What Is Wrong with Typological Thinking?*

Tim Lewens†‡

What, if anything, is wrong with typological thinking? The question is important, for some evolutionary developmental biologists appear to espouse a form of typology. I isolate four allegations that have been brought against it. They include the claim that typological thinking is mystical; the claim that typological thinking is at odds with the fact of evolution; the claim that typological thinking is committed to an objectionable metaphysical view, which Elliott Sober calls the 'natural state model'; and finally the view (endorsed by Ron Amundson and Günter Wagner) that typological thinking—and specifically evolutionary developmental biology's typological thinking—is committed to a peculiar form of causation that does not fit neatly into the causal models endorsed by population genetics. I argue that, properly understood, the typological thinking of evolutionary developmental biology does not run into any of these problems.

1. A Basic Outline of Typological Thinking. Population thinking and typological thinking have been defined in many ways, by many people, and for many purposes (see Chung 2003, inter alia). In this paper, I will begin with what I see as one of the core senses of Ernst Mayr's ([1959] 1976) characterization of typological thinking. The typological thinker believes there is some limited number of stable 'types' or 'forms', which explain the observed patterns of diversity in the biological world. The 'vertebrate archetype' of Richard Owen, for example, was an effort to represent a common structural plan, modified to various degrees in particular species,

*Received April 2008; revised August 2009.

†To contact the author, please write to: Department of History and Philosophy of Science, University of Cambridge, Free School Lane, CB2 3RH Cambridge, United Kingdom; e-mail: tml1000@cam.ac.uk.

‡A much shorter 'abstract' of this paper has appeared as Lewens 2009. I am grateful to audiences at the IHPST (Paris), the University of Leeds, and the University of Cambridge, where earlier versions of this article were presented. I am also grateful to Günther Wagner and Roberta Millstein for comments. Finally, I am grateful to the IHPST (Paris), for accepting me as a visitor while this work was being completed. This work was supported by grants from the Leverhulme Trust and the Isaac Newton Trust.

Philosophy of Science, 76 (July 2009) pp. 355–371. 0031-8248/2009/7603-0006$10.00
Copyright 2009 by the Philosophy of Science Association. All rights reserved.

https://doi.org/10.1086/649810 Published online by Cambridge University Press

which underlies all vertebrates. We can think of 'types' as explanatory posits: some forms are seen rarely or not at all, because there is no corresponding type. Others are seen frequently because they are variations on an underlying type (see Sober 1980; the presentation of typological thinking in this section and the next follows Lewens 2007, chap. 3).

The question for this paper is what, if anything, is objectionable about this basic form of typological thinking. One might think such a question is irrelevant: haven't all modern biologists followed Mayr in rejecting typology? Surely typological thinking is no longer a serious stance for a modern biologist to adopt? But consider these comments by Rudolf Raff:

> Diversity is not merely an inconvenience. It has also been regarded as a sort of epiphenomenon, the frills and digressions surrounding the real elements of development. To developmental biologists, there is a mechanistic universality in developmental processes despite any diversity of ultimate outcome. (1996, 22)

These views coincide strongly with Mayr's notion that the typologist considers variation to conceal underlying unity, while the population thinker regards variation, in some sense, as basic. While Mayr is clear in his view that typological thinking is a bad thing, some evolutionary developmental biologists seem to endorse a view that sounds a lot like typological thinking. If there is something wrong with typological thinking, it is important to identify it, and to determine whether the apparent typological thinking of evolutionary developmental biology is guilty of the same mistakes.

In this paper I isolate four allegations that have been brought against typological thinking. The first claim, which we owe primarily to Mayr, is that typological thinking is mystical, other-worldly, or committed to some kind of dubious or obscure ontology. The second claim, once again due primarily to Mayr, is that typological thinking is at odds with the fact of evolution. The third claim, championed by Elliott Sober (1980), is that typological thinking is committed to an objectionable metaphysical view, which Sober calls the 'natural state model'. Finally, Ron Amundson (2005) has argued that typological thinking—and specifically evolutionary developmental biology's typological thinking—appears committed to a peculiar form of causation, one that does not fit neatly into the causal models endorsed by population genetics. I argue that properly understood, the typological thinking of evolutionary developmental biology does not run into any of these problems. Moreover, typological thinking is compatible with the variety of population thinking endorsed by population genetics. There is nothing wrong with the form of typological thinking that features in modern evolutionary developmental biology.

https://doi.org/10.1086/649810 Published online by Cambridge University Press

2. Typological Thinking Is Other Worldly. Here is what Mayr says about the typological thinker in his 1959 paper:

> According to [typological thinking], there are a limited number of fixed, unchangeable 'ideas' underlying the observed variability, with the eidos (idea) being the only thing that is fixed and real, while the observed variability has no more reality than the shadows of an object on a cave wall. . . . The discontinuities between these natural 'ideas' (types), it was believed, account for the frequency of gaps in nature. . . . Since there is no gradation between types, gradual evolution is basically a logical impossibility for the typologist. Evolution, if it occurs at all, has to proceed in steps or jumps. ([1959] 1976, 27)

Sometimes Mayr writes as though the typologist also denies the uniqueness of individuals; however, the view that types explain why individual variation is concentrated in certain areas is compatible with the view that no two individuals are alike. As Sober has argued, unless we are to see the typologist as a straw man who denies that there is variation, we should cast her position as one that sees the pattern of variation as expressive of underlying explanatory types (1980). Population thinkers do not object to 'types' as statistical *summaries* of the average form of a trait, but for the population thinker such types do not *explain* why variation centers on that average.

Mayr's explicitly Platonic language might lead us to the view that typological thinking is both essentialist and nonnaturalistic: types, whatever they are, are not natural entities of the sort usually discussed by scientists. But we can reject both of these connotations for typological thinking. Let us begin at the conceptual level. Moving away from biology for a moment, something like a typological explanation seems appropriate when we try to understand why some crystal structures are seen frequently, while others are not seen at all. We can take reference to types here to be shorthand for sets of physical facts that make some crystalline forms stable, others unstable. Perhaps we can think of organic types in a similar way. The typologist claims that only a few basic organic configurations are stable. These stable configurations then explain the diversity of forms manifested by individual organisms. Whatever we think about the merits of this view, it is neither idealistic, nor is it committed to any particular metaphysical view about essences.

Moving from conceptual to more historical considerations, recent work by Winsor (2006) and Amundson undermines Mayr's characterization of pre-Darwinian naturalists as Platonists and essentialists. Amundson, for example, has argued that in Owen's work Platonism played a largely cosmetic role. Chung's work on Mayr's own changing conceptions of the population/typological distinction is also instructive. He points out that

https://doi.org/10.1086/649810 Published online by Cambridge University Press

in a comparatively early discussion in *Systematics and the Origin of Species*, Mayr begins to draw a distinction between the 'old systematics', typically focused on 'types', and the 'new systematics', which makes essential use of the notion of a population in its employment of the biological species concept (1942). In a work of 1953 Mayr begins to link what he then calls 'the type concept' in biology with Platonism (Mayr, Linsley, and Usinger 1953). And Mayr does not associate Darwin with the demise of typological thinking until 1959; in the 1953 work he instead claims that the replacement of the type concept began in 1878, nearly twenty years after the publication of the *Origin of Species*. The general message of Chung's discussion is that Mayr himself may have been too harsh in his treatment of typologists.

3. Typological Thinking Is Antievolutionary. The evolutionary developmental biologist Günter Wagner has also pointed out that one might think of types as biological analogues of stable physical configurations, but he goes on to suggest another source of opposition to typological thinking:

> The regularities of the chemical properties of elements are explained by the quantum mechanical principles governing the electron arrangement in the atomic shell. Why not expect the same for the living world, as long as evolution was not an established fact? (1989, 53)

One might pause here and ask why establishing the hypothesis of evolution excludes this typological manner of thinking. By itself, it doesn't. Ron Amundson has recently pointed out that for many nineteenth century biologists, morphological types were meant to capture the unity underlying groups of species, not members within individual species (Amundson 2005, 80). Owen's Vertebrate Archetype is a prime example. Clearly, a typologist of this sort need not be a fixist about species: consistent with this form of typology, species might change over time in ways that explore the possible incarnations of a single archetype. Indeed, this may have been the view eventually held by Owen. Darwin's bulldog himself, Thomas Henry Huxley, disagreed with Darwin's gradualism, and although he was personally opposed to Owen, his own views regarding evolution might be viewed as a form of descent with modification within a typological framework. Amundson adds that "timelessness of types still does not imply species fixism unless species themselves are types" (2005, 80). But logically speaking, one could be a transmutationist even if one thought that species corresponded one-to-one with types. Just as it is not contradictory to claim that there are a few stable forms of Carbon, and that a particular sample of graphite might be transformed into a sample of diamond, so it is no contradiction to claim that there are a few stable organic types

https://doi.org/10.1086/649810 Published online by Cambridge University Press

(the species) and that individuals of one type (one species, that is) might give birth to individuals of another.

The existence of stable forms is thus perfectly compatible with an evolutionary process that explores the limits of, and transitions between, such forms. Such a view is not merely possible; it seems to be the view actually held by Francis Galton. He believed that the analysis of populations reveals the existence of underlying 'positions of organic stability', a thoroughly typological notion. As a result of this, Galton was skeptical of the efficacy of selection. He believed we need to distinguish two senses of 'variation': 'variations proper', and 'sports'. Variations proper are minor disturbances from particular positions of stability, but because these positions are stable, organisms will generally tend to return to them, rather like Weebles, which wobble when pushed but always right themselves. Sports, on the other hand, are major mutations—saltations—towards new positions of stability. Galton's view was that selection can act on variation to produce temporary change, but only saltation has the permanence to produce new species.

4. Typologists Are Committed to the "Natural State" Model. I have suggested that Francis Galton looks like a good example of an evolutionary typological thinker. Why does Elliott Sober make Galton the hero of population thinking in his classic paper on this topic (Sober 1980)? Sober is well aware of Galton's typological views, but he is most interested in those aspects of Galton's work where, according to Sober, Galton invokes population-level features to explain further population-level features. Sober seems to cast Galton is a population thinker malgré lui: one who endows statistical properties of populations with explanatory efficacy, thereby inadvertently undermining the need for the types he elsewhere endorses.

Here, in very condensed terms, is how Sober portrays the situation. On Sober's view, the typologist is committed to some version of the *Natural State Model*—that is, a view of the biological world that distinguishes between 'proper' or 'representative' instances of a species, and 'aberrant' or 'defective' instances. In general, the type specifies the natural state (which will usually be the statistically normal state), while organisms which depart from the type form are in some sense abnormal. Both Galton and Quetelet recognized that a population reliably manifests a characteristic distribution of trait values, centering on a mean. For Quetelet, atypical organisms are produced by a particular class of cause—the causes of error—while typical organisms are produced by constant causes: "For Quetelet, variability within a population is caused by deviation from type. . . . Our belief that there is variation in a population is no mistake on our part. Rather, it is the result of interferences confounding the expression

https://doi.org/10.1086/649810 Published online by Cambridge University Press

of a prototype" (Sober 1980, 367). Galton represents a move towards population thinking because (according to Sober) Galton denies that individual variation should be explained as a result of interference with a prototype; "Rather, variability within one generation is explained by appeal to variability in the previous generation and to facts about the transmission of variability. Galton used the law of errors, but no longer viewed it as a law about errors" (Sober 1980, 368).

At this point I want to pause. In denying that variation should be explained in terms of characteristic error-inducing causes interfering with a prototype, does Galton thereby remove the explanatory need to posit types? It seems to me that he does not. Consider a die, loaded to land six up. For such a die, six is more stable, comparatively speaking, than other orientations. We should expect alternative numbers to come up with regularity, albeit less often than six. Indeed, the facts about the distribution of mass within the die, which make it the case that the die has a particularly high chance of landing six up, are the very same facts which make it the case that the die also has a good chance (a lower one, but still significant) of landing three up, or two up. Twos and threes are less likely than sixes, but their appearance is not anomalous. It is to be expected, just not so often as sixes. Finally, the sorts of causes that lead the die to land six up are of the same type as those which cause it to land two up, or three up. There are no characteristic 'error-inducing' causes which cause the die to land on three or two, nor is there any way of isolating a characteristic set of causes such that were those causes absent, the die would always land six up. A 'position of stability', understood as a set of physical facts determining which orientations of the die are more and less likely to appear, can therefore constitute a characteristically typological notion, which explains a series of varied events, and which demands no distinction between constant causes and the causes of error.

The same is true if we think of 'positions of organic stability' as sets of physical facts that dictate which organic forms are more and less likely to appear in a population, and which thereby explain constancy in observed patterns of variation over time. Indeed, it appears that for Galton, the existence of positions of organic stability explains the phenomena of reversion to the mean (see Gayon 1998). For Galton, a population has a tendency to show similar distributions in traits from one generation to another because there is a conservative 'pull', constraining the tendency of the bell curve to spread outwards. This pull is exerted by the position of organic stability, and it manifests itself as reversion. For Sober, Galton is a population thinker because the inheritance from one generation to the next of a *population-level* bell-shaped distribution of traits is explained by appealing to *population-level* phenomena, such as reversion. But reversion in turn is explained by appeal to an underlying notion of type.

https://doi.org/10.1086/649810 Published online by Cambridge University Press

All this rather abstract argument shows is that it is possible to be a typologist and still reject some of the central elements of a Natural State model. Sober sometimes suggests that the typologist is committed to unsound implications of the Natural State Model. But logically speaking, the element of typological thinking which involves an appeal to explanatory types is separable from the Natural State Model's distinction between constant causes and causes of error.

5. Interlude: Typology with Population Thinking. If evolution is compatible with typological thinking, is there any sense in which Darwin's ideas are opposed to those of the typological thinker? There is. Darwin denies that we can only explain species coherence by reference to the stability of underlying forms. On Darwin's view, species are 'tolerably well-defined objects' in virtue of the corralling forces of local environments, which discipline the tendencies of individuals to vary, and thereby maintain coherence over time at the level of the population. This population-level coherence is achieved in spite of differences constantly being introduced among individuals, not because of something—a stable type—instantiated by all individuals. If we are interested in explaining the nonappearance of organic forms, this populational mode of thinking gives us an alternative to typology.

Note, though, that even if the forms we observe are a subset of possible forms, namely those that reflect the changing demands of local environments, there might also be important structural factors that explain the limits of possible forms. So while the population explanation offers an alternative to the typological explanation, the two are not mutually exclusive. Note, also, that while a strong form of typological thinking appeals to eternally stable forms, a somewhat weaker form of typological thinking is available according to which the nature of stable forms is itself something that can change over time. In principle, at least, it is possible to explain the distribution of organic forms by appeal to a combination of (first) contingent and changeable biasing forces affecting the range of stable variation that can be produced in a set of species, and (second) by the winnowing effects of local environmental forces. So here, in effect, is a response to a further criticism of typological thinking. Someone who wishes to endorse typological thinking is not thereby committed to rejecting population thinking.

Again, this mixed stance is not a mere conceptual possibility. It appears to be the one held by many workers in contemporary evolutionary-developmental biology. It is, for example, precisely the stance expressed in Wallace Arthur's (2004) 'biased embryos' program. Arthur argues that embryos show characteristic forms of bias: developmental processes mean that different variations are not equiprobable, and this needs to be taken

https://doi.org/10.1086/649810 Published online by Cambridge University Press

into account in explaining evolutionary trends. Facts about how members of a species (or of a broader taxonomic category) develop are understood here, in effect, as facts about 'positions of organic stability' for that species: they are facts that make some variations in organic form more likely than others.

6. Typological Thinking Is Incompatible with Population Genetic Causation. As we have now seen, there are typological themes in some evolutionary developmental work. Consider, once again, these comments by Rudolf Raff:

> Diversity is not merely an inconvenience. It has also been regarded as a sort of epiphenomenon, the frills and digressions surrounding the real elements of development. To developmental biologists, there is a mechanistic universality in developmental processes despite any diversity of ultimate outcome. (1996, 22)

This reference to variability as an *epiphenomenon* gets very close to Mayr's characterization of the typologist as one who thinks that "there are a limited number of fixed, unchangeable 'ideas' underlying the observed variability, with the eidos (idea) being the only thing that is fixed and real, while the observed variability has no more reality than the shadows of an object on a cave wall" ([1959] 1976, 27). A little later Raff appears to assert the existence of just such a real entity underlying observed variability:

> All chordates share a basic body organization distinct from that of any other phylum. Classes of the vertebrates, a subphylum of the chordates, share a basic set of anatomical features characteristic of the phylum Chordata despite the substantial distinctness of the anatomical features of the classes from each other. (1996, 30)

Raff seems committed to the view that there is some commonality underlying the diversity observed in nature. Here he is asserting the existence of *body plans*—structures that can be investigated, even depicted, and which are manifested in slightly different ways across different species in a phylum. Clearly these views have a good deal in common with some canonical typological notions, such as Richard Owen's vertebrate archetype, a general structural scheme which appears in various different incarnations in all vertebrate species.

We should remind ourselves once again that while some of the more radical proponents of the structuralist school refer to 'timeless laws' of organic form, most credit nature with more flexibility. Just as the weighting on a die can change over time, leading to changing 'positions of stability', so evolutionary forces can alter the developmental facts that determine

https://doi.org/10.1086/649810 Published online by Cambridge University Press

the probabilities of different forms arising as variants in a species. As Brian Hall, another evolutionary-developmental biologist says:

> The need is not to regard the Bauplan as the idealized, unchangeable abstraction of Geoffroy, but to treat it as a fundamental, structural, phylogenetic organization that is constantly being maintained and preserved because of how ontogeny is structured. (as quoted in Amundson 2005, 235)

Such thinkers seem committed to types understood as real, albeit changeable entities that explain clustering of variation across species at a time. But what could these entities be? Is there any real entity that affects and explains the general probability distribution at a time of the likely variants that will arise in future generations?

In an important recent work, Ron Amundson (2005) has tried to expose the tensions between evolutionary developmental biology, and the mainstream of population genetic thinking. He claims that theorists who argue that development is relevant to evolution are indeed typologists of a sort. This is because they try to describe what Amundson calls 'developmental types'. These are developmental structures such as *the tetrapod limb* which, it is claimed, have explanatory relevance that simultaneously ranges over many different species.

For the 'population thinker', it is hard to see what sorts of entities these types could be, and how they could come to have a causal role that extends beyond species boundaries. Günther Wagner, a leading evolutionary developmental biologist, puts Amundson's problem like this:

> For the kinds of causes that the Neo-Darwinan theory accepts as real, i.e., population processes like selection and drift, the limit of their reach are the limits of species. . . . Speciation irreversibly breaks the causal nexus that flows from population processes. In contrast, however, entities like the tetrapod limb transcend the limits of species, and there can be no population genetic [meaning 'evolutionary'] mechanism which lends cohesion to these entities. (2007, 148)

Amundson and Wagner's worries will occupy us for the remainder of this paper.

7. Nominalist Types. Amundson is certainly right to say that evolutionary developmental biologists talk in a way that appears to commit them to developmental types. Sean Carroll tells us that "the different architectures of these wings [in bats, birds and pterosaurs] reflect different developmental modifications of a common tetrapod forelimb design" (Carroll 2005, 190).

There is, it seems, some single entity—the tetrapod forelimb—that is

https://doi.org/10.1086/649810 Published online by Cambridge University Press

variously instantiated in bats, birds and pterosaurs. The question is whether this might be written off as a mere façon de parler. Indeed, a rephrasing of these commitments in more pedestrian language is offered by Carroll himself. He begins by saying that "while all arthropod limbs have a common design, an incredible spectrum of variations on this design have evolved" (2005, 170). But only a page later this is put in a way that suggests a kind of resemblance nominalism about the notion of a 'common design': "None of these later structures were invented from scratch; they are all variations on an ancient limb design" (171). One need not believe some single entity is literally shared by these different species. Rather, each species has limbs that resemble the limbs of the others. They resemble each other because they are descended from a common ancestor. Similarly, the resemblance nominalist (e.g., Rodriguez-Pereyra 2002) denies that there is any one entity—redness—literally shared by a red tomato and a red pillar box: when we say their colors are the same, we commit ourselves only to a resemblance between distinct entities.

On the face of things, then, one might worry that Amundson and Wagner have made a simple mistake. They have assumed that in speaking of a structure shared across taxa, the evolutionary developmental biologist is committed to a metaphysically rich notion of a single entity multiply instantiated in distinct species, something akin to a universal. The truth is that a nominalist recasting of developmental types is available.

Amundson and Wagner have not, in fact, made a mistake of this sort. Ultimately, an account of types that is nominalist in spirit is, I will argue, the right one. But we cannot arrive at this point without attempting to explain, using the conceptual repertoire of population genetics, why we should find resembling structures across distinct taxa.

8. Generative Entrenchment. It might seem, in contradiction to Amundson and Wagner's contention, that there is a perfectly easy way to explain shared structures like the tetrapod limb using concepts from population genetics, such as natural selection. Structures which arise early in evolutionary history are likely to acquire a key foundational role in the development of many diverse functional structures that arise later in evolutionary time. We should consequently expect these structures to remain largely unchanged across long periods of evolutionary time, because alterations of them are likely to be extremely costly in fitness terms. William Wimsatt calls this phenomenon 'generative entrenchment' (e.g., Wimsatt 1986). Here, shared structures are explained by ongoing shared selection processes at work in each of the populations in which the structure is preserved. If functional requirements on the internal organization of related species are constant over long periods of evolutionary time, then internal selection pressures will also be shared across diverse species, and

https://doi.org/10.1086/649810 Published online by Cambridge University Press

we should expect similar developmental processes to appear, too. This, in turn, might allow structuralists to imply that there are entities such as the tetrapod forelimb, which do indeed express shared patterns of development across taxa, in a way that is perfectly in tune with the causal assumptions of population genetics.

9. Fitness and Probability. Amundson rejects this apparent reconciliation of population genetics and evo-devo, and with good reason. He points to the fact that some evolutionary developmental biologists feel able to explain some evolutionary trajectories with no appeal to fitness, and hence no appeal to selection, at all (see Stadler et al. 2001 for a partial elaboration of this approach). The important distinction is between an explanation of conserved traits in terms of the *low fitness* of alternative variants, and an explanation of conserved traits in terms of the *low probability* of alternative variants. The generative entrenchment explanation for conserved traits is compatible with alternative traits arising quite regularly, and being selected against because of low functional performance. In contrast to this, the structuralist claims that some traits simply never arise at all, or arise only rarely, because they are unlikely to do so. These patterns of probability are themselves conserved across diverse taxa. In an echo of Galton's 'positions of organic stability', the 'developmental type' is posited as a structure shared across taxa, which determines which structures are more and less likely to arise in mutation, and hence which governs the probabilities of various evolutionary trajectories independently of the population-level 'forces' (selection, drift and so forth) acting on species.

We can use Wagner's work (e.g., 1989, 2001) to fashion a very general framework for resolving Amundson's conundrum. We begin with a truism. Development in any given organism is produced by the interaction of numerous resources of many different kinds. Large networks of genes act against complex environmental backgrounds. When the organism reproduces, it is conceivable that any of these elements might change, and with such a change, an altered phenotype may or may not be produced in the offspring generation. Different probabilities can be attached to these different phenotypic alterations. The probabilities we assign will be a function of the configuration of the entire developmental system. The chances of given phenotypic alterations occurring will depend in part on the chances of alterations occurring in specific elements of the system that produces the phenotype (so, e.g., alterations that would require variation in the strength of gravity will be very unlikely), and in part on the general nature of the system that interacts with those specific elements (so, e.g., even if changes in some gene are likely, this need not make phenotypic change likely if the mutation in question is silent). What is more, we should

https://doi.org/10.1086/649810 Published online by Cambridge University Press

remember that population-level facts can also determine the chances of different forms arising, for example by affecting the chances of different sorts of mate pairings.

This general framework, applied to an individual organism, allows us to assign different probabilities to different phenotypes arising through mutation. Note that these issues are conceptually prior to issues relating to the fitness of different phenotypes. If a phenotype would be very fit, but has a very low probability of arising through mutation, then there is a very low chance that it will be available for selection to find it. And there is no guarantee that it will arise over time. For suppose the chances of mutation from A to B are very high, the chances of mutation from A to C very low, and the chances of mutation from B to C even lower. Suppose, moreover, that C is fitter than B and A, and B is fitter than A. Given a population of A individuals, they are more likely to mutate to the B form than to the C form. B's may then replace the A's in the population, making the chances of mutation to C even lower than they were before. So far, nothing distasteful to the population thinker has been introduced. Even so, we show by this highly schematized example how fitness-independent facts of development can introduce biasing forces on the direction of evolution. A purely selection-based approach, that regarded all phenotypic mutations as equally likely, would not be able to adequately explain the nonappearance in the population of C.

In the highly schematized discussion above, the chances of phenotypic alterations were assigned on the basis of the developmental matrix of a single organism. But note that there is nothing to stop us from giving a characterization of the chances of phenotypic alterations arising in a population of organisms. These chances will be a function of the developmental matrices of each organism in the chosen population, and of the numbers of those different developmental matrices. So, on this view, a developmental type is indeed an abstraction of a nominalist variety, albeit an abstraction from a population of individual ontogenies, giving rise to a probability distribution across various phenotypic alterations.

Note that the proposed framework is deliberately stated in the most generic way possible—the probabilities of traits arising in future generations are a function of the entire populational developmental matrix. One might choose to simplify this by introducing constant mapping rules from genotype to phenotype, and assessing how likely different phenotypes are to appear, given the nature of these rules and the chances of genetic mutations and recombinations occurring. This is to presuppose that there are no salient forms of nongenetic inheritance. But this form of simplifying assumption is by no means obligatory. Moreover, it becomes hard to justify. For consider that new variant phenotypes can be introduced simply by a change in environment, exposing a new element of a

https://doi.org/10.1086/649810 Published online by Cambridge University Press

gene's norm of reaction. Hence the probabilities of alterations in various environmental parameters can become important when we ask how we should expect the generation of new phenotypic traits to be constrained or facilitated.

How far does this get us in resolving Amundson's conundrum? Only part of the way. When focusing on a particular population, we can and should draw a distinction between the question of how likely different phenotypic alterations are to arise within that population, and the question of the relative fitnesses of those altered phenotypes. There is no guarantee, then, that an exclusive focus on relative fitnesses of alternative phenotypes will fully explain the evolutionary trajectory taken by the population. This helps us to understand the distinctive evolutionary importance of an evo-devo approach, and the way in which it can provide explanations that elude adaptationists. But it still leaves us with a fundamental worry. As Amundson and Wagner point out, breeding populations are relevant units in a standard evolutionary model, whereas 'the tetrapod forelimb', if it describes a structure underlying the probabilities of phenotypic mutation, would have to describe a structure constructed from the developmental matrices of many reproductively isolated groups. Why lump such isolated groups together?

As a matter of fact, so long as ontogeny is reasonably conservative—so long as offspring tend not to depart too radically from their parents—we will find that developmental structures remain shared to a greater or lesser degree across reproductively isolated groups simply in virtue of those groups' descent from common ancestors. If ontogeny is conservative in this way, then on many occasions the similarities will be close enough to justify the description of a shared abstract structure governing the transition probabilities of the clade as a whole. In other words, the description of developmental types need not be in tension with populational causation, so long as ontogeny has a conservative character. But why should ontogeny be conservative, and if it is conservative, what explains this? The final section addresses these questions, and in so doing completes the resolution of Amundson's concerns.

10. Populational Types. Let us begin by asking what we might expect to see if ontogeny were not conservative. If the tendency to vary were nearly limitless, then we might expect selection to be the only force available that might restrict that tendency. Every trait of every population would tend to follow the particular demands of its local environment. We would be surprised to find developmental processes shared across different species, unless those species also happened to share selection pressures, such as shared internal selection pressures. And suppose, further, that evo-devo succeeded in describing developmental types even when we had no reason

https://doi.org/10.1086/649810 Published online by Cambridge University Press

to think that the taxa across which those types ranged were subject to similar selection pressures. In such circumstances, we would be right to feel the sort of perplexity that Amundson articulates. Moreover, if we instead relied on shared selection pressures to explain shared developmental processes, then evo-devo would explain nothing that could not be captured more simply by the adaptationist notion of selection. One might think that in some sense this gives natural selection priority over developmental constraint, for developmental constraints are explained by natural selection acting to stabilize development. In other words, one might argue that this vindicates Darwin's assertion that "the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type" ([1859] 1985, 233).

This is far too hasty. First, the notion of shared developmental processes sketched here is at best an explanatory consequence of natural selection. It is not logically prior to it. One can make perfect sense of the concept of a shared probabilistic bias on variant phenotypes without needing to invoke natural selection; natural selection is simply invoked as an account of why such biases should come to exist. And once we see this, we also see that it is an empirical question as to whether natural selection is always the proper explanation for the existence of such shared biases.

It is, however, exceptionally implausible to think that the tendency to vary is limitless in this way, or that selection is the only force that can explain why some limited range of variation is observed. Sometimes generic thermodynamic considerations may come into play. Perhaps we can explain the stability in the face of mutation of some three-dimensional protein structures by pointing to their energetic stability, rather than by pointing to selection in favor of epigenetic processes that chaperone their folding in such a way. More generally, suppose we ask what sort of change in developmental resources would be necessary to enable a particular phenotypic alteration to appear in the next generation. The answer might be a change in some environmental factor, or even a change in physical laws. If these developmental resources are unlikely to change, then the phenotypes they give rise to will be unlikely to change, too. Since both environmental factors and physical laws are the sorts of things that can be shared by reproductively isolated taxa, it follows that there is no principled problem in the thought that the grounds for the conservative nature of ontogeny need not reside wholly in shared selective regimes. To give another example, in cases where mutation rates are low, we might anticipate that developmental processes will remain reasonably similar in closely related taxa, even when those taxa are reproductively isolated. Finally, recall that generative entrenchment predicts that if there are alterations in early developmental stages, these will often tend to disrupt many later functions. Suppose that natural selection renders these early

https://doi.org/10.1086/649810 Published online by Cambridge University Press

structures developmentally robust—especially unlikely to be altered by mutation—in an ancestral breeding population. As I understand it, this is the underlying view of Rupert Riedl, whose notion of 'functional burden' is more or less the same as Wimsatt's (2007) notion of generative entrenchment. If this developmental robustness is itself inherited in new species that split off from this ancestral population, then once again we may find similar developmental processes even when the species themselves no longer share selection pressures. Here, then, are a number of factors which can explain the robustness of developmental patterns across distinct species, hence which justify the description of those patterns as 'developmental types'. In articulating the nature of these types, one thereby says something about the general nature of variation permitted across a broad taxon, in a way that permits genuine explanation of the evolutionary pathways followed within that taxon.

This very schematic presentation receives empirical support from a paper by Newman and Müller (2001). They take "the physical nature of living organisms to be their most salient property" (564). Claims about what the 'most salient' property of organisms might be are hard to justify in any objective way: the important message to take from Newman and Müller draws on their explanation of common features of organic form in terms of generic physical and chemical properties of aggregates of living cells, understood as 'excitable media'. They do not deny, of course, that selection (acting on genetic variation) can act to stabilize and refine the developmental outcomes underpinned by these generic physical and chemical processes. Their work does, however, make a strong case for the role of these processes not only in explaining the conservative nature of ontogeny in early evolutionary history, but also in explaining the ongoing nature of repeated forms even after the advent of selective stabilization and refinement.

This brief discussion of the sorts of processes that explain the robustness of developmental patterns allows us to rebut the accusation that on the view offered here, developmental types amount to nothing more than coincidentally shared patterns of development across distinct species. I do not discuss in any detail here the important question of what it takes for the developmental processes of distinct species to constitute a bona fide 'developmental type'. By way of a sketch, let me note that on the broadly nominalist account offered here we should expect no firm answer to the question of when resembling developmental patterns are close enough in their phenomenology to license the description of a genuine 'type'. But so long as there are underlying factors or some kind or another that help to explain why reproductively isolated species nonetheless display similarly structured developmental processes, then these cross-species 'types' will qualify as so called 'natural kinds' on at least one influential

https://doi.org/10.1086/649810 Published online by Cambridge University Press

philosophical account of kinds, namely the 'homeostatic property cluster' theory (Boyd 1991).

We have seen that there is no reason to be especially perplexed by the thought that factors other shared selection regimes could be invoked to explain why patterns of development should be similar in reproductively isolated populations. There is, consequently, no reason to be especially surprised to find that ontogeny has the sort of character that permits the description of developmental types that range across population boundaries. Finally, these developmental types have just the roles in biological enquiry that Amundson says they do: their nature can be reconstructed from observed patterns of morphological variation, and once they are characterized, they enable the explanation of pathways of evolutionary change independently of adaptationist concerns about relative fitness.

The considerations offered here are exclusively conceptual. Explaining why ontogeny is conservative is an enormous project—it is the project of explaining reproduction. It is not my goal to assert, of any particular trait, why it takes the form it does, and what underpins the limited range of morphological variation that it manifests. The point of this essay is merely to gesture at the sorts of processes or properties that these explanations can appeal to, and in so doing to render evo-devo's appeal to developmental types respectable in principle, without making the empirical case for any specific evo-devo claim.

In summary, what is offered in this paper is a populational account of developmental types: it is a typology for population thinkers. The question of which variants are likely to become available in a population is a function of the makeup of the population as a whole. But although *populational*, this does not mean that the nature of developmental types can be captured solely through the concepts of *population genetics*. The general framework provides an ontology that makes evo-devo's typological thinking respectable, while retaining the explanatory novelty of the evo-devo approach.

REFERENCES

Amundson, Ronald (2005), *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo*. Cambridge: Cambridge University Press.

Arthur, Wallace (2004), *Biased Embryos*. Cambridge: Cambridge University Press.

Boyd, Richard (1991), "Realism, Anti-foundationalism, and the Enthusiasm for Natural Kinds", *Philosophical Studies* 61: 127–148.

Carroll, Sean (2005), *Endless Forms Most Beautiful*. London: Weidenfeld & Nicholson.

Chung, Carl (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.

Darwin, Charles ([1859] 1985), *On the Origin of Species*. Edited by J. W. Barrow. Reprint. Originally published (London: John Murray). London: Penguin.

https://doi.org/10.1086/649810 Published online by Cambridge University Press

Gayon, Jean (1998), *Darwinism's Struggle for Survival*. Cambridge: Cambridge University Press.
Lewens, Tim (2007), *Darwin*. London: Routledge.
——— (2009), "Evo-Devo and Typological Thinking: An Exculpation", *Journal of Experimental Zoology B—Molecular and Developmental Evolution* 312: 789–796.
Mayr, Ernst (1942), *Systematics and the Origin of Species*. New York: Columbia University Press.
——— ([1959] 1976), "Typological versus Population Thinking", in *Evolution and the Diversity of Life*. Reprint. Originally published as "Darwin and the Evolutionary Theory in Biology", in J. Meggers (ed.), *Evolution and Anthropology: A Centennial Appraisal* (Washington, DC: Anthropological Society of Washington), 1–10. Cambridge, MA: Harvard University Press, 26–29.
Mayr, Ernst, Earle Gorton Linsley, and Robert Usinger (1953), *Methods and Principles of Systematic Zoology*. New York: McGraw-Hill.
Newman, Stuart, and Gerd Müller (2001), "Epigenetic Mechanisms of Character Origination", in Günter Wagner (ed.), *The Character Concept in Evolutionary Biology*. San Diego, CA: Academic Press, 561–581.
Raff, Rudolf (1996), *The Shape of Life*. Chicago: University of Chicago Press.
Rodriguez-Pereyra, Gonzalo (2002), *Resemblance Nominalism: A Solution to the Problem of Universals*. Oxford: Oxford University Press.
Sober, Elliott (1980), "Evolution, Population Thinking, and Essentialism", *Philosophy of Science* 47: 350–383.
Stadler, Barbel, et al. (2001), "The Topology of the Possible: Formal Spaces Underlying Patterns of Evolutionary Change", *Journal of Theoretical Biology* 213: 241–274.
Wagner, Günter (1989), "The Biological Homology Concept", *Annual Review of Ecology and Systematics* 20: 51–69.
——— (2001), "What Is the Promise of Developmental Evolution?", part 2, "A Causal Explanantion of Evolutionary Innovations May Be Impossible", *Journal of Experimental Zoology—Molecular Developmental Evolution* 291: 305–309.
——— (2007), "How Wide and How Deep Is the Divide between Population Genetics and Developmental Evolution?", *Biology and Philosophy* 22: 145–153.
Wimsatt, William (1986), "Developmental Constraints, Generative Entrenchment, and the Innate-Acquired distinction", in William Bechtel (ed.), *Integrating Scientific Disciplines: Case Studies from the Life Sciences.* Dordrecht: Martinus-Nijhoff, 185–208.
——— (2007), "Echoes of Haekel? Retrenching Development in Evolution", in Manfred Laublicher and Jane Maienschein (eds.), *From Embryology to Evo-Devo: A History of Developmental Evolution*. Cambridge, MA: MIT Press, 309–356.
Winsor, Polly (2006), "The Creation of the Essentialism Story: An Exercise in Metahistory", *History and Philosophy of the Life Sciences* 28: 149–174.

https://doi.org/10.1086/649810 Published online by Cambridge University Press