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"A temporary oversimplification": Mayr, Simpson, Dobzhansky, and the origins of the typology/population dichotomy (part 2 of 2)

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ABSTRACT

The dichotomy between 'typological thinking' and 'population thinking' features in a range of debates in contemporary and historical biology. The origins of this dichotomy are often traced to Ernst Mayr, who is said to have coined it in the 1950s as a rhetorical device that could be used to shield the Modern Synthesis from attacks by the opponents of population biology. In this two-part essay, I argue that the origins of the typology/population dichotomy are considerably more complicated and more interesting than is commonly thought. In the first part, I argued that Mayr's dichotomy was based on two distinct type/population contrasts that had been articulated much earlier by George Gaylord Simpson and Theodosius Dobzhansky. Their distinctions made eminent sense in their own, isolated contexts. In this second part, I will show how Mayr conflated these type/population distinctions and blended in some of his own, unrelated concerns with 'types' of a rather different sort. Although Mayr told his early critics that he was merely making "a temporary oversimplification," he ended up burdening the history and philosophy of biology with a troubled dichotomy.

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1. Mayr's mixed tape

In part one of this two-part article, we have seen that Simpson and Dobzhansky each developed their own typology/population distinction in relative isolation from the other. This is not to say that they independently came up with the *term* 'typology,' but rather that the *arguments* they formulated under this banner were of their own making.[1] Until the 1960s, Simpson and Dobzhansky indeed never cited each other when discussing types or typology. This is not all that surprising, since each of them drew the distinction in a context that was of marginal professional interest to the other. The methodology of taxonomy in a paleontological context was not a theme of direct interest to Dobzhansky.[2] Similarly, debates about race and classical/balance controversy were of little professional concern to Simpson. Delimiting species in the fossil record was hard enough, dealing with subspecies and races fell largely outside the purview of the paleontologist. For the same reasons, it would have been hard to see the relevance of the classical/balance controversy for paleontology.

In this regard, Dobzhansky and Simpson differed quite a bit form Mayr. As a neontological systematist with a strong interest in speciation, his area of expertise overlapped with that of Simpson on questions about classification, and with Dobzhansky on the genetics of races and species. More than each of his friends, Mayr was

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[1] We will see shortly that they likely had a common source for the term: Mayr.

[2] The book by Simpson that Dobzhansky was most interested in, *Tempo and Mode in Evolution* (Simpson, 1944), did not make any reference to Simpson's type/population distinction. The intricacies of taxonomic methodology were not discussed in this book (see Part 1, Section 2.5).

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aware of what the others were writing about in various domains. Yet, as we will see next, this did not result in Mayr managing to successfully *integrate* what he read about types.

1.1. In Simpson's footsteps, out of step

In 1964, a reprint was issued of Mayr's influential *Systematics and the Origin of Species* from 1942. In a newly written introduction, Mayr reminisced how back in the day he had set out "to demolish the typologically defined species" (Mayr, 1942 [1964]). In 1999, in another reprint of the original, Mayr again called to mind how his 1942 self had been "appalled by the typological spirit dominating taxonomy" (Mayr, 1942 [1999]). Readers of these reprints might have been surprised to discover that the word 'typology' and its cognates did not occur in the remainder of the reprinted book. But, surely, we should interpret Mayr's remarks the way we interpreted Simpson's reflections on his reprinted article from 1937. That is, Mayr was pointing to his 1942 book as the first exposition of an argument against a position that he would only later label 'typological.'

However, this does not imply that *Systematics* presented the outlines of a coherent position or argument against typology. Instead, we will see that this book presented a number of different, thematically unrelated concerns with types, which Mayr 'compressed' into a single charge on typology in later writings. This was a hugely problematic move: not only because it amounted to a conflation of entirely different sorts of argument, but also because many of the separate arguments Mayr outlined in *Systematics* were already on shaky grounds.

Let's begin by reviewing what Mayr had to say about types in 1942. Mayr started out by treading in Simpson's footsteps, and argued that a type specimen "is not necessarily the most typical specimen of the species" but only serves "to fix the correct name to a definite individual and thus to the species or subspecies to which this individual belongs" (Mayr, 1942, p. 15). However, in the course of his book, Mayr gradually transformed Simpson's methodological argument against the use of types as classificatory standards into something much bolder. A hundred pages into *Systematics* we read that the classificatory use of type specimens was somehow part and parcel of a particular species concept: the morphological species concept:

> The taxonomist who follows this [morphological] species concept sets up a number of standards ('types') to which he applies his species names. As he receives additional specimens from new localities, he compares them with his standards. If they are different, he describes them as new species, if they agree more or less, he unites them with the known species.
>
> Mayr (1942, p. 109)

Mayr argued that this morphological species concept, on which a species was defined as "a group of individuals or populations with the same or similar morphological characteristics," was fundamentally flawed, since "it does not delimit true species from subspecies below or genera above" (Mayr, 1942, p. 115). By defining species morphologically one would fail to identify *the* distinctive features of taxa at the species rank, to wit, "the interbreeding of the populations that belong to the species, and the 'reproductive isolation' against the populations, which do not belong to the species" (Mayr, 1942, p. 119).

Here Mayr departed significantly from how Simpson had presented the type/population distinction. Simpson had never suggested that the difference between type- and population-based taxonomic *methodologies* was correlated with a difference in *species concepts*. On the contrary, in his view population-based methods remained wedded to the practice of delimiting morphological resemblance groupings. The interbreeding relations that formed the basis for the biological species concept could seldomly be determined without making an inference from character distributions. On this ground, Simpson also concluded that the morphological and biological species concepts were not at all incompatible. "[The] morphological definition is merely a description of the usual result of the situation involved in the [biological] definition. Therefore, morphological species tend to correspond closely to [biological] species" (Simpson, 1943, p. 154).[3] Simpson pointed out that in everyday taxonomic practice the morphological approach was the actual approach used by both neontologists and paleontologists to infer species boundaries, respectively "for practical reasons" and "from necessity" (Simpson, 1943, p. 147).

Mayr clearly had a different understanding of the difference between the morphological and the biological species concepts. Although he admitted that, in practice "the potential capacity for interbreeding can be decided only by inference, based on a careful analysis of the morphological differences of the compared forms" he was quick to add that "this does not mean that I am retracing my steps and now propose to accept a morphological species definition" (Mayr, 1942, p. 121). Mayr's problem with the morphological definition was that it took the study of characters to be the final word, whereas on a biological definition this verdict was "always subordinated in importance to biological factors." What Mayr meant was that on a biological definition knowledge about breeding patterns could trump inferences about morphological resemblance groupings. This had important implications in the several cases of recently discovered 'sibling species': breeding populations that are morphologically indistinguishable but whose members fail to produce fertile offspring when crossed. Mayr had discussed the topic of sibling species at length in preceding chapters of *Systematics* as well as in earlier publications (Mayr, 1940a,b). The specific distinctness of these populations from a 'biological' point of view would be missed from a 'morphological' resemblance-based perspective. For this reason, Mayr strongly disagreed with Simpson's judgement that "it is not a serious error to reduce two such species, certainly very closely related, to subspecific status or even to fuse them completely in the taxonomic system" (Simpson, 1943, p. 154). Mayr instead viewed sibling species as "all-important borderline cases" that formed "the most serious objection to a morphological species definition" (Mayr, 1942, p. 116). Hence, the existence of sibling species showed that defining species as morphological resemblance groupings fell short. Only the addition of further 'biological' information about breeding relations would lead one to draw the right boundaries. Therefore, even the use of statistical methods to infer morphological distributions from samples of specimens would have to be "superimposed on a biological analysis" (Mayr, 1942, p. 135).

It is clear, then, that Mayr and Simpson had a genuine disagreement about the meaning and legitimacy of the morphological species concept. But Mayr's position in this dispute fails to justify his suggestion that the morphological species concept—however it be interpreted—was wound up with the use of type specimens as classificatory standards. Mayr would have to admit that this method of inference could be replaced with a

[3] I have substituted 'biological species' for Simpson's somewhat confusing term 'genetic species.' The symposium this paper was part of was held at the AMNH in April 1942 (Bogert, 1943), i.e. before Mayr submitted his manuscript of Systematics later that year. (The book was published in November.) Mayr also presented a paper at this symposium (Mayr, 1943), in which he made remarks similar to those that will be assessed in the remainder of this section.

statistical one without needing to abandon the morphological species concept. In addition, his position clearly allowed for the possibility of embracing the biological species concept while continuing to use the method of setting up type specimens as a morphological proxies for determining gaps between breeding units. Simpson, in contrast, had been distinctly aware of the latter possibility. He emphasized that his argument against the use of type specimens as classificatory standards was relevant to all biologists who used morphological material as a means of delimiting breeding groups (Simpson, 1943, p. 147).

What this shows, it that Mayr's attempt to integrate Simpson's *methodological* criticism with his arguments against a species *concept* simply did not work. As a result, the first argument against types that emerged from *Systematics* was rather confusing, if not plainly incoherent.

1.2. Biotypes and typology

Mayr's failed attempt to amalgamate Simpson's methodological type/population distinction with a distinction between species concepts would have been easy to undo in a future publication. But instead of nuancing and correcting his treatment of type specimens later in the 1940s, Mayr added to the confusion by merging his critique of type specimens with an entirely different argument directed at a different notion of type: the *biotype* concept.

Mayr had already discussed this notion of types in *Systematics*, in the context of yet another species concept: the genetic species concept.[4] Mayr pointed out that early nineteenth century botanists such as Wilhelm Johannsen (1857–1927) and Hugo de Vries (1848–1935) had invoked the concept of a biotype to refer to highly inbred populations of individuals with identical genotypical constitutions. Some experimentalists argued that only these groups of genotypically identical individuals merited the name 'species.' The Dutch botanist Johannes Lotsy (1867–1931), for instance, asserted that "a species is a group of genetically identical individuals" (Lotsy, 1918, quoted in Mayr, 1942, p. 118) and thus concluded that "the Linnean [sexual] species is no species" (Lotsy, 1916, p. 22). This genetic 'biotype' species concept was obviously antithetical to Mayr's preferred definition of a species as a reproductively isolated natural breeding unit. The biotype concept resulted in absurdities when applied to natural populations of sexual organisms. It would entail that "except for identical twins, every individual in a bisexually reproducing species is a different biotype" (Mayr, 1942, p. 118).[5] The biological species concept, on the other hand, made salient that speciation in the wild proceeds by geographical isolation of interbreeding populations. Because of its obvious shortcomings, Mayr saw no reason to pay further attention to the notion of biotypes in the remainder of *Systematics* and in his later articles on species concepts (Mayr & Dobzhansky, 1945; Mayr, 1946a,b,c).

However, Mayr did return to the biotype concept in the context of a rather different debate, about theories of speciation. In the mid-1940s, Mayr noticed with concern how theories of ecological speciation—which he thought he had refuted in *Systematics*—began to regain support (Test, 1946; Thorpe, 1945; Valentine, 1945). Theorists of ecological speciation expressed doubt about geographical isolation being the only driver of speciation and suggested that local differences in ecology could be an alternative cause. This meant that sympatric speciation—speciation without geographic isolation—was a genuine possibility. Mayr regarded such suggestions as deeply confused. In reality, geographical speciation was perfectly compatible with ecological speciation; they were different aspects of the same process. In a letter to William Thorpe (1902–1986), Mayr expressed his belief that their there was no argument between them "about the facts but merely about their interpretation." He did admit, though, that his presentation "of the process of speciation in *Systematics and the Origin of Species* was perhaps oversimplified," and he told Thorpe that he was working on an article that would "present a synthesis of our ideas."[6]

Mayr's article, published a few months later, delivered on the promise of synthesis by filling in the ecological side of geographical speciation. But in addition, Mayr took several pages to criticize the suggestion that ecological speciation might also be compatible with sympatric speciation. And here, he made a surprising move. Theories of sympatric speciation, he argued, were rooted in a latent adherence to the biotype concept. Mayr complained that "the whole subject [of sympatric speciation] is still dominated by the early De Vriesian thesis of the origin of species by single mutations …[which] produce new 'types' as if genetic change was an 'all or nothing' mechanism" (Mayr, 1947, p. 276). Mayr accused his opponents of failing to realize that "all individuals in sexually reproducing species (except identical twins) can be expected to be genetically different" (Mayr, 1947, p. 278).

This attack on the sympatric dimension of ecological speciation quite obviously missed its target. The biologists Mayr was addressing certainly did not view species as internally homogeneous biotypes, but sided with him in defining species as groups of breeding populations. What Mayr had delivered in terms of a synthesis in the first part of his article, he molded into a misrepresentation of his opponents' views in the second part.

Mayr's remarks on biotypes were premeditated. They were part of another 'synthesis' he had been working on concurrently. A few months later, he published an article in which he suggested that the biotype concept and the use of type specimens in classification were two sides of the same coin. In a section of that article on 'The Recognition of the Population as the Basic Taxonomic Unit,' he noted:

> The individual was considered the basic unit by most of the older naturalists. The type specimen was thought to be 'typical' and other specimens that did not agree with the type were described as varieties. Eventually, however, it was realized after painstaking genetic and biometric analysis that in sexually reproducing animals no two specimens (except identical twins) are exactly alike.
>
> Mayr (1948, p. 206)

This passage shows nicely how Mayr began to interweave two lines of criticism that he had kept strictly separate in *Systematics*.

[4] Besides the morphological, biological, and genetic species concepts, Mayr also discussed the 'practical species concept' and the 'sterility species concept' in *Systematics*. In Mayr's later writings these species concepts either vanished, were merged with others, or were given a different status than other species concepts (e.g. 'philosophical' vs. 'practical' (Mayr, 1955a)). Mayr's juggling with species concepts has given rise to a cottage industry of inquiries into Mayr's changing views on species (e.g. Beurton, 2002; Bock, 2004; Ghiselin, 2004; Hey, 2006; Magnus, 1996; Queiroz, 2005). I doubt that the many changes in Mayr's taxonomy of species concepts can all be explained on substantive (theoretical) grounds, as the remainder of this section will make clear.

[5] In an article from two years earlier Mayr had similarly rejected this 'genetic distinctness' criterion of species by noting that it resulted in the view that "in fact every individual is a different biotype" (Mayr, 1940b, p. 255).

[6] Mayr to Thorpe, 30 April 1947, Mayr Papers. An earlier letter to Dobzhansky shows that a rebuttal to theorists of ecological speciation already ranked high on Mayr's to-do list. In June 1946, Mayr wrote Dobzhansky that "a thorough discussion of this subject would be very timely" (Mayr to Dobzhansky, 18 June 1946, Theodosius Dobzhansky Papers at the American Philosophical Society [hereafter: 'Dobzhansky Papers']).

The first two sentences, about the use of type specimens as classificatory standards, were clearly taken from his critique of the morphological species concept, whereas the final sentence was lifted from his critical discussion of the biotype concept. By stitching these arguments together, Mayr effectively suggested that the erroneous use of types *of* species (i.e. the use of type specimens as classificatory standards) had been rooted in a conception of types *as* species (i.e. the view that species are genetically homogeneous biotypes). The suggestion was puzzling. In reality, the two notions of type Mayr mentioned in one breath each came with entirely different sets of conceptual, methodological, and empirical commitments.[7] It is easy to grasp that there was an almost diametrical opposition between, on the one hand, the experimentalist's controlled setups that were needed to isolate pure strains of biotypes, and, on the other hand, the naturalist's informed judgment that guided the selection of typical specimens around which species could be grouped.

Mayr, however, continued confidently on the path he had begun to pave. A few months later he equated de Vries's "typological concept of species" with "[t]he old 'type concept' of the species … founded on a morphological species definition" (Mayr, 1949, p. 514). This was the first time Mayr spoke of 'typology' and '*the* type concept,' terms that suited his aim of pointing to a supposedly hidden unity underlying a diversity of uses of the word 'type'. He immediately began harnessing the power of this terminology to structure most of his work on systematics and evolution. When he received an invitation in December 1949 to participate in a symposium on systematics and anthropology, he suggested to the organizers that his talk be titled 'The Population Approach versus Typology,'[8] and in his next articles he consistently spoke of the 'typological species concept' (Mayr, 1950; Mayr & Stresemann, 1950). In his next big book, *Methods and Principles of Systematic Zoology* (1953), Mayr presented a strict contrast between "the population concept" and "the type concept" as his guiding theme (Mayr, Linsley, & Usinger, 1953, p. 15). But in explaining that the type concept "postulates that all members of a taxonomic category conform to a 'type,'" he continued to cloud what his problems with 'types' really came down to. Was he objecting to the use of type specimens as classificatory devices, or did he object to defining species as biotypes? Mayr purposely left his readers guessing. His vocabulary of 'types' and 'typology' enabled him to seemingly kill two birds with one stone, but concealed the fact that he was dealing with two very different birds.[9]

1.3. Disunity in hiding

It can hardly be a coincidence that the term 'typology' and its derivatives began to show up in Simpson's and Dobzhansky's writings shortly after Mayr had used it for the first time in April 1949 (Mayr, 1949). Simpson appears to have first referred to Schindewolf as a typologist in June 1949 (Simpson, 1949). Dobzhansky criticized the "early typologists" of race in his closing talk of a Cold Spring Harbor symposium in 1950 (Dobzhansky, 1950), with Mayr and Simpson in the audience. In earlier sessions of the symposium, Mayr had already made several references typology, in his own talk and in discussions that followed other talks.[10]

The anthropologist Sherwood Washburn (1911–2000), who had co-organized this symposium with Dobzhansky, later reminisced that "population vs. type" was a hot topic at the symposium, but "probably too fundamental an issue to be discussed usefully in a public meeting" (Washburn, 1983, p. 16). On the surface, it must indeed have seemed that Mayr, Simpson, and Dobzhansky were talking about one and the same distinction, but this impression was misleading. We have already seen that Simpson and Dobzhansky were broadcasting their own, distinct lines of argument under the banner of 'typology vs. population.' Meanwhile, Mayr was about to deploy this distinction in an even looser, even more confusing manner.

The internal tensions in Mayr's presentations of typology from the 1950s become particularly clear when we turn to his comments on several historical and contemporary scientists: Linnaeus, Goldschmidt, and Schindewolf. First, take the case of Linnaeus. In the 1950s, Mayr often presented Linnaeus as someone who "defined species typologically" (Mayr, 1958b), because of his use of typical specimens as classificatory standards. (Also see Mayr, 1951; 1953; 1957; 1960). However, whenever Mayr also touched on the biotype concept within the same discussion, he presented Linnaeus differently. In those instances, Mayr presented the adherents of the biotype conception as typologists, and portrayed Linnaeus as a (budding) population thinker who had initiated "the study of natural populations … an entirely independent conceptual stream [from typology]" (Mayr, 1957, p. 5; also see Mayr, 1953; 1955a; 1955b). As a result, Mayr sometimes made contradictory statements about Linnaeus within the span of a single publication (e.g. Mayr et al., 1953; Mayr, 1957).

Similar tensions and internal conflicts can be found in Mayr's treatment of Goldschmidt and Schindewolf. Mayr had been rather critical of Goldschmidt in *Systematics*, because of his saltationist (sympatric) theory of speciation (Goldschmidt, 1940). In his writings from the 1960s and after, Mayr invariably presented Goldschmidt as a staunch typologist for this reason (Mayr, 1963a, 1982b, 1997). Yet, in the early days of his talk about typology Mayr took a very different stance. In the publication that introduced the term 'typology,' Mayr contrasted Goldschmidt with De Vries, and argued that the former had shown that "species are not the uniform, homogeneous 'types' which the typologists made them out to be" (Mayr, 1949, p. 515). What is more, he later listed Goldschmidt among those who had helped to "introduce the population concept of the taxonomist into genetics" (Mayr et al., 1953, p. 12). It was only in the late 1950s that Mayr suddenly positioned Goldschmidt alongside De Vries among "the many well-known biologists … who are essentially typologists" (Mayr, 1958b, p. 13). Around this time he also stopped associating Goldschmidt with the introduction of the 'population concept' into genetics (Mayr, 1959c, p. 2).

[7] I do not have space here to enter here into a detailed historical discussion of the notions of a type specimen and/or a biotype, but see Witteveen (in press) for the former and Rietz (1930); Roll-Hansen (2009, 2014) for the latter.

[8] Washburn to Mayr, 5 and 23 December 1949; Mayr to Washburn, 12 and 30 December 1949, Mayr Papers.

[9] What is more, it looks like Mayr still had not fully internalized Simpson's argument against the use of type specimens as bases for classification or description. This is suggested by what Mayr wrote in a draft of the chapter 'The type method and its significance' for his (co-authored) 1953 book. In late 1950, Mayr sent this draft to Simpson for feedback. Simpson replied that he had found the chapter "rather unsatisfactory." One sentence bothered him in particular: "I disagree violently with the statement that 'The description itself should be drawn from a single specimen (the type) … ' This might not be too bad for diagnosis … but even so, proper diagnosis often demands consideration of other specimens than the type. Definition always demands such consideration, and of course proper *description* should involve *all* specimens studied" (Simpson to Mayr, 15 December 1950, Simpson Papers).

[10] The proceedings of this symposium include transcriptions of the discussions that followed several talks. They reveal that, apart from criticizing the "typological species concept" in his own talk (Mayr, 1950), Mayr objected to the "typological race concept" in a response to anthropologist Ashley Montagu. As usual, Mayr was very vague about what this came down to: "It implies that every individual of a race conforms to the 'type' of that race" (Montagu, 1950, p. 336).

A similar shift can be detected in Mayr's attitude towards Schindewolf. As Winsor (2006) has pointed out, Mayr was already critical of Schindewolf in *Systematics*. He took issue with Schindewolf's 1936 hypothesis that higher taxa could emerge nearly instantaneously on geological time scales, calling it "so far as I can judge, exaggerated or untrue" (Mayr, 1942, p. 296). However—*pace* Winsor, —Mayr moved closer to Schindewolf in the early 1950s, when he turned his attention to a puzzling phenomenon in speciation studies. Mayr had noticed that peripherally isolated populations of certain bird species showed striking morphological differences compared to the main population—differences that could not be explained by standard population-genetic theories of speciation. In an important paper, Mayr introduced a new theory of 'genetic revolutions' to account for this phenomenon (Mayr, 1954). Interestingly, he presented his theory as an explanation for the puzzling phenomenon of "typostrophic variation" (a term he explicitly attributed to Schindewolf) and explained how his theory could account for the almost instantaneous evolution of "species or incipient species of an entirely new type" (Mayr, 1954, p. 160).[11] It thus seems that by the early 1950s Mayr was generally appreciative of Schindewolf's view about types and typostrophism, and took these as a neutral basis for further theory development.

And yet, in the same publication in which Mayr suddenly labeled Goldschmidt a typological thinker he also categorized Schindewolf as such (Mayr, 1958b). Moreover, in none of his later writings on genetic revolutions did he make any reference to 'typostrophic variation' or to Schindewolf's notion of types (Mayr, 1959b,c, 1963a, 1982a). Mayr's shift in attitude towards Goldschmidt and Schindewolf was likely due to his encounter with Simpson's *The Major Features of Evolution* (1953), his first detailed presentation of the 'typological systematics' of Schindewolf and Goldschmidt.[12] In fact, Mayr referred the readers of his 1958 paper to "Simpson's (1953, pp. 340–348) masterly analysis" for further discussion of the trouble with typology.[13]

1.4. Typology expanded

The fact that Mayr brought his *talk* of 'typology' into line with that of Simpson should not be taken to imply that Mayr was gradually moving towards Simpson in terms of the *meaning* he associated with this word. On the contrary, the late 1950s was a time in which Mayr further expanded the scope of the population/typology dichotomy. An ever-increasing variety of positions, theories, concepts, and methodologies were presented by him as either typological or populationist in orientation.

Take the notion of an 'ecotype,' a term ecologists used for a population that is adapted to specific environmental conditions. Mayr himself had often used this term approvingly (e.g. Mayr, 1947, 1954, 1955b), when in the late 1950s he suddenly objected its "typological connotations" (Mayr, 1958b, 1963a).[14] The late 1950s were also a time when Mayr began to associate the typology/population dichotomy with several other conceptual distinctions he would become known for. For example, Mayr's well-known distinction between 'proximate' and 'ultimate' explanation (Mayr, 1961) was foreshadowed in his assertion that "typological thinking is still prevalent … to a considerable extent in functional biology, where the emphasis is on the performance of a single individual. The typological concept has been completely displaced in evolutionary biology by the population concept" (Mayr, 1958a, p. 352).[15] The same counts for his distinction between 'beanbag genetics'—which "suffers from typological thinking"—and the populationists doctrine of 'unity of the genotype' (Mayr, 1959c).

A still more significant move was Mayr's appropriation of Darwin as the hero of population thinking. We have seen earlier that Mayr used the centennial celebrations of the *Origin of Species* to argue that Darwin had "replaced typological thinking by population thinking," a revolutionary development that had been "almost consistently overlooked" by biologists and historians (Mayr, 1959a, p. 2). Here, the contrast with Simpson is particularly striking. He used the centennial celebrations to point to Darwin's typological thinking, because of Darwin's tendency to define "taxonomic groups in terms of a pattern of characteristics in common" (Simpson, 1959, p. 303).

Mayr's 'Darwin paper' from 1959 is also interesting for another reason. It presented the first occasion on which he drew a link between typology and racism, and between typology and natural selection. Hence, Mayr began treading on Dobzhansky's home turf in discussion's of typology.[16] Mayr's basic sketch of typological thinking in these domains was characteristically vague. In the context of race, he reiterated the dictum that the typologist "asserts that every representative of a race conforms to the type" (Mayr, 1959a, p. 3). He thus left readers to guess whether he was (1) voicing the same old criticism of using type specimens as taxonomic standards in a new context, (2) claiming that typologists about race viewed races as genetically homogenous 'biotypes', or (3) was adopting Dobzhansky's arguments against a conception of races as populations derived from ancestral types.

Mayr's brief discussion of typological thinking about natural selection was perhaps even more ambiguous and puzzling. In this context, he remarked that

[11] It worth noting that Mayr did not think lightly of this paper on genetic revolutions. In the fall of 1951 he shared a draft with several colleagues, soliciting critical feedback. With some of them he corresponded at length about the manuscript (Ernst Caspari, Bruce Wallace). In his autobiographical notes, Mayr noted that in the almost three years that it took for the paper to be published, he had been "mortally afraid that someone else would get ahead of me" (quoted in Haffer, 2007, p. 219). Also, when he was asked later in life which of his scientific contributions he was most proud of, Mayr invariably answered: "The idea of genetic revolutions" (Bock, 1997; Haffer, 2007; Provine, 2004, 2005). All this makes it very unlikely that Mayr would have unthinkingly mentioned Schindewolf's typostrophism approvingly in his 1954 paper. It nevertheless remains somewhat puzzling that Mayr used this term in such a positive light. It is possible that he was not yet familiar with Simpson's recent portrayals of Schindewolf as a typologist (Simpson, 1949, 1951), but he was certainly familiar with a very critical piece on Schindewolf's typostrophism by the German zoologist (and his old friend) Gerhard Heberer (Heberer, 1943). Years earlier, Mayr had written with enthusiasm about having received this volume from Heberer (Mayr to Dobzhansky, 16 June 1946, Dobzhansky Papers).

[12] Mayr might also have learned more about Goldschmidt's ideas on classification when the two co-taught a seminar on speciation at the University of Washington in 1952. A year later Mayr took up a professorship at Harvard, where he taught a graduate course on evolutionary biology with Simpson. That year also saw the publication of Simpson's *Major Features*.

[13] What Mayr did not mention was that Simpson remarked in a footnote on one of these pages that Mayr had shown "some tendency [in *Systematics*] to discuss lower and higher categories in terms of characters-in-common … a pseudo-idealistic approach into which we all may fall on occasion" [p. 341].

[14] Mayr's 1958b paper was based on a symposium talk from May 1957, and includes a transcript of the discussion that followed his talk. It reveals that ecologist Jens Clausen (1891–1969) took issue with Mayr's characterization of the ecotype concept as 'typological.' Mayr responded in confusing terms that although "local races may have ecotypic characteristics, there are no ecotypes in any rigid sense" (Mayr, 1958b, p. 20).

[15] Mayr made similar remarks in a symposium discussion on 'Concepts in Biology' from the same year: "As many physiologists say, '*The* frog does such-and-such.' Now, there is typological thinking" (Gerard, 1958, p. 165). In his autobiographical notes, Mayr also remember how Konrad Lorenz (1903–1989) in the 1950s "always talked about *the* Greylag Goose in a strictly typological sense" (quoted in Haffer, 2007, p. 127).

[16] Only once before had Mayr made a quick public remark about typological thinking in relation to race. See footnote 10.

> For the typologist everything in nature is either 'good' or 'bad,' 'useful' or 'detrimental.' Natural selection is an all-or-none phenomenon. It either selects or rejects, with rejection being by far more obvious and conspicuous. Evolution to him consists of the testing of newly arisen 'types.' … The populationist on the other hand, does not interpret natural selection as an all-or-none phenomenon. Every individual has thousands or tens of thousands of traits in which it may be under a given set of conditions selectively superior or inferior in comparison to the mean of the population.
>
> Mayr (1959a, p. 3)

Again, it looks like Mayr made an attempt at mixing and recombining several distinct arguments from his colleagues. The first sentence almost certainly picks up on a remark Dobzhansky had made about the conception of 'mutants' that structured Morgan's school:

> [This school] used *Drosophila* mutants chiefly to study the architecture of the germ plasm, rather than problems of evolution. For these purposes, mutants sharp enough to be recognized and easily separated from other mutants and from the ancestral form were evidently preferable to those causing minute changes. 'Good' mutants were preserved and 'bad' ones discarded. It was inevitable that discrete, clear-cut, striking mutants came to be used as models for thinking about evolutionary problems as well.
>
> Dobzhansky (1959, p. 254)[17]

By stripping Dobzhansky's point about 'good' and 'bad' mutants of its context, Mayr left it wholly unclear what he was getting at. Moreover, Mayr was happy to blend this criticism of 'types' with his other arguments against De Vriesian biotypes. Dobzhansky, on the other hand, carefully pointed out that Morgan's distinction between 'good' and 'bad' mutants "was not a reversion to de Vries's view that species arose by single mutations" (Dobzhansky, 1959, p. 254).

The second remark from Mayr's quotation, on natural selection being "an all-or-none phenomenon," was likely drawn from another publication. Mayr had been inspired by what Julian Huxley had written on natural selection a few years earlier:

> Natural selection works not by all-or-nothing elimination, involving 100 per cent death as against 100 per cent survival, but by slight average extra survival over a number of generations; further it may be concerned with all kinds of characteristics, from ability to escape detection to speed in pursuit, from passive armor-plating to greater intelligence, from extra viability of biological 'toughness' to higher fertility or success in mating.
>
> Huxley (1955, p. 275)[18]

Interestingly, Huxley intended this as a mild criticism of Darwin's conception of natural selection. Darwin had failed "to think quantitatively on the subject" (Huxley, 1960, p. 14). Mayr, on the other hand, boldly inserted this point of criticism into his eulogy of Darwin the population thinker.

2. The Coon controversy

In spite of the considerable divergence between Mayr, Simpson and Dobzhansky over the interpretation of the typology/population dichotomy, none of them ever used a public forum to draw attention to this fact. It may indeed seem surprising that Simpson and Dobzhansky adopted Mayr's term 'typology' without making clear that they were each using this term in a different (and much more disciplined) sense. Didn't they have a good reason to distance themselves from Mayr's ever more liberal, ever less coherent deployment of the typology/population dichotomy?

The simple answer is 'no.' These three men were united by much more than what divided them. As the main architects and bulwarks of the modern evolutionary synthesis, they had a vested interest in forming a united front. In this context, the typology/population dichotomy actually served as a useful tool: it created the surface impression that they formed a united front on a supposedly fundamental conceptual issue. It would be problematic, though, if one of them would get into another's way through his particular use of the typology/population contrast.

This is exactly what happened in the early 1960s, when a controversial book on the evolution of human races appeared. Carleton Coon's massive *The Origin of Races* was welcomed by Mayr (in a review for *Science*) as a book of "major scientific importance" and "a milestone in the history of anthropology" (Mayr, 1962, p. 420).[19] Coon's book finally showed that the "typological approach [has] reached the end of usefulness" in studies of human evolution (Mayr, 1962, p. 422). Instead of taking one or a few characters to be "absolutely diagnostic" for an entire taxon, Coon had realized "that all races are variable populations and that most of their characters and character combinations have only probabilistic value" (Mayr, 1962, pp. 420–21). This way of presenting the typology/population distinction was of course an application of Simpson's argument against the use of aprioristic standards in the use of classification. Simpson indeed concurred in his own appreciative review that Coon's taxonomic methodology was as nearly free from "aprioristic bias" as one could ask for (Simpson, 1963a, p. 269).

In another publication, Mayr remarked that there was a second way in which Coon had avoided the typological trap. Coon had shunned outdated "typological models" of hominid evolution, according to which one hominid species ceased to exist when a new species evolved from it. Instead, Coon realized that ancestral hominid species "were widespread polytypic species with more advanced and more conservative races. One or several of the advanced races gave rise to the next higher grade" (Mayr, 1963b, p. 337). As Coon himself put it:

> My thesis is, in essence, that at the beginning of our record, over half a million years ago, man was a single species, *Homo erectus*,

[17] Dobzhansky spoke these words at a symposium in which Mayr also took part, in April 1959. It is possible that Mayr's Darwin paper was already in press at this point. In any case, Dobzhansky had said very similar things in earlier publications, e.g. Dobzhansky & Wallace (1954).

[18] Mayr had already incorporated the same criticism into a short paper from 1956. Without referring to Huxley, he wrote strikingly similar things: "The philosophy of 'all or none' solutions is exceedingly widespread … All or none solutions are based on typological thinking and alien to the facts of variation. Multiple solutions for biological needs are the general rule in evolution. An animal is protected against a predator not by speed *or* an armor *or* by cryptic coloration *or* poison *or* bad taste *or* by hiding *or* by nocturnal habits, but always by a combination of these" (Mayr, 1956, p. 107).

[19] In a personal letter enclosing a draft of his review, Mayr also congratulated Coon with the "absolutely remarkable job" he had done (Mayr to Coon, October 11, 1962, Mayr Papers). Coon had written Mayr several times during the preparation of his book, with question about technicalities in systematics (Coon to Mayr, 27 January 1858, 17 and 18 March 1960), which Mayr answered promptly. (Mayr wrote "answered by hand" on some of Coon's letters. He did not keep copies.) Coon acknowledged the help of Mayr and Simpson (among many others) in the preface of his book. In an interview many years later, Mayr mentioned that he had been "a good friend of Carleton Coon" (Wilkins, 2002, p. 968).

> perhaps already divided into five geographic races or subspecies. *Homo erectus* then evolved into *Homo sapiens* not once but five times, as each subspecies, living in its own territory, passed a critical threshold from a more brutal to a more *sapient* state.
>
> Coon (1962, p. 656)

Coon mentioned in particular that the 'Caucasoid' white race had evolved into a *sapiens* race some 200,000 years prior to the 'Congoid' black race. The Caucasoid race had therefore "evolved the most" (Coon, 1962, x).

In stark contrast with Mayr, Dobzhansky heavily objected to Coon's thesis. In Dobzhansky's perception, it rested on a "typological way of thinking of a sort from which modern evolutionism is making itself free" (Dobzhansky, 1963a, p. 366), a conclusion he would recapitulate on numerous later occasions (Dobzhansky, 1963c,d,b, 1967b, 1968a). Coon's typological thinking revealed itself in the (hidden) assumption that *Homo erectus* and *Homo sapiens* each formed "a 'type,' of which individuals are more or less imperfect manifestations." Coon was effectively arguing that different races had at different times escaped from the pull of the *Erectus* type and come under the dominion of the *Sapiens* type; a view that represented "a relapse into a crudest form to [*sic*] typology which has no warrant in what is known about the mechanisms of biological evolution" (Dobzhansky, 1963d, p. 147). Dobzhansky herewith deployed the notion of typological thinking with a similar meaning as in earlier writings. Coon's typological thinking consisted in the unwarranted postulation of fixed centers of attraction that governed the dynamics of variation.

But more than considering Coon's book to be scientifically flawed, Dobzhansky viewed it as dangerous. Arriving amidst debates about racial segregation in the American South, Coon's thesis would inevitably be used to claim that blacks are evolutionarily inferior, primitive, and backward compared to whites.[20] In a draft of his book review, Dobzhansky chided Coon for having provided "grist to racist mills." In his position as a well-known scientist, Coon needed to take responsibility for the potential misuse of his ideas. "Scientists living in ivory towers are quaint relics of a bygone age" (Dobzhansky, 1963d, p. 366).

Dobzhansky sent a draft of his book review to Coon, who responded with outrage.[21] Coon accused Dobzhansky of defaming him and threatened him with litigation. Dobzhansky, taken aback by Coon's violent response, wrote Simpson and Mayr to ask whether they considered his review unfair. Simpson replied in a short letter that he "was surprised that I could have read the book and formed an opinion so unlike yours," and regretted having to say "yes, I do think your review is unfair to Coon."[22] Mayr, in a much longer letter, responded in a similar tone that he was "not convinced … of the validity of the accusations which you have made against Coon," and took issue with Dobzhansky's qualification of Coon as a typological thinker. If Coon was right about the Caucasoid race having "approached the *Homo sapiens* grade earlier one would have to accept this without getting emotional."[23] In Mayr's perception, it was Dobzhansky who was in the grip of typological thinking:

> We have finally understood the fact of the non-identity of individuals within populations and I do not quite see how we can turn around and deny it for mean values of groups of individuals. This would be statistical nonsense. What is important is to stress that such differences are statistical, that they represent mean values and that they not [sic] permit the ranking of individuals in view of the large overlap of all such distribution curves. Any other argument would be a sliding back into typology, as far as I am concerned.[24]
>
> Mayr to Dobzhansky, 1 November 1962, Dobzhansky Papers

Dobzhansky did not respond to this remark, but reported that after "some soul searching" he had decided "to stick to my guns."[25] He would surely have felt that Mayr had missed his point about typology. Dobzhansky was not calling into question the "non-identity of individuals." He simply wasn't using the type/population contrast in the Simpsonian, statistical sense that Mayr followed in this context. What Dobzhansky *was* taking issue with was the mistaken view about population dynamics that seemed to be at the heart of Coon's thesis. Dobzhansky was drawing a type/population contrast in his own, population dynamic sense.

The otherwise frequent correspondence between Mayr and Dobzhansky waned for almost a decade after this episode (Jackson & Depew, unpublished manuscript). But neither Mayr nor Dobzhansky appears to have been willing to turn their dispute over the typology/population dichotomy into a public controversy. In surprising twist, Dobzhansky did exactly the opposite. He closed the ranks on this topic by choosing to walk along Mayr's path of sweeping claims. In two articles for a general scientific audience, he wrote: "I agree with Mayr (1963a) that 'the replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biology.' " (Dobzhansky, 1967b, p. 2; Dobzhansky, 1968b, p. 545). "Mayr is right that 'virtually every major controversy in the field of evolution has been between a typologist and a populationist' " (Dobzhansky, 1967b, p. 2).[26]

Dobzhansky went on to make bold, broad-brush claims about the typological aspects of Christianity (original sin) and political conservatism, versus the populational nature of "Kant's doctrine that every human being is an end in itself" and of political liberal ideas as such. At this level of abstraction almost any position could be classified either way, so as to fit one's own preferred ideology. Indeed, by the time Dobzhansky had died, Mayr wrote to one of his correspondents: "'All men are created equal' was not only an ethical statement, but quite literally believed in, reinforced by the

[20] Dobzhansky was right to suspect that white supremacists would hail Coon's book as scientific support for their segregationist campaigns (Farber, 2010; Wolpoff & Caspari, 1997). What Dobzhansky did not know was that Coon had even been giving direct advice to the most radical segregationist of all, Carleton Putnam (Jackson, 2001). Putnam's tract *Race and Reason* from 1961 had already been flamed by Dobzhansky for being pseudo-scientific racist propaganda (Dobzhansky, 1961).

[21] Dobzhansky's sharing of the review prior to publication was probably the reason for it being rejected by the *Saturday Review*, the journal that had invited him to write the review (see Jackson, 2001). Dobzhansky had unknowingly violated the protocols of the journal. The review was eventually published in *Current Anthropology* (Dobzhansky, 1963d) and in *Scientific American* (Dobzhansky, 1963b).

[22] Simpson to Dobzhansky, 1 November 1962, Dobzhansky Papers. In a letter to his sister, Simpson was even more dismissive of Dobzhansky's review: "*The Origin of Races* … is being bitterly attacked by other friends of ours (including Dobzhansky), in a way I consider unfair almost the point of being underhanded" (G. G. Simpson to Martha Simpson, 16 December 1962, Simpson Papers).

[23] Mayr to Dobzhansky, 1 November 1962, Dobzhansky Papers.

[24] Mayr was even more explicit on this point in a letter to anthropologist Derek Freeman a few years later: "It is a great pity that not only the racists are typologists but the antiracist liberals as well. Right now they are in a total panic when confronted with the possibility that the blacks in this country have the mean score of 5 or 10 or 15 points below the mean score of the whites" (Mayr to Freeman, 30 July 1969, Mayr Papers).

[25] Dobzhansky to Mayr, Simpson and Strauss Jr., 9 November 1962, Dobzhansky Papers.

[26] In another article from the same year Dobzhansky also mentioned that Simpson (1961) had "discussed [the typological/population distinction] with admirable clarity and discernment" (Dobzhansky, 1967a, p. 46).

philosophy of essentialism. Natural selection … implicitly claims exactly the opposite, 'No two individuals are created equal'."[27] Dobzhansky would have turned over in his grave.

3. Conclusion

It is time to take stock. We have seen that the emergence of the typology/population dichotomy was a complex affair. From the late 1930s onwards, several type/population distinctions were being drawn in different literatures, with different meanings. These early, substantive distinctions were not due to Mayr, but were articulated by Dobzhansky and Simpson. Mayr, the likely source of the later *typology*/population terminology, was primarily responsible for misrepresenting the substantive type/population contrasts that could be found in the literature, for confounding them with each other, and for admixing some of his own conceptual distinctions. What resulted was an all-encompassing dichotomy that had been drained of any substance.

This is not to say that only Mayr is to blame for using the typology/population dichotomy to confuse rather than clarify issues in contemporary and historical biology. For a start, we have seen that Simpson and Dobzhansky were also very eager to identify historical figures as typologists, often without much justification.[28] Moreover, in the 1960s both men followed Mayr in presenting typological thinking as a unified metaphysical doctrine with deep Platonist roots.[29] But, especially in the case of Simpson, there is reason to view such references as little more than skin-deep rhetorical flourish. Simpson's concern over typology always remained the methodological one he had first presented in 1937 (e.g. Simpson, 1963b). And even Dobzhansky continued to explain "the main point" about the typology/population distinction in population dynamic terms when he began to follow Mayr by reading the entire history through its dichotomous lens (e.g. Dobzhansky, 1968b, pp. 547–48). Mayr, in contrast, never formulated anything that resembled a 'core argument' which he could build on.

It is worth reflecting on the implications of these findings for the historiography of the modern evolutionary synthesis that took shape between (roughly) 1930 and 1950. To some extent, the history of the typology/population dichotomy resonates with prominent historiographical perspectives that present the synthesis as 'constriction' of admissible theoretical variables (Provine, 1988) or as a 'hardening' around selectionist interpretations (Gould, 1983). If the account I have sketched in this essay is on the right track, it suggests that the synthesis also became constricted conceptually and hardened rhetorically around the typology/population dichotomy. On another front my narrative connects loosely to synthesis historiographies that highlight the role of Mayr as community architect (Cain, 1993, 1994; Smocovitis, 1994, 1996). It is widely acknowledged Mayr played a pivotal role in determining the shape and success of the synthesis through his extensive editorial and organizational practices. Beyond that, we have seen that he also promoted an image of unification by providing conceptual umbrellas of his own design, stitched out of a variety of fabrics. His presentation of the typology/population dichotomy gave the impression of there being a deep unity among 'populationist' synthesis defenders—sharply separated from the typological enemies—when in fact this concealed important differences and disagreements (cf. Cain, 2009).

Needless to say, Mayr himself preferred to evaluate his contributions rather differently. Overall, he thought of himself primarily as consolidator or synthesizer of ideas (Provine, 2005). In *Systematics*, Mayr already mentioned his aim to 'simplify' ongoing debates and controversies; he presented the biological species concept as a considerable "simplification of taxonomy" (Mayr, 1942, p. 125). He also highlighted the importance of simplification in a crude sketch of the history and philosophy of science: "To follow the history of the changes in the species concept is a fascinating endeavor since it sheds a good deal of light on the general principles of the growth of a scientific idea. It seems typical for all sciences that there is a continuous see-sawing between simplifying and complicating discoveries" (Mayr, 1946c, p. 274). Mayr himself had a clear preference for the simplifying moves.

He defended this stance in later works. In the introduction of *Animal Species and Evolution* he justified what could be perceived as the one-sidedness of his presentation by arguing that "to take an unequivocal stand, it seems to me, is of greater heuristic value and far more likely to stimulate constructive criticism than to evade the issue" (Mayr, 1963a, vi). In the preface of his hefty *The Growth of Biological Thought* he similarly defended his "tactic to make sweeping categorical statements. Whether or not this is a fault, in the free world of the interchange of scientific ideas, is debatable. My own feeling is that it leads more quickly to the ultimate solution of scientific problems than a cautious sitting on the fence" (Mayr, 1982b, p. 9). Stephen Jay Gould, Mayr's colleague at Harvard, commented on the upshot:

> Mayr's book tends to view the entire pageant of historical biology as a great battle between Platonic 'essentialists' who focus on unvarying types or, if evolutionarily inclined, must view the process as saltation from one essence to another, and 'population thinkers' who understand that variation is irreducible reality and become receptive to a Darwinian model of change. This 2000-year struggle culminated in the triumph of population thinking in the modern synthesis, with Mayr's own work as a prominent contribution.
>
> Gould (1984, p. 257)

Gould's verdict was clear: Mayr was using his supposedly 'deep' typology/population dichotomy as a rhetorical device for dividing historical figures into his personal heroes and villains.[30]

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[27] Mayr to Graham, 14 August 1979, Mayr Papers.

[28] For instance, Simpson's frequent claim to the effect that Linnaeus classified taxa on the basis of their characters-in-common is very questionable (Müller-Wille, 2007).

[29] Simpson once stated that "[t]ypology stems from Plato and his sources and came into taxonomy along with Aristotelian, Neo-Platonic, scholastic, and Thomist philosophy and logic" Simpson (1961, p. 46); also see Simpson, (1968, p. 8ff.). Dobzhansky went even further in claiming that "[t]he typological approach can be traced from Parmenides and Plato, through Aristotelian and Thomist philosophy, to Linnaeus, Goethe, and Owen, and to some of the conceptualizations of systematics, genetics, and comparative morphology. It is basically un-evolutionistic, if not anti-evolutionistic" (Dobzhansky, 1963c, 1132).

[30] Most other reviewers arrived at similar conclusions. See, for example, Eldredge (1982); Greene (1992); Kottler (1983); Simpson (1982). Michael Ruse (1985), in "a review of the reviews" of the book, argued that the value of the book laid exactly in the fact that it was more of an autobiography—he entitled his essay review 'Admayration.' Historian of science Richard Burkhardt Jr. (a former Ph.D. student of Mayr) later expressed the same, widely-shared sentiment about Mayr's historical writings as such: "Mayr's tendency to phrase issues starkly" often failed to "do justice to the complexity of historical circumstances and it sometimes puts readers off" (Burkhardt Jr, 1994, p. 368). It is ironic, though, that Gould later used the typology/population distinction as the organizing theme for one of his own books (Gould, 1996). Moreover, in his own magnum opus, *The Structure of Evolutionary Theory* (2002), he wrote: "As thoughtful evolutionists have always noted, and as Mayr has particularly stressed in our times by contrasting 'essentialist' and 'populational' ways of thinking, a fundamental revision in our concept of the essence of reality—from the Platonic archetype to the variable population—may represent Darwin's most pervasive and enduring contribution to human understanding" (p. 894).

Against this background, one can only read with extreme irony what Mayr wrote to a philosopher (Kenneth Schaffner) who had just read his book. Schaffner asked Mayr for "a reprint(s) or reference(s) which developed the concept of 'population thinking' more systematically."[31] Mayr did not provide him with any references, but he did make a general observation: "The trouble is that philosophers indulge too often in dichotomy. They still tend to follow the axiom of scholastic logic: 'Tertium non dat'. Actually in most philosophical and scientific controversies there are three or more alternatives."[32]

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