of animals in distinct groups, but the two always occurring in the same country & generally on the very same spot. These are most striking in insects, & I am constantly meeting with fresh instances. Moths resemble butterflies of the same country--*Papilios* in the east resemble *Euplœas*, in America *Heliconias* (Wallace 1860).

Ironically, his friend Henry Walter Bates was to discover the theory that could explain such resemblances, by means of natural selection, the very next year (1861), and publish it a year later (Bates 1862). Wallace had in a sense lost out to someone else again! Yet Wallace was as fair with Bates as he was with his admiration of Darwin; he was effusively complimentary about Bates' new theory (S96 1865). Bates had argued that rare species, palatable to predators, gain an advantage in nature if their colour patterns are similar to much commoner, unpalatable species. Predators, such as birds, learn the patterns of the common species, and rarer species without such protection benefit if they have the same colour patterns. Bates' theory chiefly argued that palatable species (dismorphiine pierids) mimicked unpalatable species (ithomiines in the genus *Melinaea* and *Mechanitis*). However, Bates also intuited that rare unpalatable species (for example, in the butterfly genus *Heliconius* (Heliconiinae) benefited by mimicking more common unpalatable species (e.g. *Melinaea*). Thus, Bates was the first to promote the idea that later became known as Müllerian mimicry, after Müller's (1879) paper. Müller's main, and indeed considerable achievement was to develop a mathematical theory to explain why it was mutually advantageous for unpalatable species to mimic one other, and estimate the relative advantage to each (see Chapter 9).

However, Bates' paper was not merely about mimicry. It was largely a systematic treatise, incorporating a somewhat understated theory of speciation by natural selection. Mimicry in particular played a major role in speciation, in Bates' view. To underpin the treatise as well as to define species from among the bewildering array of forms he found among the Amazonian butterflies, Bates had in mind a Darwinian definition of species. In his systematic discussion of ithomiines of the genus *Mechanitis* Bates describes divergent forms living together, but not intergrading, and views them as 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 (Bates 1862, 530).

In this view, he is closely following Darwin. Although reproductive isolation is clearly an important mechanism of species maintenance, it is the lack of intergradation or intermediacy in the actual specimens he has collected in the wild which leads Bates to characterise these forms as separate species. Bates argued that mimicry was an example of the kind of natural selection that can explain the origin of new species.

## Wallace's 1865 Paper "On the Phenomena of Variation and Geographical Distribution as Illustrated by the Papilionidae of the Malayan Region."

In this paper, I think Wallace is the first to lay out the Darwinian definition of species and apply it to geographic and non-geographic contexts clearly. The problem was to define species as distinct from geographical and local varieties, and Wallace, after his travels on the Amazons and in the Malay Archipelago, had unrivalled experience on which to base his opinions:

> 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--…1. *simple variability* [probably equivalent to quantitative variation]…2. *polymorphism or dimorphism* [discrete forms separated by morphological gaps, which nonetheless belong to the same species]…3. *local form, or variety* [gradually varying forms differing from place to place]…4. *coexisting varieties*…a somewhat doubtful case [reserved for coexisting forms which differ in very few constant characters, but which may be separate species; "sibling species" would perhaps be the modern equivalent]…5. *race, or subspecies*…6. [true] species (S96 1865, 5-14).

I have argued elsewhere that this is the forerunner of similar and highly influential classifications of geographic and non-geographic variation by the evolutionists E.B. Poulton, Karl Jordan and Ernst Mayr (Mallet 2004). Wallace gives his definition of species thus: "Species are merely those strongly marked races or local forms which, when in contact, do not intermix, and when inhabiting distinct areas are generally believed to have had a separate origin, and to be incapable of producing a fertile hybrid offspring" (S96, 12). This statement so far approximates the pre-Darwinian understanding of species, but as we shall see is followed by a partial rebuttal. As a Darwinian, Wallace instead believes that all species derive from one another and do not, in fact, have a separate origin. He argues also that the use of the sterility of hybrids as a species definition is tautological. Although he doesn't define here exactly what he means by a species, he clearly agrees with Darwin's view that species cannot easily be distinguished from varieties. He goes on:

> 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 separate 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 (S96, 12).

Wallace has already introduced a major difficulty: how to define species when distinct populations are found on different islands:

> The rule…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 distinctions between the two forms to become inconsiderable and indefinite…I class one of the forms as a variety of the other (S96, 4).

Wallace here attacks the problem of geographic variation, a complication which has blocked agreement on the definition of species even today. There are still "splitters" who would argue that every geographic form with a fixed difference should be defined as separate species, and "lumpers" who in contrast argue that such forms should as far as possible be defined as subspecies within much more widely-distributed species (Isaac *et al.* 2004).

Wallace was also among the first to appreciate that Darwin's idea of species being morphologically different from one other is problematic for a group of special cases, such as mimetic butterflies. *Papilio memnon* males appear to be different species from the females, as they have entirely different colour patterns, and the females themselves are polymorphic, some with tails and some without, each one mimicking a different species of poisonous Papilionidae. Wallace was able to apply Bates' mimicry theory to this situation, citing data showing forms that were reared from eggs laid by mothers with different colour patterns than their own. He gives a graphic illustration of how extraordinary it is that all these markedly different forms of *Papilio memnon* belong to the same species:

> 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 (S96, 10, footnote).

Clearly, these forms have morphological gaps between them, but Wallace does not in any way view them as equivalent to species. In this paper, Wallace built up perhaps the most complete theory of species and speciation put forward in the early days of Darwinism. His theory was based both on his novel biogeographic ideas, and his knowledge of many details of local natural history, variation, polymorphism, and evidence for natural selection. In the taxonomic sections of this same paper, he tends to assign geographic races as separate species rather more than we would today, but he admits this quite frankly, feeling that the important geographic subspecies in many *Papilio*s across the archipelago of South East Asia would be lost if he did not name them as taxonomic species (Mallet 2008b). At this time, it would have been possible to name a local form as a variety (usually written as "var."), but this risked confusion of strongly-marked, geographically informative subspecies with trivial local sports and variants; the subspecies had not yet formally been accepted in the formal trinomial system of nomenclature developed in the period 1890-1910 by ornithologists and lepidopterists, among them David Starr Jordan, Karl Jordan, and Walter Rothschild (Stresemann 1975; Rothschild 1983; Mallet 2004). Essentially, Wallace, in 1865, had laid out the full understanding of what later came to be known as the polytypic or "biological" species concept, even though he had, with Darwin, rejected too great a dependency for his own concept on reproductive isolation. It was no accident that K. Jordan and E. B. Poulton (a good friend of Wallace's in the latter's old age), both acknowledged pioneers of the biological species concept that Mayr (1942) later adopted, were also both experts on the Papilionidae. They had read and absorbed Wallace's paper on the topic (Mallet 2004).

## Benjamin D. Walsh in U.S.A. in the 1860s.

Walsh was a correspondent of Darwin's, and one of the earliest Americans to appreciate fully and apply the Darwin-Wallace theory of species and speciation, in his case to insects. In over 90 pages, Walsh argues with great verve and verbosity for Darwin's idea of species:

> The only valid practical criterion of specific distinctness is the general non-existence…of intermediate grades in the distinctive characters, whence we may reasonably conclude that the two supposed species are distinct, i.e. that they do not now in general mix sexually together, or if geographically separated that they would not do so supposing them to be placed in juxtaposition. …They may even now mix sexually together in some few rare instances [*i.e.* hybridization between species] and yet if they do not commonly and habitually mix together the species will remain distinct. Hence all experiments on artificial hybridization seem to me to prove nothing as to the distinctness of species unless they are conducted, as they necessarily cannot be, on the same gigantic scale as that upon which Nature works. …Immediately we assume any other criterion of specific distinctness than the general non-existence in a state of nature of the intermediate grades, either proved by actually examining numerous specimens or inferred from the analogy of allied species, all is chaos and confusion... (Walsh 1863, 220).

On p. 221 he continues: "I am not ignorant of the existence in the Vegetable Kingdom of what are called Dimorphous species..."

There follows a long list of polymorphisms and dimorphisms without intermediates in insects. Examples include: neuters in social insects, gynandromorphs in *Dytiscus*, *Papilio*, and *Colias*, orange females of the dragonfly *Agrion ramburii*, dimorphism of horns in male *Siagonium* beetles and allies, brachyptery/macroptery in Orthoptera, Hymenoptera, Heteroptera, Homoptera; agamous species of dimorphic forms of a sexual species, trimorphic heterostyly in plants, soldier castes in *Atta* ants and in termites, forms of females in the butterfly *Vanessa interrogationis* [= *Polygonia interrogationis*]. However,

> In the meantime, the general non-existence of intermediate grades between two closely-allied forms may and must be taken as prima facie evidence of their specific distinctness. That "the exception proves the rule" is an old and not very philosophical saying; but that there are exceptions to almost all rules in Natural History is undoubtedly true. Monomorphism is the rule; Dimorphism is the exception (Walsh 1863, 221).

This article was cited by Wallace in his 1865 article, particularly with respect to the case of *Papilio memnon* as described above. Walsh had discovered in Illinois a similar case of sexual dimorphism and female-limited polymorphism in what is now *Papilio glaucus*, which has some females that are black, mimics of *Battus philenor*, and some yellow, and non-mimetic, like the male. The very next year, 1864, Walsh addressed the extraordinary case of the host races of *Rhagoletis pomonella*, and again came up with a reproductive isolation definition of species and mechanism of speciation, similar to Poulton's (Berlocher and Feder 2002).

## Wallace's Views on Species in Later Life

Wallace differed with Darwin on a number of issues, such as the evolution of man and sexual selection by female choice (S729 1905), but he never seems to have had strong disagreements with Darwin on species. In the 1860s, he wrote to Darwin with a suggestion that hybrid sterility might be explained via natural selection (Wallace 1868). This was perhaps in response to the apparent problem T.H. Huxley had raised: that in order for natural selection to be a complete theory of the origin of species, it must also explain hybrid sterility. Darwin replied to Wallace arguing that he could not entertain this idea (Darwin 1868): natural selection can never act to reduce fertility of individuals, even if it may eventually be advantageous to species divergence to lack gene flow. As sterility was not a necessary or sufficient characteristic of species, its explanation was not crucial to the theory of the origin of species by natural selection. Wallace seems to have accepted this, and did not publish his theory. Twenty-one years later he described the episode in print (Wallace 1889).

Wallace also demolished a later theory to explain hybrid sterility between species by natural selection, a phenomenon called "Physiological Selection" (Romanes 1886), by means of a numerical

argument (S389 1886, S724 1889). George Romanes had been an earnest and devoted disciple of Darwin's, but as Wallace points out, argued by assertion rather than marshalling any facts in support of his ideas. In *Darwinism* Wallace includes a long chapter "On the Infertility of Crosses…" (S724, 152-86) in which he is in complete agreement with Darwin's argument that sterility is a by-product of evolution, rather than an "intended" consequence of natural selection. Nonetheless, Wallace himself still seems dissatisfied, and produces a somewhat rambling, five-page theory of his own to explain sterility; yet, as is typical of Wallace's honesty, recognizing his theory's tortuousness, he attempts a brief summary of his argument, in footnotes lasting a good three pages ("As this argument is a rather difficult one to follow…I add here the following briefer exposition…", pp. 179-81). The important additional ideas he lays out here are that, provided divergence takes place in different environments, natural selection for ecological divergence may exceed the power of natural selection to prevent the evolution of intersterility, and that selection for a "disinclination to crossed unions" may occur.

> The constant preference of animals for their like, even in the case of slightly different varieties of the same species, is evidently a fact of great importance in considering the origin of species by natural selection, since it shows us that, so soon as a slight differentiation of form or colour has been effected, isolation will at once arise by the selective association of the animals themselves… (S724, 172-73).

Wallace is here proposing what later became known as "reinforcement," an idea now generally attributed to Dobzhansky (1940). This is somewhat surprising, as the idea has been dubbed the "Wallace effect" by Grant (1966) and Murray (1972). Recent evidence has abundantly proved that the idea is correct, although we don't yet know how common it is in a state of nature (Coyne and Orr 2004; see also Chapter 10).

Much later, in 1900, Wallace was involved in correspondence about species concepts with Henry Bernard, reprinted in Cock (1977). In his letter of reply, late in life, and this time with the aid of a diagram, Wallace again expounds his (and Darwin's) theory of speciation via extinction of intermediates. Interestingly, Mayr (1982) chooses this single, casual, and unpublished example to demonstrate Wallace's primitive and "typological" lack of understanding of species. Mayr apparently does not realize that his own geographic, polytypic, biological species concept stems ultimately from Wallace's original work with papilionid butterflies, as well as his vast knowledge of birds of South East Asia. I think one can easily argue, based on the 1865 monograph and 1889 book, that Wallace knew exactly what he was talking about: Mayr, who cut his own teeth as a bird collector on a much shorter trip to New Guinea, simply does not do Wallace justice.

## Conclusion

Wallace, in 1865 and 1889, developed and supported perhaps the clearest conceptualization of species of all the early Darwinians. In this, he did not in the slightest bit deviate from Darwin's own conception of species, although he clarified and greatly extended its geographic scope. He had always found Darwin's arguments on this topic both convincing and worthy of admiration. Even 30 years after the *Origin*, Wallace sides with him:

> Generally speaking, it may be said that the varieties of any one species, however different they may be in external appearance, are perfectly fertile when crossed, and their mongrel offspring are equally fertile when bred among themselves; while distinct species, on the other hand, however closely they may resemble each other externally, are usually infertile when crossed, and their hybrid offspring absolutely sterile. This used to be considered a fixed law of nature…[however]…The elaborate and careful examination of the whole subject by Mr. Darwin, who has brought together a vast mass of evidence from the experience of agriculturists and horticulturists, as well as from scientific experimenters, has demonstrated that there is no such fixed law in nature as was formerly supposed (S724, 152-53).

Species were, to Darwin, Wallace, Bates, and Walsh exactly the same kinds of things as varieties, differing only in the presence of morphological gaps between them. To erect a theory of the transmutation of species, they had to reject the old creationist idea that species were intersterile, while varieties within species were interfertile. They didn't deny that hybrid sterility was a tendency to which species are prone,

but there are exceptions to this rule, and the very odd laws of sterility rule out hybrid sterility as a good definition. Wallace in particular enunciated a clear species concept that combined Darwinism with his knowledge of the geography of biodiversity in South America and South East Asia (S96 1865). He saw the logic in Darwin's stance on species, and stuck with it. Furthermore, Wallace's extension of the Darwinian species concept to broader geographic regions, far from being superseded by the polytypic or biological species concept of Mayr in the 1940s, in fact forms a clear forerunner of the geographic parts of that idea.

Subsequent generations of evolutionary biologists ignored these subtleties, and eventually, by the 1960s accepted a new species concept, based on the very essence of reproductive isolation that Darwin and Wallace had recommended discarding. These post-World War II ideas weren't so much wrong, as lacking the depth already explored by the early Darwinists. By the 1980s, species concepts were again becoming a battleground for evolutionary biologists, with the rise of the phylogenetic species concepts. Now we seem again to be on the verge of entering a new age of enlightenment about the complexity of species and speciation. Is the wheel of ideas ready to turn again?

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