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Darwin and species

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One would have thought that, by now, 150 years after 'The Origin,' biologists could agree on a single definition of species. Many biologists had indeed begun to settle on the 'biological species concept' in the late Modern Synthesis (1940-1970), when new findings in genetics became integrated into evolutionary biology. However, the consensus was shortlived. From the 1980s until the present it seems not unfair to say that there arose more disagreement than ever before about what species are. How did we get into this situation? And what does it have to do with Darwin? Here, I argue that a series of historical misunderstandings of Darwin's statements in the 'Origin' contributed at least in part to the saga of continued conflict among biologists about species, and that it continues to this day. Today, Darwinian ideas about species are becoming better understood. At long last the outlines of a new and more robust Darwinian synthesis are becoming evident. This "re-synthesis" (as it perhaps should be called) mixes Darwin's original evolutionary ideas about species with evidence from modern molecular and population genetics.

What did Darwin mean by species?

Darwin realized he had convincing proof that species evolved, rather than were created. But this understanding caused a terminological problem that he had to address in his book. Species were defined in the minds of many of his readers as members of real groups related by means of descent: all members of a species were related by descent, whereas no individual was descended from members of another species. A second idea, which had been promoted especially by the French naturalist Buffon, was that the intersterility of species was a protective mechanism with which species which had been endowed by the Creator to maintain their purity. Thus, the famous anatomist Richard Owen, a powerful creationist opponent of Darwin, had given this succinct definition in his 1858 treatise on chimpanzees and orang-utans:

"… an originally distinct creation, maintaining its primitive distinction by obstructive generative peculiarities" (as cited by (Huxley, 1860), p. 544).

In order that he could make the argument that species evolved under his theory of "descent with modification", Darwin required a new definition of species. In particular, descent must now be allowed to extend across the species boundary, and ultimately to encompass all living things, as well as within species. Descent could no longer be used as part of the definition of species. If species evolved, we would also expect hybrid sterility to show evidence of continuous evolution across the species boundary. This terminological problem about species did not, apparently, trouble Darwin greatly (except for the matter of hybrid sterility – see below), and he spent only a little space discussing what he meant by species. Perhaps, as a naturalist, he thought that the existence and nature of species would be self-evident to his readers. Even in later editions of *The Origin*, to which he added a glossary, there is no formal definition of species.

Nonetheless, Darwin did, in my view, clearly indicate what he meant by species, and the conception of species in *The Origin* is now generally recognized by philosophers and historians to have been a useful one for his purpose, that is to demonstrate evidence for their transmutation

(Lovejoy, 1968; Ghiselin, 1969; Kottler, 1978; Beatty, 1985; Ruse, 1987; McOuat, 1996; Stamos, 2006; Kohn, 2009; Ereshefsky, 2009; Sloan, 2009). Darwin's definition was the simplest that allowed for multiple species to originate from a single ancestral species. One of his clearest short statements on species is in the summary at the end of *The Origin*: "Hereafter we shall be compelled to acknowledge that 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, whereas species were formerly thus connected" ((Darwin, 1859): 485).

In *The Origin*, Darwin devoted a large portion of Chapter II ("Variation under nature") to discussing what species and varieties were, and how difficult they can be to distinguish. His method of distinguishing varieties from species in this chapter was: "Practically, when a naturalist can unite two forms together by others having intermediate characters, he treats the one as a variety of the other, ranking the most common, but sometimes the one first described, as the species, and the other as the variety" (p. 47). Of course, it is really a statement about varieties, not species: forms lacking morphological gaps between them are varieties; but a species definition is implicit: forms that have gaps between them are separate species.

But then Darwin immediately qualified this statement, and in doing so, unwittingly confused many of his subsequent readers: "But cases of great difficulty, which I will not here enumerate, sometimes occur ... 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" (p. 47). Many subsequent authors have cited the latter sentence as evidence of Darwin's nihilism about species, while ignoring the foregoing statements. In fact, if the unwary reader fails to concentrate, Darwin seems to tack back and forth, with statements such as: "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" (p. 177), which sounds almost like the opposite of what he has said in Chapter II.

Later, in *The Descent of Man* (Darwin, 1871), there is perhaps a rather clearer statement: "Independently of blending from intercrossing, the complete absence, in a well-investigated region, of varieties linking together any two closely-allied forms, is probably the most important of all the criterions of their specific distinctness". Darwin used this definition to argue that all of the races of Man belong to the same species[1] (pp. 214-215).

It seems quite clear to me, even from the few excerpts cited here, that Darwin never claimed that species didn't exist or were "unreal," however many biologists, philosophers of science, and historians of science would have us believe the converse (a more detailed textual analysis is given in (Mallet, 2010b). Darwin was not arguing that all

[1] Darwin's bitter opponent, Richard Owen, while deprecating the idea that humans evolved from ape-like ancestors, nonetheless categorized species the same way as Darwin: that all human races belonged to the same species, whereas the orang, chimpanzee, and gorilla were separate species (Owen, 1859). He did this for very much the same anatomical and morphological reasons as Darwin – the presence or absence of intermediates. The last thing that Darwin would have wanted was to invent a definition of species that played havoc with existing taxonomy. In *The Origin* he needed only to explain how generally accepted taxonomic species, those recognized by "naturalists having sound judgement," could have evolved. He intentionally adopted the practical methods that most naturalists were using in

species are arbitrary. The statement "the opinion of naturalists having sound judgement and wide experience seems the only guide do follow" did not imply that "naturalists of sound mind" were required to use educated guesswork. Darwin was was certainly arguing that species were similar to "varieties", but only up to a point. Species differed from varieties in that they lacked morphological intermediates: there were gaps between them. In his view, Darwin had indicated adequately what he meant by species, and then moved on. A more important task, and a major one in *The Origin*, was to show that there were many fuzzy borderline cases – these provided evidence for continuous evolution between species. Good evidence for this interpretation is that the pages containing Darwin's most disputed passages about species in Chapter II all have the header "DOUBTFUL SPECIES" in the first edition (Mallet, 2010b). Darwin was merely showing here that, in *doubtful* cases, it is difficult to tell species from varieties, as a necessary prelude to arguments about how species might evolve. He never intended the message, now widely believed to be Darwin's goal by latter-day readers, that *all* species blended together "in an inextricable chaos of varying and intermediate links."

The myth of "Darwin's failure"

It is an extraordinary paradox that what to Darwin was the most important theme of *The Origin* also became the most doubtful in the minds of his readers, even today. Almost everybody, at least by the mid-20th Century, agreed that Darwin had written a great book, that he had proved that species had evolved from varieties, and that natural

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1859, while separating his definition of species from the creationist theoretical baggage it had carried hitherto.

selection was an important process in nature. What they found increasingly hard to accept, however, was that Darwin had understood what species were, and had made any effort to explain the origin species from varieties, or that natural selection was involved (Mallet, 2008b). By the time of the "Modern Synthesis," this view hardened into a dogma that Darwin had completely failed:

"Darwin succeeded in convincing the world of the occurrence of evolution and ... he found (in natural selection) the mechanism that is responsible for evolutionary change and adaptation. It is not nearly so widely recognized that Darwin failed to solve the problem indicated by the title of his work. Although he demonstrated the modification of species in the time dimension, he never seriously attempted a rigorous analysis of the problem of the multiplication of species, the splitting of one species into two" ((Mayr, 1963), p. 12).

"In retrospect, it is apparent that Darwin's failure … resulted to a large extent from a misunderstanding of the true nature of species" (Mayr 1963, p. 14).

Mayr's critique came from the Modern Synthesis standpoint of his own 'biological species concept', in which species were defined as populations reproductively isolated from one another by 'reproductive isolating mechanisms.' Darwin, argued Mayr, had not understood the fundamental importance of reproductive isolation in speciation implied by the biological species concept. The undoubted primary reason why Mayr found Darwin's pronouncements on species illogical was that Darwin strenuously argued in his chapter "Hybridism" against the importance of hybrid sterility in providing either useful definition of species or an explanation of speciation; "It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties" (Darwin 1859: 248). To Mayr, in contrast, hybrid sterility and other 'isolating mechanisms' were the key differences between species and varieties, and the elucidation of their origin constituted an understanding of speciation. Mayr's isolating mechanism of hybrid sterility was to Darwin an incidental by-product of other evolutionary changes between species, that would not have warranted the term 'mechanism' at all, since it could not be explained directly by natural selection[2]. Darwin certainly appreciated and discussed how species intersterility and reluctance to mate allowed the coexistence of species, and that these traits were strongly associated with what taxonomists recognized as separate species (Mallet, 2010b). Yet to Darwin it was the failure of direct natural selection to explain the evolution of hybrid sterility, the fertility of many hybrids between generally accepted 'good species', as well as the existence of some kinds of infertility within species, that forced him to abandon an idea that species could be defined via reproductive isolation.

However, let us not just blame Mayr and the Modern Synthesis for this misunderstanding. The problems for the understanding of Darwin's ideas about species go back much further than the middle of the 20th Century. The seeds of the difficulty can be seen even in one of the most positive reviews ever published of *The Origin*, by the very man

[2] Mayr, unlike Dobzhansky, agreed with Darwin that there was no evidence that sterility and inviability had evolved via natural selection. Nonetheless, Mayr clearly agreed with Dobzhansky that isolating mechanisms were in some sense adaptive, that they were useful to species as a means of keeping them apart from other species (Mallet, 2010a).

nicknamed “Darwin’s bulldog,” Thomas Henry Huxley. While generally complimentary about natural selection and that species arose by evolution, he also wrote: “…There is no positive evidence, at present, that any group of animals has, by variation and selective breeding, given rise to another group which was even in the least degree, infertile with the first. Mr. Darwin is perfectly aware of this weak point, and brings forward a multitude of ingenious and important arguments to diminish the force of the objection. … but still, as the case stands, this ‘little rift in the lute’ is not to be disguised or overlooked” ((Huxley, 1860), p. 74-75). This statement forms a conclusion to a long discussion of Darwin’s evidence on the nature of species, with which Huxley largely agrees.

But the “rift in the lute” turned out (and was perhaps intended) to be a very British understatement. Wallace wrote that it was “one of the greatest, or perhaps we may say the greatest, of all the difficulties in the way of accepting the theory of natural selection as a complete explanation of the origin of species” (Wallace, 1889): 152. Much later, “the remarkable difference between varieties and species with respect to fertility when crossed” became seen by one of the major 20th Century historians of evolutionary ideas as “the greatest of all the difficulties in the way of accepting the theory of natural selection as a complete explanation of the origin of species” (Lovejoy, 1968)[3].

[3] This paper was originally published for the first Darwin centenary in 1909, and revised for the centenary of “The Origin” in 1959. To my mind, it remains one of the best pieces of scholarship documenting not only precisely what it was that Darwin and Wallace discovered, but also exploring and partly explaining the great mystery of why other great biologists, such as Thomas Henry Huxley did not discover it themselves, even though many of Darwin’s conclusions in retrospect immediately seemed quite obvious. As Huxley himself remarked: “My reflection, when I first made myself master

The problem arises with the second part of Owen's definition "maintaining its primitive distinction by obstructive generative peculiarities". Darwin had argued so vehemently against reproductive isolation as a definition of species because creationists, from Buffon onwards, had proposed hybrid sterility to be evidence of the Creator's wisdom. Darwin probably felt he had to show that sterility wasn't, in fact, a valid definition in order to disabuse his readership of the idea. But to those, like Owen and Huxley, for whom it was key to explain hybrid sterility in a theory of speciation, Darwin's belittling of its importance seemed to duck the issue, while his partial explanation of sterility as a by-product of other forces seemed weak. Darwin was very clear that his greatest theory, natural selection, failed to explain hybrid sterility. What then did Darwin think had caused it? "The foregoing rules and facts … appear to me clearly to indicate that the sterility, both of the first crosses and of hybrids is simply incidental or dependent on unknown differences, chiefly in the reproductive systems, of the species which are crossed. The differences being of so peculiar and limited a nature, that in reciprocal crosses between two species the male sexual element in one will often freely act on the female sexual element of the other, but not in reversed direction." (p. 260-261). "…sterility of first crosses and of hybrids … is not a special endowment, but is incidental on slowly acquired modifications, more especially in the reproductive systems of the forms which are crossed" (p. 272)

In other words, Darwin really didn't know what caused hybrid sterility, although some causes could be ruled out. However, hybrid sterility was

of the central idea of the 'Origin' was, 'How extremely stupid not to have thought of that!' " (Huxley, 1887).

far from universal among species, and was so scattered and "incidental" that it seemed most unlikely that it was either a naturally selected adaptation or an attribute provided by God to preserve the purity of species. It must instead be "incidental on slowly acquired modifications" – a by-product of evolutionary divergence in general, or a 'pleiotropy' to use today's genetic term. We will see evidence in correspondence from Darwin to Wallace in 1968 (see below) that Darwin himself was dissatisfied with his partial explanation, although it was clearly more of a problem for Huxley and others. Today, whatever their view of Darwin's ideas about speciation, evolutionary biologists accept Darwin's opinion that hybrid sterility is not an adaptation. With hindsight, I believe we can forgive Darwin for not explaining sterility: it is only now that its precise causes are becoming understood. Sterility represents a failure in hybrids of normal beneficial interactions among genes that have diverged in different populations for a sufficiently long time. Although such genes are often popularly referred to as "speciation genes", it is now generally recognized that many, and probably most of the differences that cause negative interactions in hybrids evolved long after speciation is complete, and rarely, if ever cause species to divide (Coyne and Orr, 2004; Orr, 2009).

Physiological species versus morphological species

Returning again to 1860, we now follow the thread that led to the rejection of Darwin's view of what species were. Huxley argued that Darwin's use of the term 'species' was indeed useful, but that it was based only on morphology. But to Huxley, another very important difference between species was what he called 'physiological.' 'Physiological species' are those that are unable to interbreed successfully ((Huxley, 1860), p. 26). It is not entirely clear whether Huxley invented the term 'physiological species,' which does not appear in Darwin's writings, or whether he co-opted it from other sources that were generally read then. Regardless of the source of the idea, 'physiological species' became a touchstone for an argument that dogged evolutionary biology for the next 150 years. The morphological vs. physiological species ideas was also the major reason for the rejection of the Darwinian notion of species, as well as of their origin.

Henry Walter Bates, writing in 1863 about *Heliconius* butterflies alluded, one assumes, to Huxley's critique of 'The Origin,' in the following terms: "In the controversy which is being waged among Naturalists, since the publication of the Darwinian theory of the origin of species, it has been rightly said that no proof at present existed of the production of a physiological species, - that is, a form which will not interbreed with the one from which it was derived, although given ample opportunities of doing so, and does not exhibit signs of reverting to its parent form when placed under the same conditions with it." Bates argued that his study of *Heliconius* butterflies in Brazil, did, on the other hand, "tend to show that a physiological species can be and is produced in nature out of the varieties of a pre-existing closely allied one". Bates purported to show that although *Heliconius melpomene* and *H. thelxiope* hybridize in some places, they also "come into contact in several places where these intermediate examples are unknown, and I never observed them to pair with each other" ((Bates, 1863), vol. 1, p. 256-262). While today's taxonomy does not, I believe, support Bates' argument in the case of *Heliconius*, this passage clearly shows that Huxley's critique and the need to explain 'physiological species' were very much the talk of the town.

In March and April of 1868, Alfred Russel Wallace and Charles Darwin corresponded extensively on the subject of hybrid sterility. Wallace asked Darwin whether he could imagine that hybrid sterility arose through natural selection, and suggested several possible schemes. Darwin, perhaps exhausted by Wallace's youthful enthusiasm, enlisted his more mathematical son George (then at Cambridge) to help; together they rebutted Wallace's arguments. But the correspondence continued, and Darwin wrote back to a second enquiry: "Let me first say that no man could have more earnestly wished for the success of N. selection in regard to sterility, than I did; & when I considered a general statement, (as in your last note) I always felt sure it could be worked out, but always failed in detail. The cause being as I believe, that natural selection cannot effect what is not good for the individual…" (Darwin to Wallace, 6 Apr 1868).

Wallace did, however, touch upon one likely argument which Darwin could not refute, that "disinclination to cross" could be effected by natural selection. Darwin again: "I know of no ghost of a fact supporting belief that disinclination to cross accompanies sterility. It cannot hold with plants, or the lower fixed aquatic animals. I saw clearly what an immense aid this would be, but gave it up. Disinclination to cross seems to have been independently acquired probably by nat. selection; & I do not see why it would not have sufficed to have prevented incipient species from blending to have simply increased sexual disinclination to cross."

Wallace wrote back: “I am sorry you should have given yourself the trouble to answer my ideas on Sterility—If you are not convinced, I have little doubt but that I am wrong; and in fact I was only half-convinced by my own arguments,—and I now think there is about an even chance that Nat. Select. may or not be able to accumulate sterility.” Prophetically, he ended the discussion with a prediction that, even so, it would be a source of controversy: “However I will say no more but leave the problem as insoluble, only fearing that it will become a formidable weapon in the hands of the enemies of Nat. Selection.” (Wallace to Darwin, 8 April 1868). As it turned out, this problem led to opposition even from within the ranks of those who called themselves Darwinists.

In 1886, George Romanes, a correspondent and self-avowed “close student” of Darwin’s, published a long and discursive paper to suggest a supposedly new mechanism of how Huxley’s physiological species separated by hybrid sterility could come into being, a process he called “physiological selection” (Romanes, 1886). His phrasing reminds one strongly of the much later statements of Mayr (above). He argued that natural selection was incompetent to cause species to diverge: “…The theory of natural selection is not, properly speaking, a theory of the origin of species: it is a theory of the development of adaptive structures” (p. 370). “…What we require in a theory of the origin of species is a theory to explain [the origin of] the primary and most constant distinction between species…[:] comparative sterility towards allied forms, with continued fertility within the varietal form.” (pp. 370-371).

Romanes agreed with another Darwin critic (Wagner, 1868; Wagner, 1873) that if populations were geographically isolated, divergent variations would not be swamped by intercrossing, and so could diverge to form separate species. However, Romanes did not believe that all speciation could be due to geographical isolation; 'physiological selection,' in his view, could have the same effect of preventing gene flow. According to Romanes, if a variation (or mutation) occurs but has no effect within an emerging variety "… such that the reproductive system, while showing some degree of sterility with the parent form, continues to be fertile within the limits of the varietal form, in this case the variation would neither be swamped by intercrossing, nor would it die out on account of sterility. On the contrary, the variation would be perpetuated with more certainty than could a variation of any other kind."

Wallace, recognizing the similarity of 'physiological selection' to earlier ideas he had himself communicated to Darwin for the evolution of intersterility by means of natural section, wrote a number of articles rebutting Romanes' suggestions (Wallace, 1886). He returned to the theme in his major work intended to update and promote Darwinism thirty years after "The Origin" (Wallace, 1889). Perhaps his most cogent criticism was that Romanes had merely asserted the importance of physiological selection (clearly evident also from the Romanes quotation reproduced above); he had failed to propose a convincing mechanism whereby it would occur, or to provide any empirical evidence for its operation. Wallace introduced a mathematical argument to show that Romanes' assertion did not work, showing that eventually a new and scarcer variety that produced infertile hybrids with the commoner 'wild-type' would die out (Wallace, 1889): 181-183. The argument assumes complete hybrid sterility, but works with partial sterility as well.

Nonetheless, Wallace himself reiterated his 1868 ideas in a lengthy and rather diffuse section (1800 words) earlier in the same chapter. He argued that natural selection could explain the evolution of hybrid sterility by means of natural selection. This passage is today difficult to interpret, and, as if anticipating the befuddlement of his readers, Wallace used a still rather lengthy footnote (850 words) to elaborate a "briefer exposition…, in a series of propositions." These propositions were almost identical to those in his 1868 letter to Darwin.

Wallace's first idea was that hybrid sterility might arise "in correlation with the different modes of life and the slight external or internal peculiarities that exist between them." If so, sterility would be a by-product of the divergent environments or inherited adaptive change of two emerging varieties, and could be stable to swamping. This can be interpreted in today's terms as a pleiotropy argument: a selective adaptation to conditions of life can evolve that outweighs the indirect or pleiotropic disadvantage of the negative side-effects of the same genes on hybrid sterility (Wallace 1889: 175-178). Wallace essentially reiterated Darwin's (1859) hypothesis for the evolution of hybrid sterility, and this the one most strongly supported today.

Wallace's second, and major argument for the evolution of sterility should probably be interpreted as a kind of selection on groups rather than Darwinian natural selection on individuals. If in one part of the range of a species diverging into two varieties under natural selection, hybrids happened to be more sterile, while in another part hybrids among the same two emerging varieties were somewhat less sterile, Wallace claimed that forms showing greater hybrid sterility would increase more rapidly as a result of their greater genetic purity due to better adaptation to conditions causing the emergence of the divergent varieties in the first place (Wallace 1889: 175). This is a tricky argument to make, as it is directly contradicted within each region by the very same Darwinian argument that he used against Romanes, outlined later in the same chapter. It relies on the idea that populations with higher sterility leave more offspring overall (due to the greater purity and better adaptation to local conditions) than populations with lower sterility (and therefore lower purity). Biologists today accept that situations under which interpopulation selection or group selection of this kind outweighs a countervailing force of natural selection within populations will be rare. If we view sterility for what it is, a problem for the individual, we can imagine that sometimes a beneficial adaptation, which also causes sterility with the parental form, will evolve *in spite of* sterility, because the benefits of the adaptation outweigh the loss of offspring. This could lead to greater hybrid sterility as a by-product (Wallace's first hypothesis). But by arguing for hybrid sterility as a direct potential advantage for populations, I think that it is correct to say (Ruse, 1980; Kottler, 1985; Johnson, 2008) that Wallace was falling into the trap of naïve group-selectionism (Wilson and Wilson, 2007).

A third suggestion by Wallace, again following on from the earlier correspondence with Darwin, was that new varieties would show a correlated "disinclination to pair" (Wallace 1889: 172-173, 175-176). Wallace argued here that adaptation to different modes of life would also bring about a reduction in tendency to pair between divergent varieties, perhaps simply because organisms specializing on different resources met less often. Darwin, as we have seen, argued that there was no evidence for this. In modern terms, this is arguing for what has been lightheartedly termed a 'magic trait,' that is a pleiotropic effect that automatically aids speciation (Gavrilets, 2004). Pleiotropic effects of ecological adaptation on mate choice are today thought to provide an important route to ecological speciation (Drès and Mallet, 2002; Hendry et al., 2007).

There is a fourth and final suggestion, which Wallace could have made in 1868 or 1889, but apparently did not. As Darwin had briefly mentioned in his letter of reply to Wallace (above), "disinclination to pair" with individuals of a different type would seem likely to be enhanced by natural selection because it would reduce the number of useless offspring that might become sterile. This argument was revived again by Theodosius Dobzhansky in 1940 and became variously known as 'reinforcement' (Blair, 1955; Levin, 1970; Butlin, 1985), or the 'Wallace effect' (Grant, 1966; Murray, 1972). Today reinforcement is generally accepted as a possibly common means whereby reproductive isolation is acquired via natural selection (Coyne and Orr, 2004; Johnson, 2008).

Post-Mendelian ideas of physiological species

By around the turn of the century, many people were beginning to argue, in contrast to Darwin and Wallace, that species should be defined physiologically, i.e. by means of their reproductive isolation

(Cockerell, 1897; Petersen, 1903; Poulton, 1904; Jordan, 1905). With the rediscovery of Mendelian heredity, William Bateson and the Mendelians approached the understanding of species from a new, experimental genetics viewpoint; sterility could now be investigated in the laboratory. Bateson argued that Darwin's definition of species ignored what was their most important feature, their physiological tendency to produce sterile hybrids (Bateson, 1913; Bateson, 1922). Darwin's was an incomplete theory of speciation since it could not explain this important "specificity" of species in nature, as Bateson called it. By 1926, the Russian geneticist Sergei Chetverikov had argued that "the real source of speciation, the real cause of the origin of species is not selection, but isolation" (quoted in (Krementsov, 1994): 41).

Russian entomologists and geneticists such as Wilhelm Petersen, Sergei Chetverikov, and A.P. Semenov-Tian'-Shanskii, as well as workers in the USA and Europe, who all supported these new ideas on species, were undoubtedly strong influences on the young entomologist, and later geneticist Theodosius Dobzhansky (Krementsov, 1994). After emigration to the USA, Dobzhansky wrote the most widely read treatise of this period on the origin of species (Dobzhansky, 1937). This work blended genetical and Darwinian ideas about speciation for the first time, and supported the idea of species being definable via "physiological isolating mechanisms." "When such mechanisms have developed [between two diverging races], and the prevention of interbreeding is more or less complete, we are dealing with separate species" (Dobzhansky, 1937: 63).

In an important section, "The Origin of Isolation," Dobzhansky argued that hybrid sterility and sexual or psychological isolation could reinforce one another, and that further isolation could in some circumstances be adaptive. As applied to hybrid sterility and inviability, this again appears to be an example of naïve group selectionism (see especially pp. 257-258), even though in the same chapter he also accepted Darwin's argument that hybrid sterility was often a by-product of divergent evolution, rather than a directly selected influence on speciation. Dobzhansky was promoting a Darwinian approach to the understanding of speciation, and he seems to have been careful to avoid a direct critique of Darwin's own view of species, which of course differed from his own.

Ernst Mayr (1942, 1963) adopted Dobzhansky's reproductive isolation definition of species, and renamed it "the biological species concept." As we have seen above, he did not shy away from arguing that this "new" idea of species was very different from Darwin's, and that it demanded an entirely new view of the origin of species. In the opinion of Dobzhansky and Mayr, this new view of species and speciation represented the Modern Synthesis of Darwinism and Mendelian genetics.

Species concepts today

We have seen how Darwin seems to have failed to convince even his own chief supporter, Huxley, that species were best not to define via reproductive isolation. Huxley's invention of the term "physiological species" led eventually to a resurgence and finally, by the 1960s, almost complete acceptance of the idea that the fundamental nature of species was reproductive isolation – the very idea that Darwin had tried to disprove. This treatment of species as if they were fundamentally and physiologically distinct from varieties led, perhaps inevitably given that opinions were split about the importance of reproductive isolation, to the search for other fundamental concepts to define species. The phylogenetic concept of species is an example. In one version, a phylogenetic species is a distinct form that retains stable morphological or genetic differences, whether or not it is reproductively isolated (Cracraft, 1989). A recent version of this idea employs Bayesian statistical analyses to determine the presence of separate, phylogenetic species in a set of individual genomic sequence data. Under this idea, a pair of populations is treated as two separate species only if a model of two populations with finite time of divergence between them has a much higher Bayesian posterior probability than a model of a single population (itself equivalent to two imaginary separate populations that have been diverging for zero time) (Yang and Rannala, 2010).

The validity of a Darwinian notion of species in 2011

However, another view is that a Darwinian delimitation of species still today has some validity: species are separate 'genotypic clusters' when considered in a molecular genetic sense (Mallet, 1995). Arguing for two species based on genetic data is equivalent to arguing that there are two sets of individuals each coming from a population which differ in at least some gene frequencies. In other words, one needs only to disprove the null hypothesis that there is a single population in the array of individual genetic or genomic data, in order to prove that two populations is a better hypothesis; and the method can be extended to multiple populations. If we plot the distribution of individuals along axes representing multilocus gene frequencies, the distribution will be bimodal if there are two species, or single-peaked if there is only one. Data can be treated statistically by means of a Bayesian Markov-Chain Monte-Carlo approach (Pritchard et al., 2000; Huelsenbeck and Andolfatto, 2007). This procedure is called an "assignment test" because it determines the appropriate number of distinct populations into which to assign each of the genotyped individuals in a sample. It should also be mentioned that the Bayesian method of Yang and Rannala is somewhat similar to an assignment test, but it is a more complex one based on a precise mathematical model of genealogical divergence. Gene frequencies may of course differ if populations are spatially isolated without necessarily implying speciation, but if distinguishable populations occur together in the same region and yet retain differences at multiple loci, the two populations will generally be accepted to be different species. Intermediates may occur, but provided they are rare in areas of overlap, these populations can also be considered separately delimited species.

Today assignment tests are useful in delimiting cryptic species in many groups, such as flowering plants (Larson et al., 2010; Zeng et al., 2010), corals (Pinzón and LaJeunesse, 2011), butterflies (Dasmahapatra et al., 2010), or primates such as mouse lemurs (Weisrock et al., 2010). These methods are also useful for identification of genetically distinguishable ecological taxa normally considered below the species level in taxa such as aphids (Peccoud et al., 2009) or social-group forms of mammals such as the orca (killer whale) (Hoelzel et al., 2007). In Darwinian terms, such ecological races represent exactly the “doubtful cases” that Darwin used to suggest that species evolved from varieties (Mallet, 2008a).

It seems we have come full circle from a general disregard for Darwin’s view of species, to using statistical methods employing a recognizably Darwinian notion of species, although today’s methods tend to be based on genetic rather than purely morphological data. Physiological and biological concepts of species can be seen as explanations of the scarcity of intermediates between species, and so genotypic bimodality generally makes as much practical sense to those who support phylogenetic or biological concepts of species as it does to those who feel that Darwin was correct about species all along. Perhaps now “we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species” (Darwin 1859: 485). We shall see!

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