



On the origin of the typological/population distinction in Ernst Mayr's changing views of species, 1942–1959

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Abstract

Ernst Mayr's typological/population distinction is a conceptual thread that runs throughout much of his work in systematics, evolutionary biology, and the history and philosophy of biology. Mayr himself claims that typological thinking originated in the philosophy of Plato and that population thinking was first introduced by Charles Darwin and field naturalists. A more proximate origin of the typological/population thinking, however, is found in Mayr's own work on species. This paper traces the antecedents of the typological/population distinction by detailing Mayr's changing views of species between 1942 and 1955. During this period, Mayr struggles to refine the biological species concept in the face of tensions that exist between studying species locally and studying them as geographically distributed collections of variable populations. The typological/population distinction is first formulated in 1955, when Mayr generalizes from the type concept versus the population concept in taxonomy to typological versus population thinking in biology more generally. Mayr's appeal to the more general distinction between typological and population thinking coincides with the waning status of natural history and evolutionary biology that occurs in the early 1950s and the distinction plays an important role in Mayr's efforts to legitimate the natural historical sciences.

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Ernst Mayr's contributions to evolutionary biology rightfully place him on any

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short list of the greatest evolutionary biologists of the twentieth century. But Mayr's accomplishments have extended beyond the boundaries of any one discipline. He has made important contributions to the popular understanding of natural history and evolution, he has been a tireless defender of the naturalist tradition in biology, and he has produced a body of insightful and provocative work in the history and philosophy of biology (Bock, 1994; Gould, 1984; Junker, 1996; Shermer & Sulloway, 2000). Given the sheer volume, range, and depth of Mayr's published works, he occupies a unique place in the developments of twentieth century evolutionary biology, and to adequately understand those developments we need to understand his work.

The purpose of this paper is to shed some light on the historical origin of one important facet of Mayr's work, namely, the distinction between 'typological' and 'population' thinking. While some attention has been paid to the distinction itself (Amundson, 1998; Ghiselin, 1969, 1997; Gould, 1984; Hull, 1965, 1990, 1994; Sober, 1980), a comprehensive analysis of Mayr's presentation and use of this distinction has yet to appear. Focusing on the typological/population distinction is worthwhile for two main reasons:

First, after its 'official' appearance in 1959, the typological/population became a central conceptual thread that ran throughout Mayr's work. For example, both *Animal species and evolution* (1963) and *The growth of biological thought* (1982) are structured throughout as an ongoing interchange and struggle between typologists and population thinkers. More specifically: Mayr continues appealing to the distinction in his later, more detailed interpretation of Darwin and the Darwinian revolution;¹ he uses it to help explain the origin and development of the biological species concept and his own theories of speciation;² he uses it as part of his interpretation of the evolutionary synthesis and his critique of the early Mendelians, classical genetics, and early population genetics;³ it plays a major role in his attack on racism;⁴ and, finally, it is part of his reasoning for defending the autonomy of biology.⁵ As such, clarifying the distinction's origins and meaning provides a useful vantage point from which to scrutinize Mayr's work as a whole.

Second, by detailing how specific components of Mayr's work on species are pressed into service as key components of the typological/population distinction, we see how one scientist uses 'scientific concepts' to forge a conceptual tool with a wider range of historical and philosophical applicability.

¹ For example, in *The growth of biological thought* (1982); *Toward a new philosophy of biology* (1988), Essay 13; and *One long argument* (1991a).

² For example, in *Animal species and evolution* (1963); *Principles of systematic zoology* (1969); *Evolution and the diversity of life* (1976), Essays 10, 13, 33, 35; *Toward a new philosophy of biology* (1988), Essays 19–21.

³ For example, in *The evolutionary synthesis* (1980), co-edited with William Provine; 'Where are we?' (1959c); *Animal species and evolution* (1963); *The growth of biological thought* (1982), p. 41.

⁴ For example, see 'Darwin and the evolutionary theory in biology' (1959); *Animal species and evolution* (1963), pp. 646 ff.; *Evolution and the diversity of life* (1976), Essay 36.

⁵ For example, see *The growth of biological thought* (1982), Chapter 2; *Toward a new philosophy of biology* (1988), Essay 1.

1. An introduction to the typological/population distinction

Mayr introduces the typological/population distinction in ‘Darwin and the evolutionary theory in biology’ (1959a). Here, Mayr summarizes what he takes to be ‘the significance of the scientific contribution made by Darwin’ (1959a, p. 1): (1) Darwin collected and presented evidence demonstrating the occurrence of evolution; (2) Darwin proposed the mechanism of natural selection to explain evolutionary change; and (3) Darwin ‘replaced typological thinking by population thinking’ (*ibid.*). After noting that the first two points are uncontroversial, he continues, ‘Equally important but almost consistently overlooked is the fact that Darwin introduced into the scientific literature a new way of thinking, “population thinking”’ (*ibid.*, p. 2).

This ‘new way of thinking’ is contrasted with typological thinking, which Mayr characterizes as follows:

Typological thinking no doubt had its roots in the earliest efforts of primitive man to classify the bewildering diversity of nature into categories. The *eidos* of Plato is the formal philosophical codification of this form of thinking. According to it there are a limited number of fixed, unchangeable ‘ideas’ underlying the observed variability, with the *eidos* (idea) being the only thing that is fixed and real while the observed variability has no more reality than the shadows of an object on a cave wall, as it is stated in Plato’s allegory. The discontinuities between these natural ‘ideas’ (types), it was believed, account for the frequency of gaps in nature. Most of the great philosophers of the 17th, 18th, and 19th centuries were influenced by the idealistic philosophy of Plato, and the thinking of this school dominated the thinking of the period. Since there is no gradation between types, gradual evolution is basically a logical impossibility for the typologist. Evolution, if it occurs at all, has to proceed in steps or jumps. (*Ibid.*, p. 2)

By contrast:

The assumptions of population thinking are diametrically opposed to those of the typologist. The populationist stresses the uniqueness of everything in the organic world. What is true for the human species—that no two individuals are alike—is equally true for all other species of animals and plants. Indeed, even the same individual changes continuously throughout his lifetime and when placed into different environments. All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and statistics of variation. Averages are merely statistical abstractions, only the individuals of which the populations are composed have reality. The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstrac-

tion and only the variation is real. No two ways of looking at nature could be more different. (*Ibid.*)

As I argue elsewhere (Chung, 2000), the 1959 presentation hardly amounts to a ‘full articulation’ of the distinction between typological and population thinking as Mayr claims (Mayr, 1976, p. 26). But scrutinizing more closely what Mayr has to say about the Darwinian revolution points to Mayr’s own work on the species problem and the biological species concept as key to understanding the distinction.

2. A word on ‘the species problem’

To provide some context for the more detailed historical discussion that follows, a brief overview of the species problem will prove useful. Basically, the species problem turns on answering questions like the following: What are species? Are species real biological entities or convenient conventions? Is there anything special about species that distinguishes them from the other taxonomic categories? How do species originate and how are they maintained? What role(s) do species play in different areas of biology? The reason there is a problem is that biologists cannot seem to agree on answers to these questions.

For present purposes, however, I want to present two specific and more focused problems relating to species that Mayr himself sees as crucial to his own work on species concepts. One problem, for Mayr, is to ‘reconcile the sharp demarcation of species in a local fauna and flora with the Darwinian concept of gradual evolution’ (1993, p. 35). That is, if evolution is in fact gradual as maintained by Darwin and if species must evolve from each other, then the Darwinian view seems to require a plethora of intermediate gradations between distinct species—and yet in the local situation, the naturalist finds sharply delineated, clearly demarcated gaps between species (cf. 1991b, p. 7). This problem, then, involves an apparent inconsistency between the species of the local naturalist (species are separated by a distinct gap), and the Darwinian view of evolution (species ought to be connected by a series of gradations).

A second problem, for Mayr, involves a tension between the definition of species derived from the local situation and the application of this definition to polytypic species, which comprise groups of geographically distributed variable populations. The problem is that the definition hinges on reproductive isolation—species are delineated by being reproductively isolated from each other—and yet this criterion is simply impossible, in practice, to apply when species do not come into contact with each other.

Both problems involve conflicting sets of intuitions: the intuitions of the traditional local naturalist against those of (i) the Darwinian regarding gradual evolution and (ii) the more recent defenders of polytypic species. Mayr’s solution to the two problems tries to incorporate the intuitions of the local naturalist, the Darwinian, and the defender of polytypic species. As we shall see, it is in the course of grappling with

these problems that Mayr develops the ideas and language that eventually become the typological/population distinction.

In the next section, I present an overview of Mayr's changing views of species between 1942 and 1955. My main purposes in presenting such an overview are (1) to identify and trace the antecedents of 'typological thinking' and 'population thinking' in Mayr's work on species and (2) to determine at what moment and in what context the typological/population distinction first appears.

3. The development of Mayr's views of species between 1942 and 1955

3.1. 1942

In 1942, Mayr published his first major work, *Systematics and the origin of species*, in which he attempts to reconcile recent changes in systematics and taxonomy with a Darwinian interpretation of evolution. Mayr completed the book after spending some ten years working with and thinking about bird species at the American Museum of Natural History, where he was curator of the extensive South Sea Island collection. In particular, Mayr had just completed his *List of New Guinea birds* the year before, in which he had identified, described, and ranked 1501 species and subspecies (Mayr, 1941, p. vii). So when Mayr talks about important shifts in both systematics and species concepts, he is drawing upon his own experience as a practicing systematist.

In *Systematics and the origin of species*, Mayr discusses a number of species concepts:

1. The 'static and strictly morphological species concept' of Linnaeus (Mayr, 1942, pp. 109ff., 115), based on striking differences in appearance.
2. The 'practical species concept', based on the subjective judgment of a 'competent systematist' (*ibid.*, p. 117).
3. The 'genetic species concept', based on genetic identity (*ibid.*, p. 118).
4. The 'species concept based on sterility', based on interfertility (*ibid.*, p. 119).
5. The 'biological species definition', based on the practical need of the taxonomist and synthesizing elements from the other concepts, reads as follows (*ibid.*, pp. 119–120):

A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.

Or shorter: Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.

In his discussion of these concepts, Mayr argues that neither (2), (3), nor (4) can serve as an adequate species concept by itself. Instead, the biological species definition incorporates what Mayr takes to be the basic insights of (2)–(4). Mayr's main point is to highlight the transition from the morphological species concept to the biological species concept, a move he explicitly associates with the transition from the 'old' to the 'new' systematics. In fact, Mayr portrays the morphological approach as being perfectly legitimate in the initial study of a species (*ibid.*, p. 109). But this approach breaks down in 'better-known groups' due to the widespread occurrence of geographic variation (*ibid.*, pp. 110–111). More specifically, as more specimens were collected, naturalists found that what were originally thought to be two separate species were actually connected by a series of 'intergrading' populations (*ibid.*). Using the morphological approach of Linnaeus, each of the populations would be labeled a separate species (because each population was morphologically distinguishable from the others). In better-known groups such as birds this morphological approach soon generated practical difficulties: for example, some populations could be assigned to two different morphologically defined species, depending upon which morphological characters one decided to look at.

Eventually, bird taxonomists⁶ revised their understanding of what the term 'species' meant. Instead of identifying a series of interconnected but distinct morphological species, the bird taxonomists came to think of the whole series of intergrading populations as forming a single 'collective' species that was distributed geographically (*ibid.*, p. 111). To distinguish this newer conception of species, some taxonomists began employing trinomial names (beyond the traditional binomial procedure) and eventually called such species 'polytypic' (*ibid.*, pp. 111–113).

For Mayr, it is this change from the traditional morphological conception of species to the collective, polytypic conception that marks the difference between the old and new systematics. Mayr's formulation of this development also, however, contains a glimmer of the ideas that will later become 'typological thinking' and 'population thinking'. As he writes (*ibid.*, pp. 6–7, italics in original):

The old systematics is characterized by the central position of the species. No work, or very little, is done on infraspecific categories (subspecies). A purely morphological species definition is employed. Many species are known only from single or at best very few specimens; the individual is therefore the basic taxonomic unit. There is great interest in purely technical questions and nomenclature and 'types'. The major problems are those of a cataloguer or bibliographer, rather than those of a biologist.

The new systematics may be characterized as follows: The importance of the species as such is reduced, since most of the actual work is done with subdivisions of the species, such as subspecies and populations. The population or rather an

⁶ Given his education in Berlin under Erwin Stresemann, clearly this is the tradition out of which Mayr himself came.

adequate sample of it, the ‘series’ of the museum worker, has become the basic taxonomic unit. The purely morphological species definition has been replaced by a biological one, which takes ecological, geographical, genetic, and other factors into consideration.

Note that the main differences between the old and new systematics are expressed exclusively in terms of species:

Old systematics	New systematics
<ul style="list-style-type: none"> – species central – variation within species not emphasized – a single individual represents a species – morphological species concept, based on type 	<ul style="list-style-type: none"> – species not central – variation within species emphasized – a population sample (a series of individuals) represents a species – biological species concept based on ecological, geographical, genetic factors

Note also how closely the differences between the old and the new systematics parallel the differences between typological and population thinking: recall that the typologist downplays the importance of variation and focuses on underlying types, while the population thinker emphasizes the importance of variation and focuses on populations (1959a, p. 2). So even though Mayr has yet to formulate the distinction, the basic ideas are already present in 1942. This is especially apparent in the case of what Mayr later calls ‘population thinking’.

In his later 1959 presentation, the significance of ‘unique individuals’, ‘populations’, and ‘variation’ is not clearly motivated—that is, the emphasis on populations seems to come out of nowhere. But if we look at what Mayr has to say about populations in 1942, in the context of elaborating on the new systematics, the significance of uniqueness, individuals, and populations becomes clear. As Mayr writes (1942, p. 24):

The population concept, which has been used in these definitions and which will play an important role in many of our subsequent discussions, is based on the practical experience of the taxonomist, but it is difficult to define adequately. The concept is based on a certain genetic similarity and on the possibility of interbreeding . . . In fact, the term population connotes, in general, a geographical coexistence . . . Under ideal conditions a population consists of a small group of individuals clearly separated from other individuals of the species by a physical barrier.

This quote provides a succinct snapshot of what Mayr means by ‘population’: populations are the basic units that the taxonomist studies in nature, they have particular biological attributes (genetic similarity, interbreeding), and they are geographically circumscribed. But the significance of populations is intimately bound up with the taxonomist’s goals in studying species (*ibid.*, p. 25):

If we want to compare a form or species with another one, we compare samples (‘series’ of the taxonomist), we do not compare individuals; this is one of the basic principles of modern systematics. It is therefore the first task of the taxonomist to study variation within the population, the so-called individual variation, in order to determine the characteristic attributes of that population.

So, in order to study and understand a species we must study population samples, and to get at the attributes of a population, we must study individual variation within that population. In other words, individual variation is the key to understanding populations, and populations are the key to understanding species. The significance of individual variation and populations flows directly from their role in the approach of the new systematics to studying species.

It is this emphasis upon populations and their variation that affords Mayr and the new systematics a solution to the first problem relating to species. Recall that this problem involved a conflict between the sharply delineated species of the local, traditional naturalist and the gradualism posited by Darwinian evolution. By focusing on the polytypic nature of many animal species (and especially birds), Mayr argued that there was in fact no conflict between the existence of sharp local gaps between species and the gradual nature of evolutionary change (cf. Mayr, 1942, 1991b, 1993). He accomplished this by emphasizing that species are in fact aggregates of geographically distributed populations and that it was reasonable to suppose that sometimes these populations would become separated by some geographic barrier (such as a mountain range or the changing course of a river). But once they were separated, then these populations could evolve gradually just as postulated by Darwin, until they had diverged to the point where they could no longer interbreed with each other, even if contact were to be reestablished. In this way, Mayr could explain the distinct gaps of the local species as originating via geographic isolation *and* gradual Darwinian evolution.

Mayr’s solution to the first problem, however, does not help solve the second problem. That is, in the local situation, the naturalist can simply wait and see whether the members of two different populations interbreed or not. But this is not the case with geographically distributed populations. In this case, because populations do not come into contact with each other, there is simply no way ‘to know’ whether they really are reproductively isolated or not. The naturalist must make an inference concerning reproductive isolation based on experience and other factors.⁷

⁷ See David Magnus (1996) on Mayr’s reasons for rejecting the possibility of appealing to breeding experiments in such cases and Peter Beurton (1994) for a useful analysis of this tension in Mayr’s thinking.

To summarize, in 1942 Mayr set out the rudiments of ‘population thinking’ in the context of appealing to ‘the new systematics’ and articulating ‘the biological species concept’. At this time, Mayr contrasted the morphological species concept of the old systematics with the biological species concept. What is more, his tone at this time is neutral; that is, the morphological approach is portrayed as a useful way to begin one’s study of a species, but as more is learned it needs to be supplemented by thinking of species as polytypic assemblages of variable populations.

3.2. 1946

In 1946, Mayr was awarded the Leidy Medal by the Academy of Sciences of Philadelphia. In his address, Mayr again discussed the new systematics and species. But his presentation is now more streamlined. Instead of the numerous species concepts listed in 1942, Mayr only discusses two. The species concept of the older naturalists is the morphological concept of Linnaeus and Ray (Mayr, 1946, p. 273). Mayr describes this concept as ‘that of the local naturalist’ which picks out well-defined and sharply-delimited species (*ibid.*). According to Mayr, this concept worked well enough until the avalanche of variant populations discussed above overwhelmed naturalists and prompted them to adopt a ‘biological’ (*ibid.*, p. 274) and ‘polytypic’ (*ibid.*, p. 273) conception of species. The newer biological concept is defined exactly as it was in 1942, based upon interbreeding and reproductive isolation. But Mayr also introduced a new idea in this article. In his discussion of the transition from the morphological to the biological conception of species, Mayr contended that the morphological concept ‘lost its simplicity’ (*ibid.*, p. 273) and that ‘the original Linnaean species concept had to be broadened . . .’ (*ibid.*). Mayr’s new idea is then introduced to clarify the nature of this transition. He writes:

To use an analogy from the field of geometry, we can say that the Linnaean [or morphological] species had *no dimensions*, since it dealt with the delimitation of natural populations at a single locality and at a single time level. The scientific exploration of the whole world in the post-Linnaean period resulted in the addition of longitude and latitude to the domain of the taxonomist. Taxonomy thus became *two-dimensional* and it became necessary to replace the simple binomial species of Linnaeus by the polytypic, trinomial species of recent authors. (*Ibid.*, my emphasis)

Most of the content here is familiar territory. And yet this new distinction between ‘no dimensions’ and ‘two dimensions’ comes to play an important role in Mayr’s subsequent thinking regarding species. Here in 1946, note that Mayr’s tone is still neutral. In fact, he uses the new distinction to emphasize the *continuity* from the simpler morphological case of the local naturalist to the more complicated cases of the new systematics. Both the Linnaean and the polytypic species involve the ‘delimi-

tation of natural populations’, either locally or more globally. Finally, note that ‘the biological species concept’ is characterized as polytypic or two-dimensional.⁸

3.3. 1953

In 1953 as the lead author of *Methods and principles of systematic zoology*, Mayr continues to contrast the older morphological species concept with the newer biological one (Mayr *et al.*, 1953, pp. 24–25). But several aspects of the presentation depart significantly from the earlier work. First, Mayr explicitly calls the morphological species concept ‘typological’. For example, in his description of the old systematics, he writes that it ‘is characterized by the central position of a species, typologically conceived, morphologically defined, and essentially nondimensional’ (*ibid.*, p. 13). And concerning the Linnaean period, Mayr states that ‘The thinking of this period was characterized by the concepts of classical typological taxonomy. The species was the nondimensional species of the local naturalist’ (*ibid.*, p. 7). Here the species concept of the older tradition of naturalists is still morphological and nondimensional, but now it is also situated in the context of ‘classical typological taxonomy’. To understand what Mayr might mean by classical typological taxonomy we must consider a second point. In particular, Mayr’s introduction of ‘typological’ coincides with a discussion of Plato. This occurs in the context of Mayr’s contrasting what he calls ‘the type concept’ with ‘the population concept’. He writes (*ibid.*, pp. 15–16):

Another way of bringing out the revolutionary change in the thinking of the taxonomist is to define the two concepts that are most characteristic for early and for recent taxonomy.

The type concept. Taxonomy in its early history was completely dominated by the type concept. The type concept goes back to Greek philosophy. The ‘ideas’ of Plato are such ‘types’ . . . Applied to taxonomy, the type concept postulates that all members of a taxonomic category conform to a ‘type’. Whether a taxonomist adhered to the type concept consciously or unconsciously, it inevitably affected his methods and results. In particular, the type concept tended to exaggerate the constancy of the categories and the gaps that separate them and to minimize variability. Typologists have often either denied evolution altogether or explained its operation by macromutations . . .

The population concept. During the past seventy-five years [1878–1953] the population concept has gradually replaced the type concept, but by no means completely. According to this view, species are composed of variable populations . . . The impact of this change of concept on the working methods and results of the taxonomist has been enormous. Populations are variable and, consequently,

⁸ Mayr subsequently uses the term ‘multidimensional’ instead of ‘two-dimensional’. It would be worthwhile pinpointing when this change occurs.

the description, measurement, and evaluation of variation has become one of the principal preoccupations of the student of lower categories . . .

There are definite similarities between the 1953 presentation of ‘the type concept’ versus ‘the population concept’ and the 1959 presentation of ‘typological thinking’ versus ‘population thinking’. In fact, the paragraph on ‘the type concept’ can reasonably be seen as a skeletal outline for the 1959 discussion of typological thinking. The connection between the paragraph on ‘the population concept’ and the later discussion of population thinking is not as strong. But the differences between the two are provocative. Most intriguing is that Mayr does not even mention Darwin here and the time frame he gives for the replacement of the type concepts begins in 1878, not 1859!⁹ I take this as an indication that Mayr has not yet made the move from the specific distinction between the type and population concepts to the more general distinction between typological and population thinking, and that he has not yet had occasion to consider Darwin’s relationship with regard to types or populations.

Mayr’s change of tone is also noteworthy. For example, he uses more polemical language such as ‘*the revolutionary change* in the thinking of the taxonomist’, ‘in its early history [taxonomy] was *completely dominated* by the type concept’, and ‘the impact of this change of concept on the working methods and results of the taxonomist has been *enormous*’. This change coincides with Mayr’s discussion of Plato, and it foreshadows the more polemical tone of ‘Darwin and the evolutionary theory in biology’.

In many respects, then, the 1953 presentation of species concepts still centers on contrasting the morphological and nondimensional approach of the old naturalists with the biological, polytypic, and multidimensional approach of the new systematics. The change that occurs here is the greater emphasis on ‘type talk’—for the first time Mayr labels the morphological, nondimensional species concept as typological and he associates the type concept with the philosophical tradition of Plato. This goes beyond the almost ‘by the way’ mention of types in 1942. More striking, however, is the change in Mayr’s tone. Through 1946, Mayr’s tone was neutral and stressed the continuity from the old approach to the new approach. Now, however, he talks about ‘the revolutionary change’ from the morphological, nondimensional, typological approach of the old naturalists to the polytypic, multidimensional, biological approach of the new naturalists.

⁹ Mayr does discuss Darwin earlier in his historical overview of taxonomy, but there is no mention whatsoever of Darwin’s contributions to ‘the population concept’ (Mayr et al., 1953, pp. 8–9). In fact, Mayr summarizes the period in which Darwin played a major role as being ‘dominated by the study of evolution of the higher categories, with a great interest in ancestral forms or missing links . . .’ (*ibid.*, p. 9), and he explicitly contrasts this with ‘the most recent phase in the history of taxonomy’ in which ‘taxonomy is characterized by a study of the evolution *within* species’ (*ibid.*, italics in original).

3.4. 1955

Just two years later, in 1955, Mayr presents a dramatically reconfigured view of species and formulates for the first time the distinction between typological and population *thinking*. This occurs in an in-depth paper on Karl Jordan, a German entomologist and taxonomist, entitled ‘Karl Jordan’s contribution to current concepts in systematics and evolution’ (Mayr, 1955 [1976]). In reading through this paper, it becomes clear that Mayr views Jordan as an early pioneer and advocate of many ideas that Mayr himself came to defend later.¹⁰ Another thing that becomes clear, though, is that Mayr’s more general formulation of the difference between typological and population thinking is ‘correlated’ with his reconfiguration of his views on species.¹¹ To motivate this point, I begin with the distinction between typological and population thinking and then discuss species.

In a one-paragraph section on ‘The meaning of variability’ Mayr segues to praising Jordan with the following (1955 [1976], p. 301):

One of the most revolutionary changes of concept in biology has been the replacement of typological thinking by thinking in terms of populations. According to this concept [of population thinking], no two individuals or biological events are exactly the same and processes in biology can be understood only by a study of variation.

This passage marks a significant development in Mayr’s thought. For as far as I can tell, up to this point, Mayr’s discussion of types, populations, and variation has always occurred with respect to the new systematics, taxonomic practice, or the species problem. But here the ‘revolutionary change’ from types to populations is no longer just important for systematics, understanding species, or even just evolutionary biology—instead the importance of the change from typological to popu-

¹⁰ This paper raises a number of important historical questions. First, to what extent did Mayr’s early training in Germany shape his later thinking on species, speciation, and Darwin? For both Jordan and Mayr were products of the same scientific milieu (see Junker, 1996; Bock, 1994; and Mayr, 1980). Second, given how ‘modern’ Mayr makes Jordan out to be, to what extent does Jordan’s work impact Mayr’s views? Or is it more accurate to say that Mayr somewhat whiggishly ‘reads in’ his own favored views back onto Jordan’s work? A third question is more historiographical: to what extent does Mayr’s treatment of Jordan presage Mayr’s treatment of Darwin? The organization and specific sections of the Jordan paper would seem to constitute a useful template for a careful look at Darwin’s work and contributions to systematics, species concepts, and speciation.

¹¹ I use the word ‘correlated’ because I cannot determine which came first, Mayr’s formulation of a more general distinction between typological and population thinking or his revised analysis of species concepts. Given the content of this 1955 paper and what Mayr says here, it seems reasonable to hypothesize that he did carefully study Jordan’s work (as well as the work of others) on species, then he revised his views on species, and then he generalized from these revised views to the more general typological/population distinction. But it is an intriguing possibility that Mayr had the more general distinction in mind *first* and that this had an impact on how he carves out the three species concepts in this 1955 presentation.

lation thinking is extended to ‘biological events’ and ‘processes in biology’ *in general*.

Mayr’s bold formulation of the change from typological to population thinking is accompanied, later in the paper, by a more confident and forceful presentation regarding species. Mayr’s discussion begins definitively (1955 [1976], p. 485):

After a thorough study of most of the literature on this subject, I have come to the startling conclusion that the disagreement is actually due to the fact that there are in existence not merely one but actually three entirely different species concepts. All past arguments and discussions have suffered from the fact that an author has either championed one of the three concepts against others or has wavered between two of these without realizing it.

Mayr then discusses these three species concepts in turn. First there is the ‘typological’ species concept:

... which goes back to the *eidōs* of Plato. Such a species is a ‘different thing’. Implicit in this concept is that variation as such is unimportant since it represents only the ‘shadows’ of the *eidōs*. Translated into biology, the typological concept becomes the morphological species concept. (*Ibid.*)

This passage indicates an interesting change in Mayr’s thinking. Through 1953, Mayr sticks with ‘the morphological species concept’ as a basic way of defining species and as the main contrast to the biological conception. But whereas in 1953 the morphological species concept was described as nondimensional and typological, now Mayr implies that the morphological species concept is simply an application of typological thinking to biological phenomena. In other words, Mayr’s change of terminology indicates that he now sees the typological concept as basic and the morphological concept as derived from it. From here on, Mayr contrasts the biological approach to species with the typological conception.

The second species concept

... is altogether different from the typological species. It does not deal with things, describing their degree of difference, but specifies a relationship. It is a concept like the word *brother*, which has a meaning only with reference to some other object. This ‘biological’ or ‘nondimensional’ species concept describes the relationship of two natural populations that coexist at the same locality and specifies this relationship as ‘noninterbreeding’. (*Ibid.*, p. 486, italics in original)

Here we have the ‘biological species concept’ from early discussions, but now it is described as ‘nondimensional’, a word that had originally been applied to the morphological species concept beginning in 1946! Just a bit later, Mayr indicates that he is now switching terminology as well:

Indeed, it is this concept of the nondimensional species, expressing the relationship of noninterbreeding among sympatric populations of a single locality, which

was the foundation of the original biological species concept of John Ray (1686), of that of Linnaeus, and of that of all local naturalists since. (*Ibid.*)

Here Mayr also states that this nondimensional species concept fits the local situation and the thinking of Ray and Linnaeus. This conflicts with Mayr's earlier discussions where the species concept of the local naturalist, of Ray and Linnaeus, was *morphological*. So the original connection between the early local naturalists and the morphological species concept is severed in the 1955 paper. The morphological species concept is relegated to being merely an application of typological thinking to biology, and the early naturalists are now seen as embracing a biological species concept that is relational, nondimensional, and based on reproductive isolation. In making this change, Mayr no longer stresses any sort of continuity between the typological/morphological concept and the newer biological concept—they are 'altogether different'. This heightened contrast between 'the typological' and the 'the biological' with respect to species concepts correlates with Mayr's earlier quoted description of the 'revolutionary change . . . of concept' from 'typological thinking' to 'thinking in terms of populations'; as we saw, in 1959 Mayr describes the difference between typological thinking and population thinking similarly: 'No two ways of looking at nature could be more different' (1959a, p. 2).

Finally,

The third species concept is that of the multidimensional species. While the nondimensional species defines a relationship of two populations, the multidimensional species is a grouping of populations . . . This third species concept, then, is a collective concept . . . It was an inevitable consequence of the great period of geographical exploration that the nondimensional species of the local naturalist had to be expanded into a multidimensional species, a geographically variable species. (Mayr, 1955 [1976], pp. 487–488)

Here we have the notion of 'polytypic species' that originated in the new systematics rendered into yet a third species concept. Note that in this quote Mayr again implies a continuity between the nondimensional species of the early local naturalist and the multidimensional species of the later naturalists. This is the same sort of continuity that Mayr portrayed as holding between the nondimensional *morphological* concept and the multidimensional biological (polytypic) concept. But now, 'nondimensional species of the local naturalist' is clearly meant to refer to a species concept based on reproductive isolation or noninterbreeding. What is going on here?

Mayr's new presentation of species in 1955 can be clarified by briefly considering what Mayr does in 1957. There Mayr keeps the three-fold distinction from 1955 (among typological, nondimensional, and multidimensional), but he characterizes them as theoretical, primary, or philosophical concepts from which biologists need to derive practical species concepts. For example, one could formulate a genetic typological species concept, a genetic nondimensional species concept, or a genetic multidimensional concept (Mayr, 1957, p. 504). All in all, though, Mayr argues that any biological species definition will be based on both the nondimensional and multi-

dimensional concepts (ibid., p. 505), which he calls a synthetic definition of species. In this sense, the continuity I noted in the 1955 quote on the multidimensional species concept indicates that both the nondimensional and the multidimensional concepts are ‘biological’ and they are both meant to contrast with the typological approach.

Mayr’s somewhat confusing 1955 presentation can best be explained by examining both internal and external factors. Internally, I believe Mayr is struggling to clarify an inherent ambiguity in the term ‘biological species concept’. That is, ‘biological’ seems to encompass two different sets of intuitions. One set of intuitions derives from the work of the early, local naturalists, and emphasizes the gaps between species at a particular time and place—that is, the nondimensional situation. As Mayr continues publishing on ‘the species problem’ I think he realizes that his own favored definition of species as reproductively isolated populations most closely connects with this *older* tradition in systematics. And yet, Mayr’s own work in taxonomy and on speciation—all of which is just as ‘biological’ as the early work—connects to another set of intuitions, based on more recent trends in systematics. In particular, the new systematics grew out of the discovery and study of geographically distributed populations—that is, the multidimensional situation. And as Mayr makes clear in 1957, a multidimensional approach emphasizes the flow of genes between populations (ibid., p. 505).

Internally, then, Mayr is trying to work out how these two sets of intuitions mesh. In the local, nondimensional case, reproductive isolation and the gaps between populations stand out. In the more global multidimensional case, it is gene flow among populations that stands out. By bringing both the nondimensional and the multidimensional species concepts under the rubric of ‘biological’ and stressing their ‘synthesis’, Mayr is attempting to deal with the second problem noted earlier (that the definition of species based on the local, nondimensional case does not work well in the global, multidimensional case). Part of the reason why Mayr needs to worry about this no doubt involves the book *Animal species and evolution* (1963), his second major work in evolutionary biology, that he is busy writing during this period (cf. Beatty, 1994). But another facet that needs to be addressed involves external factors, especially how Mayr’s perceived audience changes between 1942 and 1955.

Earlier, during the 1940s, Mayr is more interested in establishing the importance of ‘the new systematics’ vis a vis ‘the old systematics’. And so it makes sense for him to *contrast* the morphological, local, clear-cut, nondimensional domain of the old naturalists with the biological, global, more messy, multidimensional domain of the new naturalists. It also makes good sense for him to distance the work of the new naturalists from that of Ray and Linnaeus, for by doing so Mayr can stress the contributions and significance of the new systematics. Here his audience is limited to taxonomists and systematists, that is, primarily specialists.

Later, from 1953 on, when Mayr is making the transition from museum curator to Harvard professor and he is beginning to consciously take on the role of spokesman for evolutionary biology, his interests and audience shift (cf. Beatty, 1994). He is no longer just interested in clarifying recent developments in systematics and speaking to specialists. Rather, he is becoming increasingly concerned with what he

takes to be distorted views of biology¹² as a whole, and especially with a lack of appreciation of ‘the naturalist tradition’ in biology (*ibid.*). Thus the emergence of ‘typological thinking’, its links to Platonic philosophy, and the change in Mayr’s tone all correlate with a flurry of papers in 1959 that vigorously defend the whole naturalist tradition (Mayr 1959a,b,c) and address a wider audience (including anthropologists and geneticists). In this context, it makes sense for Mayr to stress the ‘unity’ within the naturalist camp. In the 1955 paper, Mayr accomplishes this by establishing a new major contrast between the typological species concept on the one hand and the two biological concepts (nondimensional and multidimensional) on the other. But in doing so, he strips the original morphological concept of *all* of its former associations to local naturalists such as Ray and Linnaeus and to the objective nondimensional situation. From now on, the morphological species concept is a product of typological thinking and it is contrasted to a more unified biological front that includes the old and new naturalists as well as the nondimensional and multidimensional situations.

In 1955, then, Mayr’s critical stance toward typological thinking crystallizes as he rethinks his stand on species. It is here that the distinction between ‘types’ and ‘populations’ is elevated from playing a role within the development of systematics to playing a role within the development of biology as a whole. The emergence of the typological/population distinction thus goes hand in hand with Mayr’s desire to defend the naturalist tradition within biology and to communicate that message to a wider audience.

4. On the emergence of the typological/population distinction between 1942 and 1955

By looking carefully at Mayr’s changing views on species between 1942 and 1955, we may clarify the origins of the distinction between typological and population thinking. In 1942, as we have seen, Mayr already has a clear idea of the importance of ‘populations’ for populations play a key role in characterizing the difference between the old and the new systematics. Mayr characterizes that difference primarily in terms of differing approaches to defining ‘species’: the old view defines species in purely morphological terms and allows a species to be characterized by a single individual; the new view defines species in terms of biological factors (ecological, geographic, genetic) and requires that a species be characterized by a series of individuals. In this way, the new systematics considers species to be populations, and it considers the study of the variation within populations as one key to understanding them. But it needs to be stressed that in 1942 Mayr does not develop any notion of ‘types’. Instead the population approach to species is contrasted with the morphological approach, which tends to disregard the variation within a species

¹² These ‘distorted’ views of biology were being promulgated by champions of genetics and ‘the new biology’, which was reductionistic, experimental, and molecular.

and instead focuses on single, representative individuals. Overall, the main contrast in 1942 is between the old and the new systematics, and Mayr's discussion of populations and his mention of types occur within the context of this larger and more important distinction.

By 1953, however, types and populations begin to stand out in Mayr's discussion. Here Mayr illustrates 'the revolutionary change in the thinking of the taxonomist' in terms of the difference between the type concept and the population concept. And while the details of the population concept largely restate his views from 1942, Mayr has much more to say about types: he links the type concept to the legacy of Plato, he uses the word 'typological', and he attributes all manner of negative outcomes to the adherents of this approach, including exaggerating constancy of species, missing the importance of variation, denying evolution completely, or explaining evolution in terms of saltations. From this list, we can also see that Mayr is beginning to think of evolutionary questions in terms of types and populations as well. Mayr's discussion of species still centers on the morphological versus the biological conceptions, but now the differences between these species concepts are couched in terms of the differences between the type concept and the population concept.

By 1955, Mayr is ready to take a further step. In 1953, the move from the type concept to the population concept constituted a revolution *in taxonomy*. But in 1955, 'the replacement of typological thinking by thinking in terms of populations' (Mayr 1955 [1976], p. 301) constitutes a revolutionary change *in biology*. By extending the scope of the distinction between the type concept and the population concept from taxonomy to biology as a whole, Mayr formulates what he will in 1959 call the typological/population distinction. In my view, this is the origin of the typological/population distinction: Mayr generalizes from the type concept versus the the population concept in taxonomy to typological thinking versus population thinking in biology more generally.

This transition I have sketched from 'type' to 'type concept' to 'typological thinking' coincides with the increasing importance that 'types' come to play in Mayr's own thinking. This is especially true with respect to species, for in 1955 Mayr replaces 'morphological species concept' with 'typological species concept'. From this point on, Mayr presents the typological species concept as 'altogether different' (*ibid.*, p. 485) from the biological species concept. Earlier, until the transition period around 1953, Mayr was more neutral toward the morphological species concept, stressing the continuity and usefulness of that approach even while contrasting it to the newer biological concept. But beginning in 1955, when Mayr introduces the typological/population distinction, he is more critical toward the typological species concept, stressing that it is 'subjective' (*ibid.*, p. 484), leads to 'inconsistencies' (*ibid.*, p. 485), and that numerous examples demonstrate its 'worthlessness' (*ibid.*). In fact, the morphological concept is stripped of its previous positive associations (with the local naturalists such as Ray and Linnaeus and as being nondimensional) and is instead portrayed simply as an application of typological thinking. The positive associations are transferred to the nondimensional species concept, which now includes Mayr's original biological species definition from 1942. This reconfigured view of species makes room for the broader scope of the typological/population

distinction. In this way, typological and population thinking become overarching and competing explanatory frameworks in biology and the reconfigured view of species ensures that any biological conception of species falls completely on the population side of the distinction.

5. Conclusion

Clarifying Mayr's changing views of species and the gradual emergence of the typological/population distinction from that work is instructive. On the one hand, given Mayr's sometimes dogmatic style of defending the biological species concept, it is somewhat surprising that his views do in fact change and evolve over time. On the other hand, Mayr skillfully employs the distinction to a variety of ends, and clarifying its origins in his own work may prove useful for understanding Mayr's appeal to the distinction to achieve two main goals.

One goal, as already mentioned, is to legitimize the natural historical sciences, including systematics, taxonomy, and evolutionary biology, against the criticisms of 'the new biology'—molecular, reductionistic, and drawing explicit inspiration from the physical sciences (cf. Beatty, 1994). The typological/population distinction helps Mayr precisely because it is a more general distinction. That is, given that 'the natural historical sciences', their concepts, and their methods were themselves subject to criticism, it would have been futile to try and appeal to those very concepts or methods in defense. Any such appeal could itself be dismissed as 'old-fashioned' and out of touch with the 'new biology'. Somehow, Mayr had to legitimate the concepts and methods of the natural historical sciences themselves. By linking the 'new biology' to typological thinking and emphasizing how population thinking flows from the natural historical sciences, this is precisely what more a general historical and philosophical approach could accomplish: historically, Mayr could demonstrate the usefulness of the naturalist approach and its connection to a respectable and powerful line of inquiry going back to Darwin; philosophically he could argue for the 'in principle' need for an evolutionary (population thinking) approach in order to offer adequate and complete explanations of biological phenomena.

Another goal, not yet discussed (and beyond the scope of this paper), is Mayr's use of the distinction to attack racism. As Walter Bock puts it, 'Nothing in Mayr's most general theoretical writings has been more important than his stand against typology in biology in the broadest sense, including his stand against racism' (Bock, 1994, p. 285). By linking racist claims to typological thinking, Mayr could easily turn to the population thinking alternative for a critical response. But again, it is the more general scope of the typological/population distinction that allows Mayr's population-based criticisms of racism to have weight—for by being typological, the racist does not simply go against the thought and practice of systematics or taxonomy or even evolutionary biology, but against 'all of biology' as it is properly understood to be informed by population thinking.

Mayr's 'development' of the broader typological/population distinction can be understood as an attempt to liberate certain key ideas of the 'students of diversity'

from their disciplinary constraints (taxonomy, systematics, evolutionary biology), and to render them more generally applicable by repackaging them into a broader historical and philosophical distinction that pertains to all of biology. However, students of Mayr's work need to exercise caution. A casual reading of Mayr's biological, historical, and philosophical writings might persuade us that Mayr 'discovered' typological and population thinking in the work of his predecessors, and that the labels 'typological thinking' and 'population thinking' have clear, fixed, and unproblematic meanings. But the account given here shows that the typological/population distinction arises out of Mayr's own work on species concepts. And it may well be the case that the fluidity we find in Mayr's work on species concepts can also be found in Mayr's use of the typological/population distinction. For example, in different contexts, Mayr portrays the typologist as a Platonist, as an adherent of the methodological ideals of the physical sciences, or as an advocate of alternative interpretations of key evolutionary concepts (cf. Chung, 2000). It may be that these all 'downplay biological variation', but surely the justifications will differ in a way that matters. Therefore, instead of casually accepting the typological/population distinction as an overarching framework applicable to all of biology, I suggest we treat Mayr's (and others') appeal to the distinction as a series of case studies, and allow for the possibility that the distinction changes or even breaks down in different contexts. In doing so, we may find that the history of biology does parse as neatly into typological and population thinkers as Mayr's account seems to imply. But, then again, we may find that it does not.

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