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“A temporary oversimplification”: Mayr, Simpson, Dobzhansky, and the origins of the typology/population dichotomy (part 1 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 this first part, I will argue 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 the 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. Introduction

In May 1956, botanist Carl Epling (1894–1968) wrote evolutionary biologist Ernst Mayr (1904–2005) to share his thoughts on a manuscript that Mayr had sent him. Mayr’s discussion of species concepts had not been entirely to Epling’s liking. He took issue with Mayr’s characterization of some (contemporary and historical) work on species as ‘typological’ in orientation, in contrast with the ‘populational’ outlook of the modern evolutionary synthesis. Epling did not think that such strongly marked conceptual dichotomy could be justified. Mayr’s division of biologists into those who mistakenly view species as unvarying types versus those who approach them as dynamic populations was a straw man. Mayr replied promptly: “I am not denying that I

may be overstating the case for or against certain concepts ... I want to make the issues clear even at the risk of a temporary oversimplification.”¹

Alas, Mayr’s oversimplification was far from temporary. Over the next decades, Mayr would give the typology/population distinction an increasingly prominent place in his writings, but without explaining in much detail what it consisted in. What did it really mean to be a ‘populationist’ and what exactly should we understand by ‘the type concept’ that Mayr rejected so resolutely? What, in practice, did ‘thinking’ in terms of populations rather than types amount to? Rather than addressing questions like these, Mayr preferred to emphasize that the distinction had deep historical roots. He traced the origins of ‘typological thinking’ back to Plato and presented Charles Darwin as the hero of ‘population thinking’

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¹ Mayr to Epling, 18 May 1956, Papers of Ernst Mayr at the Harvard University Archives [hereafter: ‘Mayr Papers’].

(Mayr, 1959b). Historians had “consistently overlooked” this foundational aspect of the Darwinian revolution, which made for a “major gap” in Darwin studies (Mayr, 1959a). By the early 1960s, Mayr liked to present the shift from typological to population thinking as “perhaps the greatest revolution that has taken place in biology” (Mayr, 1963, p. 5). Yet, Darwin’s eradication of ‘typological thinking’ from biology had not been complete. It took the modern evolutionary synthesis, which Mayr had helped to shape, to drive out the remnants of typological thinking (Mayr, 1972, 1980b, 1982).

When one of Mayr’s early historical treatments of the typology/population distinction (Mayr, 1959b) was reprinted in a collection of some of his key writings (Mayr, 1976a), he reminisced that it had constituted “the first full presentation” and “full articulation” of what this dichotomy consists in (Mayr, 1976b, p. 26).

Before long, historians began to demur. Paul Farber complained most vocally that Mayr’s talk of typology as an “allegedly archaic, fuzzy-headed metaphysical position ... does violence to the historical record and confuses contemporary debates rather than clarifies them” (Farber, 1978, p. 91). For Mayr, however, the risk of oversimplification was sufficiently offset by the rhetorical payoff of having a simple distinction that could be used to discuss a myriad of controversies in historical and contemporary biology.

In recent years, a number of philosophers and historians have begun examining the origins of the typology/population dichotomy by turning to Mayr’s early writings (e.g. Amundson, 2005; Chung, 2000, 2003; Müller-Wille, 2011; Wilkins, 2009; Winsor, 2003, 2006). In the course of doing so, they have attempted to clarify the theoretical meaning of this distinction—or the lack thereof. Polly Winsor, for example, has argued that Mayr’s dichotomy was not just “an enormously effective bit of polemic,” but was also based on a notion of types that no one recognized. What Mayr identified as ‘typological’ did not “accurately describe the avowed position of anyone, ... [it] was an error no one would want to be accused of” (Winsor, 2006, p. 159).² Carl Chung (2000, 2003), on the other hand, has argued that Mayr’s attack on typology budded from a valid concern about a substantive issue in taxonomic practice. He points to the notion of a ‘type specimen’ as being at the heart of Mayr’s concern—a possibility that Winsor eliminates (Winsor, 2006, p. 157). Yet Chung does not really tell us what Mayr’s problem with this notion of types consisted in; he does not unpack the different meanings of ‘type’ in Mayr’s writings. Thus, he ends up drawing the quasi-circular conclusion that “[the] 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” (Chung, 2003, p. 293).

In what follows, I will shed new light on the origins and content of the typology/population dichotomy. I will argue that it is more complex and more interesting than Winsor, Chung and others have suggested.³ In a nutshell, I will argue that what has been perceived

as Mayr’s dichotomy, wasn’t really *his*. Mayr rather took his cue from two close colleagues, George Gaylord Simpson (1902–1984) and Theodosius Dobzhansky (1900–1975), who had independently started drawing type/population contrasts in the late 1930s and early 1940s.⁴ Simpson drew a methodological type/population contrast in the domain of (paleontological) taxonomy, whereas Dobzhansky invoked a type/population distinction in a population dynamic context. These distinctions were individually meaningful and had little to do with each other; Dobzhansky and Simpson took issue with very different notions of ‘type.’ Yet, in Mayr’s hands, these lines of argument were ‘synthesized,’ historicized, and expanded into an all-encompassing typology/population dichotomy. What Mayr came to present as “one of the most profound intellectual and conceptual revolutions in biology” (Mayr in Gerard, 1958, p. 165), was a massive distortion of type/population distinctions that had once been individually meaningful.

This essay is published in two parts. In this first part, I will give an historical overview of the two type/population contrasts that originated with Simpson and Dobzhansky. In the second part, I show how Mayr misrepresented these distinctions individually, conflated them with each other, and admixed a number of unrelated issues. In the second part I also show how this could lead Mayr to present positions as ‘populationist’ that Dobzhansky or Simpson considered to be objectionably ‘typological’. Nevertheless, we will see that Dobzhansky and Simpson did not openly take issue with Mayr’s distortions and transformations of their ideas. These three men were united by much more than what divided them. They had a shared interest in defending the modern evolutionary synthesis that they had helped to shape. In this context Mayr’s chimeric and inflated dichotomy served its purpose.

2. Simpson on systematics and statistics

2.1. Ahead of the curve

In 1981, three years before Simpson died, some of his most important scientific publications were bundled and reissued in the collection *Why and How: Some Problems and Methods in Historical Biology* (Simpson, 1981). Simpson introduced each paper with a brief note on the context in which it had been written. About one of the included papers, ‘Patterns of phyletic evolution’ (Simpson, 1937b), he remarked that it had signaled the “abandonment of the typological thinking of my college teachers and started aiming me toward statistical biometry and the deeper investigation of evolutionary theory and taxonomic stance” (Simpson, 1981, p. 112). Interestingly, the reprinted paper contained no mention of ‘typological thinking,’ ‘typology,’ or even of ‘types.’ Yet, apparently, Simpson thought it contained the germ of a critique that he would later come to associate with these terms. So what was it that Simpson started to distance himself from in this short paper from 1937?

At heart, ‘Patterns of phyletic evolution’ was a critique of some basic methodological precepts in paleontological taxonomy. The article started by contrasting the ‘old methods’ of nineteenth century paleontology with the ‘new methods’ that were used by Simpson’s contemporaries. Simpson pointed out that the old days had been marked by unbridled speculation about phylogenetic

² More precisely, Winsor argues that Mayr set up an imaginary typologist by transferring the accepted use of ‘types’ for a supraspecific taxon down to the species level, “where no one believed they belonged” (p. 159). Several other commentators on the origins of the typology/population commentators have followed Winsor’s account quite closely on this point. Ron Amundson (2005), for example, asks “Were species thought to be types? ... Did the [notion of] types extend all the way down to the species level? I believe that the answer is clear on reading the literature. *Species are not types. Never were, never could be*” (pp. 80–81; italics in original).

³ I will not assess the historical and conceptual relations between Mayr’s objections to ‘typological thinking’ and his problems with ‘essentialism,’ which are discussed at length by Winsor (2006). Although I do believe that my account of the typology/population dichotomy introduces questions for Winsor’s historiography of the ‘essentialism story,’ I will leave discussion of this topic for another occasion. In any case, Mayr’s association of typological thinking with essentialism only started in the late 1960s (Mayr, 1968a, b, c), when his conception of the former had already crystallized (see Section 3 in Part 2 of this essay).

⁴ A few scholars have noted that Dobzhansky in the early 1950s drew between conception of ‘race as type’ and ‘race as population’ early in the 1950s (Amundson, 2005; Gannett, 2001, 2003), or that Simpson in the early 1940s was critical of a certain notion of ‘types’ (Laporte, 1994). However, these authors have not explored the connection with Mayr or the larger typology/population dichotomy in any detail.

relationships. Lavish trees were being drawn on the basis of meager evidence for the suggested lines of descent. As a reaction to these “fine optimistic years of early evolutionary paleontology” Simpson’s teachers and contemporaries had become very cautious about inferring ancestral relations (Simpson, 1937b, p. 303). But perhaps, Simpson noted, “the pendulum of scientific fashion has swung too far.” In an attempt to avoid speculation, recent taxonomic monographs included “diagrams suggesting many different lines that are parallel or that diverge but are not connected” (Simpson, 1937b, p. 304). For some good examples of the “innumerable instances in recent literature” of such diagrams, Simpson pointed to a posthumously published monograph by the famous paleontologist Henry Fairfield Osborn (1857–1935). Osborn’s (1936) phylogeny of mastodons included several diagrams like that in Fig. 1. Simpson mockingly observed about such diagrams that:

the impression is given that ... each restricted little phylum has been distinct since the beginning of time. One is almost forced to think that when primordial cells first arose on the planet there were already potentially man-cells, oyster-cells, codfish-cells, ape-cells, and every other distinct sort to correspond to every minor phylum of living things that ever was to arise, and that these various blobs of protoplasm were not on speaking terms.

Simpson (1937b, p. 304)

In the remainder of his paper, Simpson outlined how to avoid the pitfalls of this ‘new’ taxonomic methodology without relapsing into ‘old’ nineteenth century speculation. He sketched how novel taxonomic methods could enable taxonomists to reach a new and more objective middle ground.

Simpson explained the main problem with current taxonomic methodology with the aid of the toy example given in Fig. 2. It illustrates the problem of classifying a sample of slightly different specimens from the same locality or geological horizon into one or more species. The question that arises in this context is how many species are present. “Current methods, which tend to a very polyphyletic view of mammalian descent, might well lead to the recognition of three distinct groups among the specimens at hand; hence, to the conclusion that they represent three distinct phyla ... On the other hand, the whole group of specimens may belong to one race or species, and the whole difference between them may be

the range of variation within an essentially unified phylum” (Simpson, 1937b, p. 306–307). How to pass judgment on these options?

The standard answer, which Simpson had been taught in graduate school, was to use the 15 percent rule: if a specimen is more than 15 percent larger than another in any dimension, they belong to different species. But, Simpson added, “as everyone who has studied variation should know” this rule was merely a rule of thumb. In practice, taxonomists sometimes included variants that differed by more than 15 percent from another in the same species. In other cases it would be “perfectly valid” to assign individuals to different species when the difference was less than 15 percent. The reason taxonomists sometimes set aside the 15 percent rule (or one of its cognates) was their implicit awareness that

if specimens really represent distinct phyla, there must be some objective difference between them, not as individuals but as groups. Differences between the individual specimens do not in themselves necessarily have any phyletic significance, for two individuals always differ from each other, but, if such varying differences can be shown to characterize and to differentiate groups of individuals, they take on wide meaning.

Simpson (1937b, p. 307)

In other words, taxonomists were implicitly aware that a proper methodology of classification had to be group-based. They realized that comparing specimens in a one-by-one fashion, with the help of a simple taxonomic rule, could fail to result in good classifications. However, the downside of this realization was that it led taxonomists to trade communally shared taxonomic rules for opaque appeals to subjective taxonomic judgment.

At this point Simpson unveiled his strategy for putting taxonomic methodology on a firmer footing. To bring the promise of group-based taxonomy to fruition, taxonomists would need to start using modern statistical methods: “One of the most conclusive ways in which group characters can be differentiated is by means of frequency distributions” (Simpson, 1937b, p. 307). Simpson was not merely arguing for the calculation of simple *descriptive* statistics (like the mean or median for a character of a group⁵), but pointed out that *inferential* statistical methods should be used to delimit groups to start with. Returning to the example from Fig. 2, he argued that if the observed characters would lead one to infer the distribution from Fig. 3A, one would have to postulate the existence of three species. If, on the other hand, the distribution approached that of Fig. 3B, it would be safe to conclude that only one species had been discovered.

The same approach could be used to make more reliable inferences about phylogeny and ancestry. Given a sample of material as in Fig. 4A, the tools of inferential statistics could be used to determine which of several possible phylogenetic hypotheses fitted the data best. If the distribution of characters at a certain time *T* would be unimodal, the phylogenetic interpretation from Fig. 4B would be most plausible. If the distribution would tend towards bimodality, this would support the interpretation from Fig. 4C better. Simpson argued that although the latter interpretation was without doubt “the fashionable interpretation” the first interpretation must have been “so common in reality that it is surprising to note how seldom it is now invoked” (Simpson, 1937b, p. 310). It was high time for systematics to take the statistical turn.

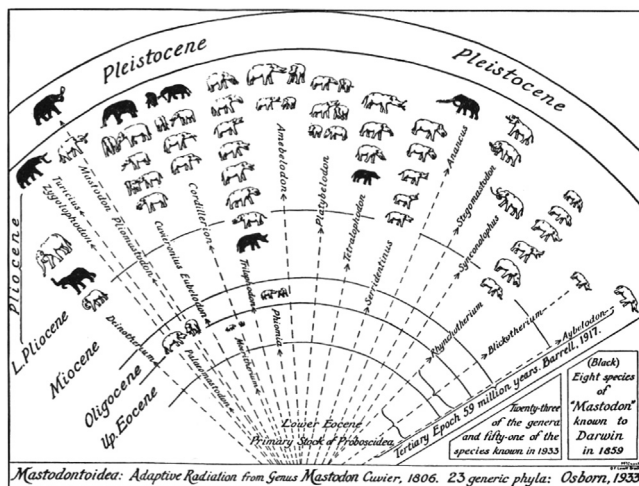


Fig. 1. Osborn’s chart of the phylogeny of the mastodons, published posthumously. Source: Osborn, 1936, xiv

⁵ By the mid–1940s, Simpson and other taxonomist had already started listing measures of central tendency in their taxonomic monographs (e.g. Simpson, 1928).

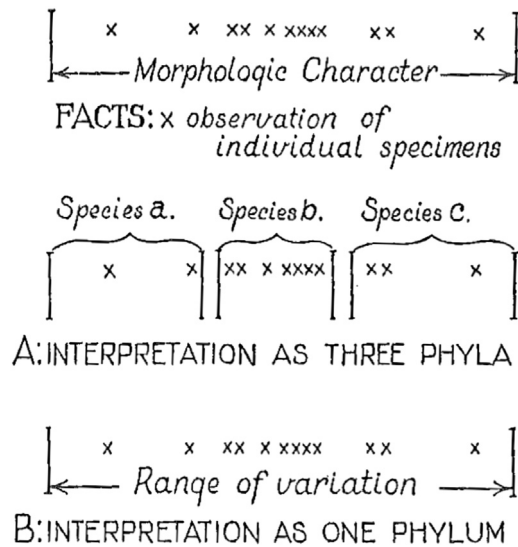


Fig. 2. A hypothetical data-set of morphological characters from similar but varying specimens from the same horizon and locality, interpreted as part of three species (A) and a single species (B).

Source: Figure 1 from Simpson, 1937b.

In two other publications from the same year, Simpson applied his methodological recommendations to actual morphological samples (Simpson, 1937a, d). He reiterated that the use of inferential statistics departed from the methodology of “the far greater part” of recent paleontological studies, in which “comparisons are made on the basis of individual specimens only. Even when groups of specimens are available and are compared, the comparison is in fact of the several individual members of the group and not of the group itself as a unit.” His own, novel approach was instead to “compare groups as such [and] to use the individual specimens only as representatives of a group rather than thinking of the group as secondary and the individuals as the essential units. Although the distinction may seem unduly subtle, it is in fact fundamental.” It harbored the potential of putting paleontology “on a more exact, more objective and less intuitive basis” (Simpson, 1937a, p. 2).

2.2. Samples, types, and typicality

Simpson’s argument for the use of statistical, group-based methods of taxonomic inference was a precursor to his later plea for ‘population thinking’ in the context of classification. Talk of ‘populations’ already appeared more prominently in a book he had begun to write in 1937, together with his soon-to-be-wife Anne Roe (1904–1991).⁶ The book, entitled *Quantitative Zoology: Numerical Concepts and Methods in the Study of Recent and Fossil Animals* (1939), contained an elaborate treatment of statistical methods that were relevant to the methodological overhaul that Simpson was advocating. The foundations of this new outlook were captured in a sentence that introduced the chapter on ‘Sampling’: “[Z]oology is, or should be, a study of populations; but a whole population cannot be brought into the laboratory or examined in the field, so that the only practical approach is by the method of samples” (Simpson & Roe, 1939, p. 166).

⁶ Roe being a clinical research psychologist with a Ph.D. from Columbia University, she had ample experience with the statistical analysis of data sets. Peeking over Simpson’s shoulder, she had remarked that paleontologists “should do more with their data statistically than just note means and ranges” (Roe, 1985, p. 313). For Simpson’s own recollections of his collaborative work with Roe, see Simpson (1978, p. 83ff.).

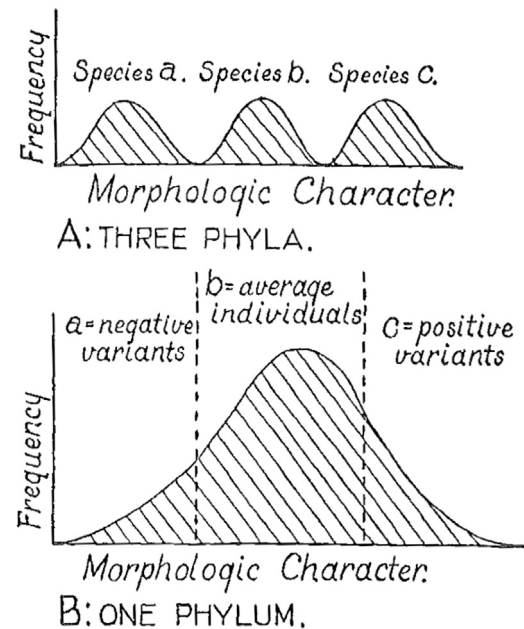


Fig. 3. Frequency distributions based on the characters of the specimens from Fig. 2. (A) Three curves corresponding to three distinct species of Fig. 2A; (B) A single curve corresponding to the interpretation of Fig. 2B.

Source: Figure 2 from Simpson, 1937b

But why would one contrast this population-based approach with anything having to do with ‘types’? What was the relation between ‘types’ and the orthodox method of one-by-one comparison that Simpson had been criticizing? The chapter on ‘Comparison of Samples’ reveals the link. In this chapter Simpson and Roe rehearsed Simpson’s earlier assessment of the problems with individual-based classification, while approaching the topic from a slightly different angle. They focused on a particular practice of one-by-one comparison, to wit, the common procedure of comparing a newfound specimen with a known *type specimen*: a select specimen that is stored in a museum collection and that has a label with a (sub)species name attached to it. Simpson and Roe explained that “[w]hen a specimen is compared with a type and decision is made as to whether it belongs to the same species, the two are really being treated as samples. The idea is to see whether the specimen to be identified was drawn from the same population, the species, as the type” (Simpson & Roe, 1939, p. 186–87). The problem with this practice was the same as Simpson had discussed before: information about samples was effectively being compressed into two individual specimens. From a statistical point of view this was therefore “a thoroughly unscientific procedure. It involves no definite criterion of significance, nor idea of what the range of variation really is, no conception of the relationship of the type to the variation of the species as a whole, and no method of relating the specimen being identified to this specific distribution beyond a vague and subjective opinion that is shown by more reliable methods to be as often wrong as right.” In the remainder of the chapter Simpson and Roe explained how information about samples from which the type specimens had been drawn could be used “to obtain definite criteria on all these points” (Simpson & Roe, 1939, p. 187).

A clear type/population contrast thus started to emerge from the pages of *Quantitative Zoology*. Taxonomists had to abandon the method of one-by-one comparison using *type specimens* and adopt sample-based methods to infer the variational spectra of *populations*. However, as Simpson explained in a separate article, this

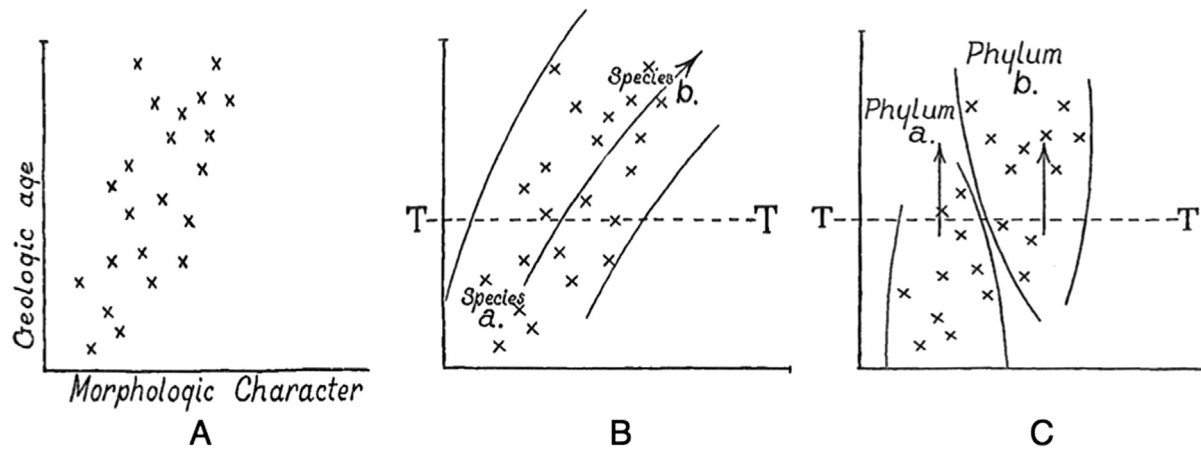


Fig. 4. A hypothetical sample of diachronic morphological variation (A) and two of its interpretations (B, C). In the middle diagram (B) the variation is interpreted to belong to one species. In the diagram to the right (C) it is interpreted to belong to two successive species. Source: Figures 3, 4, and 5 from Simpson, 1937b

did not mean that taxonomists would need to stop using type specimens altogether (Simpson, 1940). On the contrary, type specimens served a very useful role as fixed *name-bearers* for species names. The practice of anchoring species names to fixed elements of those species enabled taxonomists to agree about which name belongs to which species in spite of potential disagreements about where to draw the boundaries between species.⁷ As Simpson put it, type specimens prevented taxonomic naming from “disintegrating into an almost mystic chaos of individual systems” (Simpson, 1940, p. 416).

What Simpson objected to, was the use of type specimens for anything other than naming. The problem was that taxonomists also treated these specimens as *standards of comparison* or as *bases for description* of species. These taxonomists were making a double mistake. Not only did their classificatory practices rest on the unreliable method of one-by-one comparison between single specimens, but they were also wrong to treat type specimens “as more ‘typical,’ nearer to a norm or central tendency for a species” (Simpson, 1940, p. 417). In reality, a type specimen was often a rather aberrant member of its species, because it was usually designated as type after only a small (and possibly unrepresentative) sample from its species had been found.⁸

In short, Simpson was only objecting to the use of type specimens in the context of *classification*. He summarized this lesson by drawing an explicit contrast between populations and types:

The newer theory of taxonomy as a system of group concepts based on inferences about *populations* from samples, a theory that is rapidly gaining ground and to which I strongly adhere, is decisively incompatible with this [classificatory] use of ‘types’.

Simpson (1940, p. 417; italics added)

⁷ For more on the complex philosophical issues about naming and identity that type specimens help to address, see Witteveen (2015, under review).

⁸ Thus, Simpson concluded, the term ‘type specimen’ was very confusing, since it readily summoned up these unwarranted associations with typicality. He proposed the neologism ‘onomatophore’ (Greek for ‘name-bearer’) as suitable replacement. Yet immediately upon making this suggestion he threw in the towel: “As a matter of practical usage, however, it is evident that the word ‘type’ is so deeply rooted in our science that it is not desirable and probably not possible to uproot it” (Simpson, 1940, p. 421). Twenty years later he indeed observed that “I do not myself regularly use the term onomatophore, and I do not know of anyone who does” (Simpson, 1960).

Together with his 1937 article on ‘Patterns of phyletic evolution,’ Simpson included his 1940 article on ‘Types in modern taxonomy’ in his collection of reprints from 1981. In a brief commentary on the 1940 article he mentioned that he had made a few minor modifications to the original text. In the quotation above, he had changed the word ‘theory’ into ‘view.’ After all, he had not really been arguing for a new taxonomic theory, but he had rather presented a new outlook for taxonomy on the basis of new set of methodological precepts.

2.3. Characters-in-common and archetypal classification

Simpson’s concern with types in biology was not limited to the misguided use of type specimens as classificatory devices. There was another branch to Simpson’s critique of taxonomic methodology that he developed into another criticism of types. This branch also budded in 1937, in Simpson’s contribution to the proceedings of a symposium on classification above the species level (Simpson, 1937c).

Simpson’s symposium paper was a critical assessment of some recent work on supraspecific variation by the taxonomist Alfred Kinsey (1894–1956). For the most part, Simpson and Kinsey were on the same page when it came to methods and principles of classification. Kinsey had become famous among taxonomists for his use of very large samples of collected specimens in his studies of the gall wasp genus *Cynips*.⁹ Back in 1930 he had already warned that the reputation of biological taxonomy was suffering from the fact that “too many systematists attain their objectives when each species is ‘represented’ by a half-dozen specimens pinned in their cabinets” (Kinsey, 1930, p. 9). Simpson couldn’t agree more. He was also impressed with Kinsey’s more recent monograph *The Origin of Higher Categories in Cynips* (1936), which was similarly “based on a remarkably thorough and profound study of an exceptionally large mass of data” (Simpson, 1937c, p. 236). Nevertheless, one of the observations Kinsey made in a discussion of concepts and principles of higher classification seemed obviously wrong-headed to Simpson.

Kinsey had been discussing the widely held belief that “the characters common to all the elements of a higher category

⁹ Kinsey’s largest systematic study had been based on the measurement and description of tens of thousands of gall wasp specimens. See Bancroft (2007), Gould (1982) and Yudel (1999) for more on Kinsey’s taxonomic studies.

represent characters which were found in the ancestral stock (the species) from which the category was derived.” In Kinsey’s view, this inference was based on a false premise, since “often ... and perhaps invariably ... no single character applies to all the species of a genus” (Kinsey, 1936, p. 9). In his 1937 symposium paper Simpson concurred with the thrust of Kinsey’s point, but noted that this last remark “can not be taken literally, for it is obviously untrue” (Simpson, 1937c, p. 255). Take Kinsey’s own favorite genus *Cynips*: it is clear that all specimens of this genus *do* have certain characters-in-common. “All species of *Cynips* have wings (whatever their size), all have tracheae, all have six legs, all make galls, and so on for many characters” (Simpson, 1937c, p. 255). What Kinsey must have intended to say, is that higher ranks and their taxa do not have to *exclusively* share one or more characters. They cannot be *defined* by a set of characters-in-common. Simpson realized that this was indeed a conceptual issue worth emphasizing, because it had broad significance for the practice of classification.

In several publications from the 1940s Simpson elaborated on the shortcomings of classification “by listing characters believed to be common to all its members and not to be common, either alone or in combination, to members of morphologically contiguous groups” (Simpson, 1943, p. 153). His critique of this characters-in-common approach for higher ranks followed the same pattern as his earlier critique of the method of one-by-one comparison at the species level. He began by noting that although the identification of characters-in-common might serve as a rough-and-ready rule of thumb, “it certainly does not suffice for any real understanding of the nature and significance of the group” (Simpson, 1943, p. 153). He argued that, like in the case of species, determining the limits of higher taxa was “essentially a statistical problem ... not in a narrow sense, to which many statisticians adhere ... [but] in a broader sense [as] the science of (a) estimating the characteristics of populations from samples; and (b) describing groups, as such, rather than individuals taken singly” (Simpson, 1943, p. 151). Simpson’s conclusion sounded familiar: “The fundamental point is not so much the distinctiveness of unit characters as their distribution in the groups; these groups, and not the characters, being the objects of classification” (Simpson, 1943, p. 156).

Next, Simpson pointed out that the characters-in-common approach could lead to ill-founded evolutionary theorizing. Its methodological myopia could cause taxonomists to make flawed phylogenetic inferences. It was common, for example, to assume that certain genera could be distinguished by attending to differences in tooth formula. Simpson explained that, taken at face value, this assumption was incompatible Darwinian gradualism.

If subspecies become species in isolation and species become genera by divergence and diversification, it is inevitable that diagnostic characters should thus appear as individual variations and tend gradually to become subspecific, specific, then generic characters, and that no particular kind of character should be characteristic of a particular taxonomic level.

Simpson (1943, p. 157)

In other words, sorting characters into definite taxonomic ‘kinds’ had to be wrong if Darwinian gradualism was correct. Here the real danger of the characters-in-common approach showed its face. Those who reified this method from a mere rule of thumb into a definite criterion were bound to conclude that new ranks (with their own defining characters) emerged by saltation. They were thus driven into the arms of “the cataclysmic school, like Goldschmidt (1940),” whose theory of systemic mutations was provoking the ire of Simpson and his modern synthesis colleagues (Simpson, 1943, p. 155).

In his earliest critique of the characters-in-common approach, Simpson had made no reference to types, but in a semi-popular article from 1941 he started speaking of “archetypes” and “archetypal taxonomy” in this context:

The spread of evolutionary zoology led to the abandonment of the philosophical concept of archetypes, but the static point of view involved in it was not immediately discarded and indeed persists to considerable degree today. The diagnosis of taxonomic groups by statement of a combination of fixed characters believed to be common to all members of the group is almost exactly the same process as the delineation of an archetype, however different in intention and interpretation.

Simpson (1941, p. 12)

Simpson’s message was clear: the characters-in-common conception of higher taxa was a methodological residue from pre-Darwinian days. “Philosophical zoologists” such as Goethe, Oken, and Owen might have believed in the reality of archetypes, but true Darwinians did not. Committed Darwinians should abandon methods that were (unwittingly) based on this long-abandoned concept.

Simpson expanded on these historical remarks in his monograph *The Principles of Classification and a Classification of Mammals* (1945), where he presented the characters-in-common approach as a distinct “system of classification”:

[T]his particular method may more distinctively be called archetypal. Its basis is the grouping of animals according to the number, and to some extent the kind, of structural characteristics that they have in common. Each grade in a hierarchy corresponds with certain fixed characters possessed by all the animals included under a given rubric at that level. The lower the hierarchic rank, the more characters held in common by the included forms ... Each group of the system has a fixed model, an archetype, consisting of a given set of morphological characteristics, and any animal that agrees, in this set of peculiarities, with the archetype belongs in that group.

Simpson (1945, pp. 3–4)

Simpson claimed that this taxonomic methodology had been used “by almost all early naturalists, including Linnaeus and most of his successors before Darwin.” All of these naturalists had relied on the postulation of archetypes, albeit on different interpretations of what those archetypes represented. Some had considered the archetypal system a “subjective and arbitrary system adopted solely for convenience,” whereas others interpreted it to represent “a set of supernal models, archetypes in the philosophical sense, of which objective animals are more or less imperfect copies.” A third interpretation had been that of Darwin and many of his successors “almost up to the present,” who had retained the archetypal system “by substituting ‘common ancestor’ for ‘archetype’ ” (Simpson, 1945, p. 4). Only very recently had taxonomists like Simpson begun to free themselves completely from this archetypal system.

2.4. The Zangerl episode

Simpson finished the manuscript of *The Principles of Classification* in December 1942, days before he left the American Museum of Natural History to help in the war effort. Upon his return he continued to reiterate his objections to the archetypal system of classification with even more vigor. Whereas earlier he had addressed those who were unwittingly using its outdated methodological precepts, he now directed his attention to those who deliberately defended those precepts.

The immediate cause of Simpson's new focus was a manuscript that arrived on his desk in May 1948. It had been sent to him by Mayr, who served as the (founding) editor of the journal *Evolution*. The manuscript, entitled "The methods of comparative morphology and its contribution to the study of evolution," was from the hand of Rainer Zangerl (1912–2004), an esteemed vertebrate anatomist who worked in the tradition of the German systematic morphologists Adolf Naef and Joseph Kälin.¹⁰ In a cover letter to Mayr, Zangerl wrote that he had been spurred into action by the "great confusion" that dominated the contemporary literature on the morphological method, which "threatens to become worse with each additional paper that is published on the subject."¹¹ The most profound confusion surrounded the concepts of *structural plan* and *morphotype*, which Zangerl set out to clarify.

He defined the former concept as "the conformity to a design in the topographic (spatial) relationship of the parts of an organism to the body as a whole" (Zangerl, 1948, p. 354). These structural plans manifest themselves as a nested hierarchy that corresponds with the taxonomic hierarchy. The notion of a morphotype was closely related to that of the structural plan. It was premised on the finding that organisms with the same structural plan could nevertheless display variation in the shape, size and arrangement of their corresponding parts. A morphotype, then, was an abstraction from the form variety of organisms with the same structural plan. It could be defined as "an ideally constructed form, the norm, within a group of organisms of essentially similar structural design, from which the actual forms of that group can be ideally derived" (Zangerl, 1948, p. 373). Zangerl repeatedly emphasized that the construction of, and derivations from, the morphotype needed to be considered ideal, not actual. One had to keep in mind that the morphotype concept was part of a purely morphological method; it was "a factual morphological tool, independent from phylogenetic speculation." The potential for evolutionary interpretation of the ideal derivations would "in each case [be] a problem by itself" (Zangerl, 1948, p. 357–58).

It won't surprise that Simpson took serious issue with all of this. He wrote a long and scathing reviewer's report, focusing on the morphotype concept, which he considered "obscurantist, retrogressive, and sterile for modern biology."¹² Zangerl's entire approach hinged on the "unstated premise that classification is based on archetypes (= morphotypes?) and characters-in-common." Simpson wrote to the Mayr that he was "fundamentally in disagreement with the attitude, philosophy, and most of the procedures and conclusions of this school of morphology."¹³ He was reportedly so outraged by Zangerl's approach that he "never spoke to the man again" (Hull, 1988, p. 69).

Nevertheless, Simpson ended up recommending Zangerl's paper for publication in *Evolution*, since he deemed it useful to have a "convenient summary" of this school of comparative morphology on record.¹⁴ From an evolutionary viewpoint Zangerl's approach was relative harmless anyway, since he explicitly separated the

comparative morphologist's method from anything having to do with evolution. However, there were others who were eager to cross this bridge. The German paleontologist Otto Schindewolf (1896–1971) was getting increasingly well-known for his evolutionary interpretation of the systematic morphology of Naef. Schindewolf argued that morphotypes originated in saltationist 'typostrophic' events.¹⁵ This was exactly the kind of misguided theorizing that Simpson warned against.

A few months before Simpson received Zangerl's manuscript, he had already advised against the publication of an English translation of Schindewolf's 1936 book *Paläontologie, Entwicklungslehre, und Genetik*.¹⁶ His reason was precisely that Schindewolf's book gave "a fundamentally false impression of the true status of evolutionary theory in 1936 and a still less correct impression of its status now."¹⁷ Around the same time Simpson voiced similar concerns in a letter to the comparative anatomist D. Dwight Davis (a colleague of Zangerl at the Chicago Natural History Museum), who had just submitted his contribution to a volume Simpson was co-editing (Jepsen, Mayr, & Simpson, 1949). The main message of Davis's paper was that the divide between the "neo-classical school of idealistic or 'pure' morphology" and the modern synthesis was much less deep than commonly thought. Davis mentioned in particular that the disagreement between Schindewolf and Simpson "can be attributed far more to a mutual failure to understand concepts and terms than to differences in views" (Davis, 1949, p. 76). In a friendly letter to Davis, Simpson made clear that he disagreed about there being much convergence between Schindewolf's views and his own.¹⁸

Shortly after reviewing Zangerl's paper, Simpson read a new publication by Schindewolf in which the theory of 'typostrophism' (Typostrophismus) was explicitly presented as the more plausible alternative for the Darwinism of the modern synthesis (Schindewolf, 1945). This was not an argument that Simpson could leave unchallenged. In an essay review he strongly criticized how "the idealistic school [of comparative anatomy] has strongly affected evolutionary theory, for instance overtly in the work of Schindewolf ... [whose] 'morphotypes' and the supposed 'typostrophism' are wholly unnatural concepts arising from mere chances, of discovery and the artifices of classification" (Simpson, 1949, p. 183). Over the next few years, Simpson would frequently highlight Schindewolf's typostrophism as a prime example of how a strict adherence to the characters-in-common approach could engender flawed ideas about the evolutionary process (Simpson, 1950a, b, 1951, 1952).

Around this time Simpson began to refer to the characters-in-common approach in classification as 'typological systematics.' He made it a prominent topic in his next big book, *The Major Features of*

¹⁰ On the foundations of Naef's and Kälin's systematic morphology, see Rieppel, Williams, & Ebach (2013) and Williams & Ebach (2008).

¹¹ Zangerl to Mayr, 8 May 1948, Society for the Study of Evolution Records at the American Philosophical Association [hereafter: 'SSE Papers'].

¹² Simpson to Zangerl, 17 May 1948; SSE Papers. Simpson addressed Zangerl directly, since Zangerl had independently sent him a copy of the manuscript with a request for feedback.

¹³ Simpson to Mayr, 17 May 1948, SSE Papers.

¹⁴ Mayr concurred. When Mayr first sent Simpson the manuscript, he already mentioned that in his view Zangerl's "concepts are strictly those of scholasticism." Mayr nevertheless thought that it might be a good idea to publish Zangerl's paper (Mayr to Simpson, 13 May 1948, SSE Papers). Cain (2000) has noted that right around this time, Mayr explicitly started soliciting manuscripts from non-geneticists, out of fear that his journal might become monopolized by geneticists (who already dominated its pages).

¹⁵ Schindewolf's typostrophism involved more than just saltationism; it was also a historicist thesis about cyclism and incorporated orthogenetic elements. For details, see Reif (1986, 1997).

¹⁶ The manuscript had been translated into English by Theodor Just (1904–1960) and was presented to Simpson by the University of Chicago Press (Hemens to Simpson, 13 August 1947, George Gaylord Simpson Papers at the American Philosophical Society [hereafter: 'Simpson Papers']).

¹⁷ Simpson to Hemens, 23 October 1947, Simpson Papers.

¹⁸ Simpson to Davis, 15 December 1947, Simpson Papers. Simpson nonetheless considered Davis' manuscript "excellent" and reported that he would be "strongly recommending its inclusion in the volume without revision or abridgement." Even when Davis offered to make amendments to his manuscript in the light of Simpson's critical notes, Simpson responded that "I would like to see it published as it stands" (Davis to Simpson, 6 February 1948; Simpson to Davis, 9 February 1948; Simpson Papers).

Evolution (1953).¹⁹ In a chapter on ‘Higher classification’ he argued at length against all “covert (or occasionally overt) idealists” to whom a taxon is “a pattern, a typological concept or morphotype, and [whose] activity consists in forming concepts of patterns, comparing individual specimens with the idealized pattern, and deciding whether agreement is sufficiently close to place the specimens in the corresponding taxonomic category” (Simpson, 1953, p. 340).

Like in earlier writings, Simpson emphasized that although typology was at heart a methodological issue in taxonomy, it often engendered concepts that unduly constrained proper evolutionary theorizing. “The characters-in-common may become a morphotype in the mind of the classifier,” and subsequently induce saltationist views about evolution. An extreme example of this could be found in a recent article by Richard Goldschmidt, who wrote:

A phylum consists of a number of classes all of which are basically recognizable as belonging to the phylum but, in addition, are different from each other. The same principle is repeated at each taxonomic level. All the genera of a family have in common the traits which characterize the family; e.g., all genera of penguins are penguins. But among themselves they differ from genus to genus. So it goes on down to the level of the species. Can this mean anything but that the type of the phylum was evolved first and later separated into the types of the classes, then into orders, and so on down the line? This natural, naive interpretation of the existing hierarchy of forms actually agrees with the historical facts furnished by paleontology ... Thus logic as well as historical fact tells us that the big categories existed first, and that in time they split in the form of the genealogical tree into lower and still lower categories.

Goldschmidt (1952, pp. 91–92)

To Simpson, arguments this like illustrated the extremes which a basic methodological error could lead to. Goldschmidt’s ‘logic’ was ultimately a consequence of the characters-in-common approach he had started out with.

2.5. Typological taxonomy

We have now seen in quite some detail how, starting in 1937, Simpson developed arguments against two methodological canons in taxonomy: the method of one-by-one comparison below the species level, and the characters-in-common approach above the species level.²⁰ We have also seen that these two lines of argument were really based on one fundamental point of criticism: taxonomists should be mindful not to reify a simple rule of thumb into a definite standard for classification. Type specimens and morphotypes could serve as makeshift diagnostic tools, but not as definite standards that govern the actual construction of classifications.

Sometimes Simpson explicitly highlighted this single overarching theme of his methodological critiques. In an address before the Paleontological Society of Washington in November 1940, he objected in one breath against the delimitation of taxa “by statement of a combination of fixed characters believed to be common

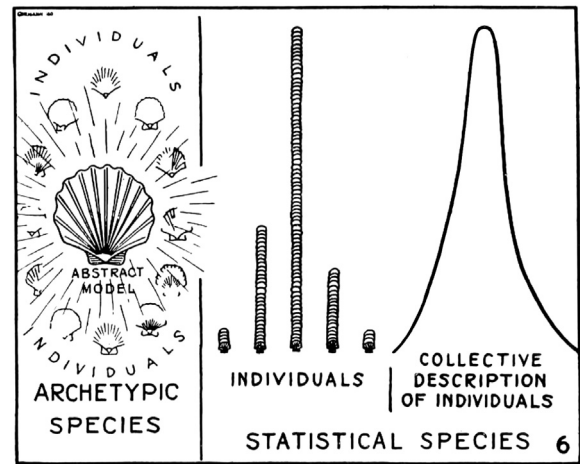


Fig. 5. The ‘archetypal’ versus the population-statistical approach to (species) taxonomy.

Source: Figure 6 from Simpson, 1941, p. 11]

to all members of the group,” or “on the basis of one or a few individuals.” In summing up his argument, Simpson advocated a shift from “the old, static, pseudo-archetypal taxonomy” towards “the new, dynamic, statistical taxonomy” (Simpson, 1941, p. 12). For the proceedings he drew Fig. 5 to illustrate his point.

In the 1950s he began to voice the same generic criticism under the new banner of “typological” versus “population systematics” (Simpson, 1951, 1952, 1959). In a revised edition of *Quantitative Zoology* (Simpson et al., 1960) the chapter on comparison of samples now included the remark that “In typological systematics, now becoming outmoded but still too commonly used, a specimen is compared with a type, and decision is made subjectively as to whether it belongs to the same species.” And a year later Simpson used his critique of typological systematics in the broad sense as the backbone for his textbook *Principles of Animal Taxonomy* (1961).

Simpson’s interpretation of the typology/population distinction as pertaining to the principles and methods of classification also helps to explain why it did not feature in what was without doubt his most important publication: the 1944 book *Tempo and Mode in Evolution*.²¹ This was the book that established Simpson as one of the ‘architects’ of the modern evolutionary synthesis together with Dobzhansky, Mayr, and a handful of others. *Tempo and Mode* certainly built on Simpson’s insights about the use of population-based, statistical methods in classification, but extended their use to the study of rates, trends and processes on a macroevolutionary scale. In the context of this project, Simpson’s critique of type-based systematics was the ladder that could be kicked away.²²

This is not to say that Simpson completely isolated his typology/population distinction from issues about evolutionary theorizing. On the contrary, we have seen that Simpson considered the rejection of typological taxonomy to be all-important for attuning biologists to the spectra of variation that underpinned the evolutionary process. More generally, Simpson’s writings on the principles and methods of classification paved the way for

¹⁹ This book was a significant revision and expansion of *Tempo and Mode* (1944), the book that established him as one of the architects of the modern evolutionary synthesis. *Tempo and Mode* counted 7 chapters and 217 pages of main text. *The Major Features* included 12 chapters and 393 pages of main text. The chapter in which Simpson discussed ‘typological systematics’ was entirely new.

²⁰ It is telling that in his autobiography Simpson recounted how his two papers from 1937 “marked the opening of two doors” towards many later writings on methods, principles and theory (Simpson, 1978, p. 81).

²¹ I thank David Sepkoski for urging me to consider the role of *Tempo and Mode* more explicitly.

²² We have seen, though, that when Simpson used *Tempo and Mode* as the basis for his *Major Features in Evolution* (1953)—a book he considered to be “more rounded and complete within its scope” (xi)—he did opt to include a long discussion of typological systematics (also see footnote 19).

taxonomists to begin “translating their data into terms that population biologists and geneticists could make use of” (Sepkoski, 2009).

At the time of writing *Tempo and Mode*, Simpson was already keenly aware of this interface with his (soon-to-be) co-architects of the modern evolutionary synthesis (Laporte, 1983). In the introduction of his book he indeed pointed out that “Like the geneticist, the paleontologist is learning to think in terms of populations rather than of individuals and is beginning to work on the meaning of changes in populations” (Simpson, 1944, xvi). We speaking of “the geneticist,” Simpson probably had Dobzhansky on his mind more than anyone else. In later writings, Simpson recounted how he had been “stimulated [by] and owed most to” Dobzhansky’s seminal 1937 book *Genetics and the Origin of Species* (Simpson, 1978, p. 155). Simpson reported that this book “profoundly changed my whole outlook” (quoted in Mayr, 1980a, p. 456). This raises the question how Simpson’s interpretation and use of typology/population distinction relates that of Dobzhansky. Did the latter understand and utilize it in a similar way? Or was the point of contact with Simpson more cosmetic than substantial?

3. Dobzhansky on heredity and population dynamics

3.1. Racial prototypes

On first inspection, it looks like Dobzhansky was making essentially the same point as Simpson when he first criticized a position that he would later label ‘typological’. The criticism can be found in *Genetics and the Origin of Species* (1937), in a brief section on ‘The genetic conception of a race.’²³ Dobzhansky took issue with the study of race “in classical morphology and anthropology, [where] races are described usually in terms of the statistical averages for characters in which they differ from each other. Once such a system of averages is arrived at, it begins to serve as a racial standard with which individuals and groups of individuals can be compared” (Dobzhansky, 1937, p. 77). This sounds a lot like Simpson’s argument against the use of rules of thumb as definite standards for classification. When we further learn that Dobzhansky started equating these ‘systems of averages’ with ‘racial types’ in the 1940s, this suggests that he was making the same point as Simpson in a different context.

But first impressions can be misleading. On a closer look it becomes clear that Dobzhansky’s issue with types and typology was importantly different from that of Simpson. For a start, Dobzhansky was not promoting the use of inferential statistics and sample-based methods in the continued handling of *morphological* material, as Simpson advocated. Instead, Dobzhansky argued that biologists had to change their very conception of races (Gannett, 2013). Races were conspecific populations that varied in their relative frequencies of certain genes (Dobzhansky, 1941). Secondly, and more importantly, Dobzhansky was not drawing a type/population contrast in a methodological context. He instead objected to certain theoretical views about *population dynamics* that were hung up on the postulation of types. In the 1940s, Dobzhansky tirelessly rehearsed that the notion of a ‘racial type’ rested on a refuted pre-Mendelian view about population dynamics: the ‘blood’ theory of heredity. He explained that

²³ In a detailed study of Dobzhansky’s ideas about race, Gannett (2013) has argued that Dobzhansky relied on a ‘taxonomic race concept’ (races as arrays or clusters of form) in his 1937 book, and only adopted the ‘genetic race concept’ around 1940. The fact that Dobzhansky entitled a section of his 1937 book ‘The genetic conception of race’ suggests that taxonomic–genetic transition was at least underway by then.

a race defined as a system of averages or modal points is a concept that belongs to the pre-Mendelian era, when the hereditary materials were pictured as a continuum subject to a diffuse and gradual modification. If germ-plasms could blend with each other as a water-soluble dye commingles with water, every interbreeding population would soon reach a reasonable uniformity, and every individual would in a very real sense be a child not only of its parents but of its race as well. A ‘pure race’ would be formed in each locality occupied by the species.

(Dobzhansky, 1941, p. 161)

Before the advent of modern genetics, this picture of a race as a community of blood had supported the view that “the racial ‘ideal’ obtained by averaging the characteristics of a group ... would approximately correspond to the type which would eventually be reached if this group were to continue intermarrying without any immigration from the outside” (Dunn & Dobzhansky, 1946, p. 100). The ‘type’ of a race was thus defined as “a kind of morphological center of gravity towards which the population ... gravitates” (Dobzhansky, 1950a pp. 112–113; also see Dobzhansky, 1942, p. 118). Dobzhansky often warned that this type-based conception of a race was not just wrong, but also dangerous: “[A] type once created ... has an insidious way of dominating its maker. It becomes ‘the race,’ a sort of noumenon of which the existing individuals are only imperfect representatives.” In an evolutionary context, this resulted in claims to the effect “that there existed at some obscure time in the past so-called primary races, which were supposedly ‘pure’ and conformed to their ideal types” (Dobzhansky, 1951c, p. 264).²⁴

Twentieth century scientists had to know better. Mendelism had thoroughly refuted the idea that heredity is diluted by crossing and that individual variation is funneled towards some racial basin of attraction. Every modern biologist knew that because of the particulate nature and structure of the germ-plasm, hereditary material is sustained intact across generations. Modern biological theory also resisted the notion of a ‘pure race.’ Races were by definition open systems that are connected by gene flow to other conspecific populations. Races *had* to be able to mix, or otherwise they would have reached the status of species. Hence, the notion of a ‘pure race’ could not even be admitted as “a legitimate abstraction: it is a subterfuge used to cloak one’s ignorance of the nature of the phenomenon of racial variation” (Dobzhansky, 1941, p. 146).

Arguing that only ‘mixed’ races exist wouldn’t help either, because it retained a commitment to a notion of pure ancestral racial types. The notion of mixed races had been made popular by the writings of late-nineteenth century physical anthropologists, who spoke of the “acquired deviations from the original types” (Virchow, 1896) and held that “nowhere in the world do we find a population completely untouched by intermixture and manifesting a single type” (Topinard, 1892).²⁵ Mid-twentieth century physical anthropologists continued to be influenced by such views. The most prominent physical anthropologist alive, Ernest Hooton (1887–1954), still aimed to “isolate pure racial types” from

²⁴ Dobzhansky argued that biologists in particular had a duty to correct the pre-Mendelian picture that lingered in the writings of several morphologists and anthropologists, whose outdated hereditarian views could be abused to support the anti-miscegenation sentiments that were on the rise the American South (Dobzhansky, 1941, p. 161). Also see Section 2 in Part 2 of this essay.

²⁵ Dobzhansky had encountered the writings of Virchow and Topinard in an anthology on the concept of race by the anthropologist Earl W. Count (1950). In later writings, Dobzhansky frequently picked quotes on racial types from this book.

contemporary mixed races (Hooton, 1926, p. 76).²⁶ To Dobzhansky this all sounded very confused. He reportedly couldn't make biological sense of "[Hooton's] method of finding several racial types in one population" (quoted in Washburn, 1983, p. 2).

By the early 1950s, Dobzhansky made frequent use of the type/population distinction in his discussions of the genetics of race. At a prominent Cold Spring Harbor Symposium on 'Origin and Evolution of Man,' Dobzhansky's theme for his concluding presentation was 'Race as a Type and as a Population' (Dobzhansky, 1950b, p. 348).²⁷ In a flurry of writings from the same year, he repeated a message that was familiar by now: Intra-racial variation needed to be understood as variation *per se*, and not as deviation from some fixed, underlying attractive state (Dobzhansky, 1950c, d, 1951a, b, c).

3.2. Typology run wild?

Although Dobzhansky first formulated his type/population contrast in discussions of race, he did not limit its application to that context. He soon started using the type/population distinction to address a concern with the idea of a 'wild type'—a notion that was at the heart of a dispute between him and the geneticist Hermann Muller (1890–1967). To understand why Dobzhansky took issue with this notion, it will help to briefly review the larger debate it was central to: the so-called 'classical/balance controversy'.²⁸

The controversy between Dobzhansky and Muller had its roots in two contrasting views about the nature of natural selection. Muller conceived of natural selection as a kind of purifying agent: a process that tends to lead a population towards a state of homozygosity for optimal alleles at all loci, counteracted only by accidental mutations and migration. The resultant optimal genotypes, fitter than all others, were what Muller called 'wild type' genotypes.²⁹ Muller argued that new species typically approximated this optimal state rather rapidly, in intense selective regimes that followed speciation events. Most extant species were therefore extremely well adapted to their environments. A typical species could thus be compared to a well-designed watch: if you prod its innards randomly you are unlikely to turn it into something that runs better, but will most likely cause considerable damage (Muller, 1929).

This picture of natural selection seemed to be confirmed by experiments with *Drosophila* in the lab of his mentor, T. H. Morgan (1866–1945). Radiation and crossing experiments sometimes resulted in the birth of mutant individuals with severe defects. Interestingly, such severely deleterious mutants were rarely encountered in natural populations. A plausible explanation was that the artificial lab conditions had mutated healthy, naturally occurring homozygotes into inferior heterozygotes for some loci (Muller, 1930).

The view of selection as a purifying agent was the reigning orthodoxy in genetics when Dobzhansky arrived from Russia in 1927 to study with T. H. Morgan. However, soon enough Dobzhansky began to consider a different hypothesis for why deleterious

mutants only showed up in the lab. He inverted the received view by suggesting that natural populations consisted almost entirely of phenotypically similar heterozygotes and argued that deleterious mutants were in fact homozygotes for recessive alleles. The reason mutants only showed up in the lab was due to the comparatively small size of laboratory populations, which increased the probability that two recessive alleles would be paired through inbreeding. As Dobzhansky put it, free-living populations consist predominantly of heterozygous "concealed mutants," whose recessive alleles are propagated "without manifesting themselves except on rare occasions" (Dobzhansky, 1939, p. 366). The mutant individuals that were bred in the lab offered glimpses at this hidden abundance of naturally occurring genetic variation.

These were not just Dobzhansky's musings, but ideas that had originated with his Russian mentor Sergei Chetverikov (1880–1959). When Dobzhansky went to the U.S., Chetverikov had just published a paper in which he argued that "mutations, originating within a 'normal' species, pass, as a result of crossing, into the heterozygous state, and are thus swallowed up, absorbed by the species, remaining in it in the form of isolated individuals. As a result, we arrive at the conclusion that a species, like a sponge, soaks up heterozygous mutations, while remaining from first to last externally (phenotypically) homogeneous" (Chetverikov, 1926 [1961], p. 178; cited in Beatty, 1987a, p. 279).³⁰

Chetverikov's sponge metaphor nicely illustrates how the Russian perspective put pressure on the received view of natural selection as a process that removes all but the most optimal homozygotes. If natural populations indeed 'soaked up' genetic variation in the form of heterozygotes that are phenotypically indistinguishable from homozygotes for wild-type alleles, then natural selection would not be able to winnow these heterozygotes from those populations. Instead, natural selection would maintain an equilibrium between homozygotes for wild-type alleles and heterozygotes containing a wild-type and a recessive allele. This outlook on population dynamics qualified Muller's picture of natural selection as being *only* driven towards the preservation of wild-type genotypes, but it was not yet a reason for Dobzhansky to take issue with the very notion of a wild type.

That changed when in the late 1940s new experimental findings led Dobzhansky to believe that heterozygotes were not just retained in population due to genetic drift—i.e., by being as fit as wild-type homozygotes—but because of their adaptive superiority relative to homozygotes.³¹ This hypothesis of heterozygote superiority posed a more direct challenge to the conception of selection as a purifying process, aimed at the preservation of wild-types. It instead called to mind a picture of selection as an active 'balancer' of variation—as a process that prevents any single type of allele from reaching fixation. To bring out the novelty of this view, Dobzhansky would later start calling it the 'balance hypothesis,' to be contrasted with Muller's 'classical hypothesis' (Dobzhansky, 1955a).

If Dobzhansky's balance hypothesis could be vindicated and natural selection indeed maintained a balance between a variety of

²⁶ Hooton was a Harvard-based physical anthropologist who "had practically created American biological anthropology single-handedly" (Brace, 2010, p. 28). He believed that isolated 'pure' races might still be intact among "savage groups in isolated wildernesses" (Hooton, 1936, p. 512).

²⁷ For background on this symposium, see Smocovitis (2012).

²⁸ For more in-depth discussions of the scientific, philosophical, and political aspects of classical/balance controversy, see Beatty (1987a, b, 1994), Lewontin (1981, 1987), and Lamm (in press).

²⁹ The term 'wild type' itself was not new with Muller, but the meaning he gave it was. The received understanding was that of his Ph.D. supervisor T. H. Morgan, who spoke of wild types as organisms or strains that were phenomenally similar to organisms in natural populations (Morgan, Sturtevant, Muller, & Bridges, 1915). Muller was responsible for giving the term a reductionist-realist interpretation at the genetic level (see Holmes, 2011; Roll-Hansen, 1978).

³⁰ Dobzhansky did not just have the advantage of knowing Chetverikov, but also of being able to read his paper. It would take until 1961 before it was translated into English. For most of the 1930s and 1940s Dobzhansky was among the very few who could keep track of developments in American and Russian population genetics research (Adams, 1980).

³¹ On the question why heterozygotes would be fitter than homozygotes Dobzhansky changed his mind at least twice. At first, he explained it as a side-effect of selection for linked genes. Later he proposed that the presence of certain adaptively superior heterozygotes was "an outcome of a historic process of adaptation to the environment" (Dobzhansky, 1951a, p. 117). Finally, he became convinced that heterozygotes as such were fitter than homozygotes. See Beatty (1987a) and Lewontin (1981) for details.

equally fit heterozygotes, this would put further pressure on the notion of a wild type. It would mean that, as a matter of fact, no wild type allele or genotype existed. In the third edition of *Genetics and the Origin of Species* Dobzhansky drew his conclusion: “The wild-type is a fiction. ‘Normal’ individuals are actually a heterogeneous collection of genotypes” (Dobzhansky, 1951a, p. 108).

The context in which Dobzhansky drew this conclusion is striking. The two sentences I just quoted were preceded by a half-page rejection of the notion of racial types, centered on Virchow’s definition of races as “acquired deviations from the original type.” Dobzhansky’s intent was unmistakable: the notions of ‘wild type’ and ‘racial type’ rested on a similar kind of mistake (also see Dobzhansky, 1955b, p. 134ff). Muller was in the grip of “a typological mode of thought” which presented natural selection as a process that would “remove, eliminate, purge from the population all the mutant genes” (Dobzhansky, 1961, p. 290; also see Dobzhansky, 1961; 1962a; 1962b; 1963; 1967). In a paper on “The invalidation of the ‘wild type’ concept,” Dobzhansky argued that this concept was a product “typological thinking, the roots of which go down to the Platonic philosophy” (Cordeiro & Dobzhansky, 1954, pp. 83–84).

3.3. Typological population dynamics

In summarizing Simpson’s views, I argued that there was something to say for how he consolidated his two critiques of types into a single argument against ‘typology.’ After all, both of Simpson’s arguments targeted a shared methodological error: that of using unwarranted standards in the practice of classification. In the case of Dobzhansky, it is not immediately clear that there is a similar overarching theme to his arguments against racial types and wild types.

One could argue that Dobzhansky’s ‘synthesis’ of his critique of racial types and wild type genotypes under the single banner of ‘typological thinking’ was a grossly unwarranted move. For, unlike the racial type concept, the wild type concept had been far from theoretically invalidated when Dobzhansky started making claims to that effect. Dobzhansky knew this. He openly admitted that “there is every reason to think that the classical hypothesis is valid to some extent” (Dobzhansky, 1957, p. 192), that the classical and balance hypotheses were “not mutually incompatible or exclusive” (Dobzhansky, 1959, p. 257), and that it would be “most probable that a whole spectrum of conditions ranging all the way from the ‘classical’ to the ‘balance’ model will be discovered when the genetic structure of different forms of life is understood better than it is at present” (Dobzhansky, 1955a, p. 4).³² Hence, it appears that Dobzhansky was dishonest when he presented his critique of wild-types under the same banner as his critique of racial types. It seems that he used the notion of ‘typological thinking’ as a mere strategic device, to insinuate that the classical hypothesis was on a par with late-nineteenth century theories about race.

However, I want to suggest that there is another, more nuanced way of looking at Dobzhansky’s deployment of the typology/population distinction. Even though his rhetoric about the ‘invalidation’ of the wild type concept was overstated, we should resist the conclusion that Dobzhansky was simply devious when he deployed the typology/population dichotomy the way he did. There was a substantive message to Dobzhansky’s use of the term ‘typological

thinking’ for both of his arguments against types. In Dobzhansky’s use of the term, typological thinking amounted to a distinctive pattern of reasoning about the dynamics of heredity and variation in biological populations. Type-based race theorists and ‘classical’ geneticists both pictured population dynamics as tending to drive extant variation towards a center of gravity. The typological thinker of this sort does not necessarily believe that the center of gravity exists (or existed) in an embodied form, but he does think that populations approach this state when unimpeded by ‘disturbing’ factors: race blending in the case of race theorist, mutation in the case of the classical geneticist. The population thinker, Dobzhansky argued, is someone who has curbed the default psychological pull of this approach to the dynamics of heredity. On a populational outlook variation is viewed as an autonomous phenomenon; it is not governed by some underlying, fixed, attractive state.

This interpretation of Dobzhansky’s use of the typology/population dichotomy—as a meaningful distinction between (views about) population dynamics—is also compatible with Dobzhansky’s moral and political objections to typology. Dobzhansky often stood up against typological thinking about race as well as about natural selection because of the support these views could lend to anti-egalitarian policies. Muller, for example, often warned against the risks of the rapid accumulation of induced mutations in humans on the basis of his views about natural selection as a purifying agent (Muller, 1950a, b). In his influent essay ‘Our load of mutations,’ Muller painted a disturbing picture of modern medicine and technology as ‘shielding’ deleterious mutations from being eliminated by natural selection. He argued that humanity was rapidly accumulating a ‘mutational load’ that would reach dangerously high levels in future generations. In the absence of an adequate form of artificial selection, humans would soon have to devote much of their time and energy “to the effort to live carefully, to spare and to prop up their own feeblenesses, to soothe their inner disharmonies and, in general, to doctor themselves as effectively as possible. For everyone would be an invalid, with his own special familial twists” (Muller, 1950b, p. 146).

Dobzhansky of course objected to this picture of genetic uniformity being optimal and genetic heterogeneity being inimical to the fitness of a human populations. He despised the kind of “typological thinking [that] makes a kind of Platonic archetype of Man the eugenic ideal ... endowed with the Optimal Genotype” (Dobzhansky, 1963, p. 1133). On Dobzhansky’s own ‘populationist’ view of genetic diversity as an adaptive device, the idea of (a small range of) optimal genotype(s) was not only scientifically unsound, but also undesirable from a moral and political point of view. The diverse ecological landscape of human societies called for people with different physical, mental, and genetic constitutions. A population of supposedly ‘optimal’ genetic clones would be hard-pressed to excel in all positions and offices of society.³³ In addition, Dobzhansky argued that the extant genetic diversity in human population could serve as a rationale for an egalitarian, democratic political system. As he wrote in his popular book *Mankind Evolving*: “Equality of opportunity tends to make the occupational differentiation comport with the genetic polymorphism of the population, and would be meaningless if all people were genetically identical”

³² Muller agreed with Dobzhansky on this point (Muller, 1956, p. 284). It must also be pointed out that Muller easily matched Dobzhansky in rhetoric by calling the ‘balance’ hypothesis “an essentially mystical doctrine, representing a revival from pre-Mendelian times” (Muller, 1958, p. 157). Beatty (1987a) provides an excellent overview of the long and sometimes acrimonious debate between Dobzhansky and Muller about the relative significance of the classical and balance positions.

³³ Dobzhansky noted that although a typologist could obviously argue that optimal homozygotes would also tend to have optimally plastic phenotypes, recent empirical evidence spoke against this. The reason heterozygotes were superior in fitness was exactly that they were thought to be more developmentally more plastic than homozygotes (Dobzhansky & Levene, 1955). Dobzhansky used the findings to bolster his argument that heterozygotes have an equal potential for ‘educability’ (Dobzhansky & Montagu, 1947).

(Dobzhansky, 1962b, p. 244). Hence, on Dobzhansky's conception of population thinking it supported liberal democratic ideals.³⁴

It may have been the case that moral and political motives were in fact the prime mover of Dobzhansky's decision to deploy the typological/population contrast the way he did. Dobzhansky was obviously worried about the societal import of Muller's views and saw a parallel with the danger that specious conceptions of race dynamics had done to society. But since this parallel had its roots in a shared gloss on the dynamics of variation in populations, the typological/population contrast could nevertheless have its home in biology. As John Beatty put it: “[Dobzhansky's] egalitarian agenda promoted his science, but that was perfectly compatible with his sincere attempt to use science to promote democracy” (Beatty, 1994, p. 216).

4. Interim conclusion

This essay started out by reappraising the widely held view that the typology/population dichotomy was first formulated by Ernst Mayr in the 1940s. We have seen that, in fact, that *annus mirabilis* for this dichotomy was 1937 and the people associated with it were Simpson and Dobzhansky instead of Mayr. Furthermore, we have seen that Simpson and Dobzhansky each developed different *kinds* of critiques of typology. They targeted different notions of ‘types’ and operated on (subtly but significantly) different understandings of ‘population thinking.’ Finally, there is no indication that Simpson and/or Dobzhansky were building on the work of Mayr in presenting their own type/population contrasts.

And yet, Mayr did play a very influential role in shaping of what we now know as the typology/population dichotomy. Not just because he popularized distinctions that Simpson and Dobzhansky had already articulated, but because he attempted to synthesize and expand them into something grander. The second installment of this essay provides a detailed exposition of how Mayr went about. It reveals how Mayr's striving for synthesis resulted in a conflation and misrepresentation of individually meaningful distinctions.

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References

- Adams, M. B. (1980). Sergei Chetverikov, the Kol'tsov Institute, and the evolutionary synthesis. In E. Mayr, & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 242–278). Cambridge, MA: Harvard University Press.
- Amundson, R. (2005). *The changing role of the Embryo in evolutionary thought: Roots of Evo-Devo*. Cambridge: Cambridge University Press.
- Bancroft, J. (2007). Kinsey, Alfred Charles. In *Complete dictionary of scientific biography* (pp. 123–130). Detroit: Charles Scribner's Sons. doi:Biography.

- Beatty, J. (1987a). Dobzhansky and drift: Facts, values, and chance in evolutionary biology. In L. Krüger, G. Gigerenzer, & M. S. Morgan (Eds.), *The Probabilistic Revolution. Volume 2: Ideas in the sciences* (pp. 271–311). The MIT Press.
- Beatty, J. (1987b). Weighing the risks: Stalemate in the classical/balance controversy. *Journal of the History of Biology*, 20, 289–319.
- Beatty, J. (1994). Dobzhansky and the biology of democracy: The moral and political significance of genetic variation. In M. B. Adams (Ed.), *The Evolution of Theodosius Dobzhansky: Essays on his life and thought in Russia and America*. Princeton, NJ: Princeton University Press.
- Brace, C. L. (2010). “Physical” anthropology at the turn of the last century. In M. A. Little, & K. A. R. Kennedy (Eds.), *Histories of American physical anthropology in the twentieth century* (pp. 25–54). Lexington Books.
- Cain, J. (2000). For the ‘promotion’ and ‘integration’ of various fields: First years of *Evolution*, 1947–1949. *Archives of Natural History*, 27, 231–259.
- Chetverikov, S. (1926 [1961]). On certain aspects of the evolutionary process from the standpoint of modern genetics (Malina Baker, Trans.) *Proceedings of the American Philosophical Society*, 105, 167–195.
- Chung, C. (2000). *Essence, variation, and evolution: An analysis of Ernst Mayr's distinction between ‘Typological’ and ‘Population’ thinking* (Ph.D. thesis). University of Minnesota.
- Chung, C. (2003). On the origin of the typological/population distinction in Ernst Mayr's changing views of species, 1942–1959. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 34, 277–296.
- Cordeiro, A. R., & Dobzhansky, T. (1954). Combining ability of certain chromosomes in *Drosophila Willistonii* and inactivation of the wild-type concept. *American Naturalist*, 88, 75–86.
- Count, E. W. (Ed.). (1950). *This is Race: An anthology selected from the International Literature on the Races of Man*. New York: Shuman.
- Davis, D. D. (1949). Comparative anatomy and the evolution of vertebrates. In G. L. Jepsen, E. Mayr, & G. G. Simpson (Eds.), *Genetics, paleontology and evolution* (pp. 64–89). Princeton, NJ: Princeton University Press.
- Dobzhansky, T. (1937). *Genetics and the origin of species* (1st ed.). New York: Columbia University Press.
- Dobzhansky, T. (1939). Experimental studies on genetics of free-living populations of *Drosophila*. *Biological Reviews*, 14, 339–368.
- Dobzhansky, T. (1941). The race concept in biology. *The Scientific Monthly*, 52, 161–165.
- Dobzhansky, T. (1942). Races and methods of their study. *Transactions of the New York Academy of Sciences*, 4, 115–123.
- Dobzhansky, T. (1950a). The genetic nature of differences among men. In S. Persons (Ed.), *Evolutionary thought in America* (pp. 86–155). New Haven, CT: Yale University Press.
- Dobzhansky, T. (1950b). Human diversity and adaptation. *Cold Spring Harbor Symposia on Quantitative Biology*, 15, 385–400.
- Dobzhansky, T. (1950c). Mendelian populations and their evolution. *The American Naturalist*, 84, 401–418.
- Dobzhansky, T. (1950d). Nature and origin of races. In *Encyclopedia Americana* (pp. 107–111). New York: Americana Corp.
- Dobzhansky, T. (1951a). *Genetics and the origin of species* (3rd ed.). New York: Columbia University Press.
- Dobzhansky, T. (1951b). Human races in the light of genetics. *International Social Sciences Bulletin*, 3, 660–663.
- Dobzhansky, T. (1951c). Race and humanity. *Science*, 113, 264–266.
- Dobzhansky, T. (1955a). A review of some fundamental concepts and problems of population genetics. *Cold Spring Harbor Symposia on Quantitative Biology*, 20, 1–15.
- Dobzhansky, T. (1955b). *Evolution, genetics, and man*. New York: John Wiley & Sons, Inc.
- Dobzhansky, T. (1957). Genetic loads in natural populations. *Science*, 126, 191–194.
- Dobzhansky, T. (1959). Variation and evolution. *Proceedings of the American Philosophical Society*, 103, 252–263.
- Dobzhansky, T. (1961). Man and natural selection. *American Scientist*, 49, 285–299.
- Dobzhansky, T. (1962a). Genetics and equality. *Science*, 137, 112–115.
- Dobzhansky, T. (1962b). *Mankind evolving: the evolution of the human species*. New Haven, CT: Yale University Press.
- Dobzhansky, T. (1963). Evolutionary and population genetics. *Science*, 142, 1131–1135.
- Dobzhansky, T. (1967). On types, genotypes, and the genetic diversity in populations. In J. N. Spuhler (Ed.), *Genetic diversity and human behavior* (pp. 1–18). Chicago, IL: Aldine Publishing Company.
- Dobzhansky, T., & Levene, H. (1955). Genetics of natural populations. XXIV. Developmental homeostasis in natural populations of *Drosophila Pseudoobscura*. *Genetics*, 40, 797–808.
- Dobzhansky, T., & Montagu, M. F. A. (1947). Natural selection and the mental capacities of mankind. *Science*, 105, 587–590.
- Dunn, L. C., & Dobzhansky, T. (1946). *Heredity, race, and society*. New York: Penguin Books.
- Farber, P. L. (1978). A historical perspective on the impact of the type concept on insect systematics. *Annual Review of Entomology*, 23, 91–99.
- Gannett, L. (2001). Racism and human genome diversity research: The ethical limits of “population thinking”. *Philosophy of Science*, 63, 479–492.
- Gannett, L. (2003). The normal genome in twentieth-century evolutionary thought. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 34, 143–185.

³⁴ See Beatty (1994) and Paul (1987) for more on the relation between science and world views in the classical/balance controversy.

- Gannett, L. (2013). Theodosius Dobzhansky and the genetic race concept. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 44, 250–261.
- Gerard, R. W. (Ed.). (1958). *Concepts of biology*. Washington, D. C.: National Academy of Sciences.
- Goldschmidt, R. (1940). *The material basis of evolution*. New Haven, CT: Yale University Press.
- Goldschmidt, R. (1952). Evolution, as viewed by one geneticist. *American Scientist*, 40, 84–135.
- Gould, S. J. (1982). Of wasps and WASPs. *Natural History Magazine*, 91, 8–15.
- Holmes, T. (2011). *The concept of wild-type in transmission genetics: Ideas of species, variation and environment amongst the Early Mendelians* (Master's thesis). University of Exeter.
- Hooton, E. A. (1926). Methods of racial analysis. *Science*, 63, 75–81.
- Hooton, E. A. (1936). Plain statements about race. *Science*, 83, 511–513.
- Hull, D. L. (1988). *Science as a process: An evolutionary account of the social and conceptual development of science*. Chicago, IL: University of Chicago Press.
- Jepsen, G., Mayr, E., & Simpson, G. G. (1949). *Genetics, paleontology and evolution*. Princeton, NJ: Princeton University Press.
- Kinsey, A. C. (1930). *The gall wasp genus Cynips: A study in the origin of species*. Bloomington, ID: Indiana University Publications.
- Kinsey, A. C. (1936). *The origin of higher categories in Cynips*. Bloomington, ID: Indiana University Publications.
- Lamm, E. (2015). Systems thinking versus population thinking: Genotype integration and chromosomal organization 1930s–1950s. *Journal of the History of Biology*. advance online publication (in press).
- Laporte, L. F. (1983). Simpson's "tempo and mode in evolution" revisited. *Proceedings of the American Philosophical Society*, 127, 365.
- Laporte, L. F. (1994). Simpson on species. *Journal of the History of Biology*, 27, 141–159.
- Lewontin, R. C. (1981). Introduction: The scientific work of Theodosius Dobzhansky. In R. C. Lewontin, J. A. Moore, & W. B. Provine (Eds.), *Dobzhansky's genetics of natural populations, Series I–LXIII* (pp. 93–115). Columbia University Press.
- Lewontin, R. C. (1987). Polymorphism and heterosis: Old wine in new bottles and vice versa. *Journal of the History of Biology*, 20, 337–349.
- Mayr, E. (1959a). Concerning a new biography of Charles Darwin, and its scientific shortcomings. *Scientific American*, 201, 209–216.
- Mayr, E. (1959b). Darwin and the evolutionary theory in biology. In *Evolution and anthropology: A centennial appraisal* (pp. 1–8). Washington, D.C.: Theo Gaus' Sons, Inc.
- Mayr, E. (1963). *Animal species and evolution*. Cambridge, MA: Harvard University Press.
- Mayr, E. (1968a). Illiger and the biological species concept. *Journal of the History of Biology*, 1, 163–178.
- Mayr, E. (1968b). The role of systematics in biology. *Science*, 159, 595–599.
- Mayr, E. (1968c). Theory of biological classification. *Nature*, 220, 545–548.
- Mayr, E. (1972). The nature of the Darwinian Revolution. *Science*, 176, 981–989.
- Mayr, E. (1976a). *Evolution and the diversity of life*. Cambridge, MA: Harvard University Press.
- Mayr, E. (1976b). Typological versus population thinking. In *Evolution and the diversity of life: Selected essays* (pp. 26–29). Cambridge, MA: Harvard University Press.
- Mayr, E. (1980a). G. G. Simpson. In E. Mayr, & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 452–463). Cambridge, MA: Harvard University Press.
- Mayr, E. (1980b). Some thoughts on the history of the evolutionary synthesis. In E. Mayr, & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 1–48). Cambridge, MA: Harvard University Press.
- Mayr, E. (1982). *The growth of biological thought: Diversity, evolution, and inheritance*. Cambridge, MA: Harvard University Press.
- Morgan, T., Sturtevant, A., Muller, H. J., & Bridges, C. (1915). *The mechanism of Mendelian heredity*. New York: Holt.
- Muller, H. J. (1929). The method of evolution. *The Scientific Monthly*, 29, 481–505.
- Muller, H. J. (1930). Radiation and genetics. *American Naturalist*, 64, 220–251.
- Muller, H. J. (1950a). Evidence of the precision of genetic adaptation. In *The Harvey Lectures, Series XLIII, 1947–1948* (Vol. 43, pp. 165–229). Springfield, IL: Chas. C. Thomas.
- Muller, H. J. (1950b). Our load of mutations. *American Journal of Human Genetics*, 2, 111–176.
- Muller, H. J. (1956). Genetic principles in human populations. *The Scientific Monthly*, 83, 277–286.
- Muller, H. J. (1958). Evolution by mutation. *Bulletin of the American Mathematical Society*, 64, 137–160.
- Müller-Wille, S. (2011). Making sense of essentialism. *Critical Quarterly*, 53, 61–67.
- Osborn, H. F. (1936). *Proboscidea: A monograph on the discovery, evolution, migration and extinction of the mastodonts and elephants of the world* (Vol. 1) New York: The American Museum Press.
- Paul, D. B. (1987). "Our load of mutations" revisited. *Journal of the History of Biology*, 20, 321–335.
- Reif, W.-E. (1986). The search for a macroevolutionary theory in German paleontology. *Journal of the History of Biology*, 19, 79–130.
- Reif, W.-E. (1997). Typology and the primacy of morphology: The concepts of O. H. Schindewolf. *Neues Jahrbuch der Geologie und Paläontologie: Abhandlungen*, 205, 355–371.
- Rieppel, O., Williams, D. M., & Ebach, M. C. (2013). Adolf Naef (1883–1949): On foundational concepts and principles of systematic morphology. *Journal of the History of Biology*, 46, 445–510.
- Roe, A. (1985). 1984 Leona Tyler Award address: Career and life. *The Counseling Psychologist*, 13, 311–326.
- Roll-Hansen, N. (1978). Drosophila genetics: A reductionist research program. *Journal of the History of Biology*, 11, 159–210.
- Schindewolf, O. H. (1936). *Paläontologie, Entwicklungslehre und Genetik: Kritik und Synthese*. Berlin: Bornträger.
- Schindewolf, O. H. (1945). Darwinismus oder typrostrophismus. *Arbeiten des ungarischen biologischen Forschungsinstituts*, 16, 104–177.
- Sepkoski, D. (2009). The emergence of paleobiology. In D. Sepkoski, & M. Ruse (Eds.), *The Paleobiological Revolution: Essays on the growth of modern paleontology* (pp. 15–42). University of Chicago Press.
- Simpson, G. G. (1928). *A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. London: British Museum (Natural History).
- Simpson, G. G. (1937a). *Notes on the Clark Fork, Upper Paleocene, fauna. Number 954 in American Museum Novitates*. New York: The American Museum of Natural History.
- Simpson, G. G. (1937b). Patterns of phyletic evolution. *Bulletin of the Geological Society of America*, 48, 303–314.
- Simpson, G. G. (1937c). Supra-specific variation in nature and in classification from the viewpoint of paleontology. *The American Naturalist*, 71, 236–267.
- Simpson, G. G. (1937d). *The Fort Union of the Crazy Mountain Field, Montana, and its Mammalian Faunas*. Washington, D. C.: United States Printing Office.
- Simpson, G. G. (1940). Types in modern taxonomy. *American Journal of Science*, 238, 413–431.
- Simpson, G. G. (1941). The role of the individual in evolution. *Journal of the Washington Academy of Sciences*, 31, 1–20.
- Simpson, G. G. (1943). Criteria for genera, species and subspecies in Zoology and Paleozoology. *Annals of the New York Academy of Sciences*, 44, 145–178.
- Simpson, G. G. (1944). *Tempo and mode in evolution*. New York: Columbia University Press.
- Simpson, G. G. (1945). *The principles of classification and a classification of mammals*. New York: American Museum of Natural History.
- Simpson, G. G. (1949). Essay-review of recent works on evolutionary theory by Rensch, Zimmermann, and Schindewolf. *Evolution*, 3, 178–184.
- Simpson, G. G. (1950a). Evolutionary determinism and the fossil record. *The Scientific Monthly*, 71, 262–267.
- Simpson, G. G. (1950b). Some principles of historical biology bearing on human origins. *Cold Spring Harbor Symposia on Quantitative Biology*, 55–66.
- Simpson, G. G. (1951). The species concept. *Evolution*, 5, 285–298.
- Simpson, G. G. (1952). Book review of *Grundfragen der Paläontologie and Der Zeitfaktor in Geologie und Paläontologie*. *Quarterly Review of Biology*, 27, 388–389.
- Simpson, G. G. (1953). *The major features of evolution*. New York: Columbia University Press.
- Simpson, G. G. (1959). Anatomy and morphology: Classification and evolution: 1859 and 1959. *Proceedings of the American Philosophical Society*, 103, 286–306.
- Simpson, G. G. (1960). Types and name-bearers. *Science*, 131, 1684.
- Simpson, G. G. (1961). *Principles of animal taxonomy*. New York: Columbia University Press.
- Simpson, G. G. (1978). *Concession to the improbable: An unconventional autobiography*. New Haven: Yale University Press.
- Simpson, G. G. (1981). *Why and how: Some problems and methods in historical biology*. Oxford: Pergamon Press.
- Simpson, G. G., & Roe, A. (1939). *Quantitative Zoology: Numerical concepts and methods in the study of recent and fossil animals*. New York: McGraw-Hill.
- Simpson, G. G., Roe, A., & Lewontin, R. C. (1960). *Quantitative Zoology*. Revised Edition. New York: Harcourt, Brace and Company, Inc.
- Smocovitis, V. B. (2012). Humanizing evolution. *Current Anthropology*, 53, S108–S125.
- Topinard, P. (1892). De la race en anthropologie. In *Congrès International d'Archéologie préhistorique et d'Anthropologie, 11e session, Moscou* (pp. 161–170). (Reprinted in Count (1950))
- Virchow, R. (1896). Rassenbildung und erblichkeit. In *Festschrift für Adolf Bastian zu seinem 70. Geburtstag 26. Juni 1896* (pp. 1–44). Berlin: Verlag von Dietrich Reimer.
- Washburn, S. L. (1983). Evolution of a teacher. *Annual Review of Anthropology*, 12, 1–24.
- Wilkins, J. S. (2009). *Species: A history of the idea*. Berkeley: University of California Press.
- Williams, D. M., & Ebach, M. C. (2008). *Foundations of systematics and biogeography*. New York: Springer.
- Winsor, M. P. (2003). Non-essentialist methods in pre-Darwinian taxonomy. *Biology and Philosophy*, 18, 387–400.
- Winsor, M. P. (2006). The creation of the essentialism story: An exercise in meta-history. *History & Philosophy of the Life Sciences*, 28, 149–174.

- Witteveen, J. (2013). *Rethinking 'Typological' vs. 'Population' thinking: A historical and philosophical reassessment of a troubled dichotomy* (Ph.D. thesis). University of Cambridge
- Witteveen, J. (2015). Naming and contingency: The type method of biological taxonomy. *Biology & Philosophy*, 30, 569–580.
- Witteveen, J. (under review). Objectivity, historicity, taxonomy.
- Yudell, M. (1999). Kinsey's other report. *Natural History Magazine*, 108, 80–82.
- Zangerl, R. (1948). The methods of comparative anatomy and its contribution to the study of evolution. *Evolution*, 2, 351–374.