Brit. J. Phil. Sci. **63** (2012), 429–448

Convergence and Parallelism in Evolution: A Neo-Gouldian Account

Trevor Pearce

ABSTRACT

Determining whether a homoplastic trait is the result of convergence or parallelism is central to many of the most important contemporary discussions in biology and philosophy: the relation between evolution and development, the importance of constraints on variation, and the role of contingency in evolution. In this article, I show that two recent attempts to draw a black-or-white distinction between convergence and parallelism fail, albeit for different reasons. Nevertheless, I argue that we should not be afraid of gray areas: a clarified version of S. J. Gould's earlier account, based on a separation of underlying developmental mechanisms from the realized trait, still represents a useful approach.

---

1 Introduction

At the end of the nineteenth century, the biologist August Weismann ([1893]) argued for the *Allmacht*—the omnipotence—of natural selection in evolutionary history. There are others who claim that selection is not all-powerful: constraints on variation may bias the production of variants, limiting the pool of variation upon which selection acts (Pearce [2011]). Defenders of the *Allmacht* position, often called externalists because they emphasize the importance of external selection pressures rather than internal constraints, offer as evidence the ubiquity of homoplasy, i.e. similar traits independently

doi:10.1093/bjps/axr046

produced by selection in similar environments.[1] But as David Wake ([1991]) points out, homoplasy can be the joint product of both external and internal factors: convergent evolution (usually seen as purely external) is often reinterpreted as parallel evolution (external + internal). According to Stephen Jay Gould, this internal–external distinction represents one of the eternal antitheses of paleontology: ‘What is the motor of organic change? [. . .] Does the external environment and its alterations set the course of change, or does change arise from some independent and internal dynamic within organisms themselves?’ (Gould [1977], p. 2).[2] Determining whether a homoplastic trait is the result of convergence or parallelism is also central to many of the most important contemporary discussions in biology and philosophy: the relation between evolution and development, the importance of constraints on variation, and the role of contingency in evolution.

Contingency, for example, has been widely discussed since Gould’s posing of his famous question: what would happen if we replayed the tape of life? Would organisms look completely different, or would they look relatively similar? (Gould [1989], p. 289). For the rest of his career, Gould denied the latter view, arguing that organic form is strongly constrained by history and highly sensitive to initial conditions. John Beatty has called this position the ‘evolutionary contingency thesis’, and has argued that it is the source of the widespread debates within biology about the relative significance of particular causal factors (Beatty [1995]). A recent debate in the *Journal of Philosophy* has demonstrated that the distinction between convergence and parallelism bears directly on Gould’s question (Beatty [2006]; Powell [2009]). Russell Powell criticizes some of Beatty’s experimental evidence against contingency in evolution by arguing that the results in question represent parallelism, not convergence. Powell’s attack depends on his earlier formulation of the distinction between convergence and parallelism, a formulation that is just beginning to reach the wider literature (Powell [2007]; Brandon [unpublished]).

While philosophers like Powell have been presenting new accounts of the difference between convergent and parallel evolution, some biologists have been arguing that the distinction should be modified or abandoned. Jeff Arendt and David Reznick ([2008]), for instance, argue that any difference between convergence and parallelism based on taxonomic distance is rendered

---

[1] Although the externalist–internalist distinction had been employed earlier by biologists such as David Wake and Stephen Jay Gould, its canonical formulation in philosophy of biology is due to Peter Godfrey-Smith ([1996]).

[2] It is not clear exactly what Gould means by ‘eternal’, but he takes these questions to be essential: they have thus persisted through the history of paleontology. Gould’s other two eternal antitheses are ‘Does the history of life have definite directions; does time have an arrow specified by some vectorial property of the organic world?’ and ‘What is the tempo of organic change? Does it proceed gradually in a continuous and stately fashion, or is it episodic?’ (Gould [1977], pp. 1–3).

incoherent by recent discoveries in developmental biology. This point has been the subject of much debate in the recent biological literature (Scotland [2011]; Wake *et al.* [2011]; Losos [forthcoming]). David Jablonski ([forthcoming]), on the other hand, claims that a simpler distinction based on phylogenetic tree topology is the best approach, since it does not depend on the messiness of developmental mechanisms.

In this article, I show that the two existing attempts to draw a black-or-white distinction between convergence and parallelism fail, albeit for different reasons. Nevertheless, I argue *contra* Arendt and Reznick that we should not be afraid of gray areas: a clarified version of Gould's earlier account, based on a separation of underlying developmental mechanisms from the realized trait, still represents a useful approach (Gould [2002], pp. 1061–89). In the first part of the article, I will present Jablonski's analysis, which, although it succeeds in making a clear distinction, divorces convergence from the broader question of externalism in evolution. In the second part, I will evaluate Powell's distinction between convergence and parallelism, demonstrating that it fails as an account, primarily due to problems with the screening-off criterion. Finally, in the third part of the article, I will argue for the coherence and utility of a neo-Gouldian analysis of the problem of convergence. This approach captures existing work in organismal and evolutionary biology without abandoning the relevance of the distinction for debates about the merits of externalist and internalist views of life.

2 The Topological Approach

David Jablonski's account of the difference between convergence and parallelism, as presented in his forthcoming book *Macroevolution*, is designed to be independent of the underlying developmental mechanisms involved in the formation of a homoplastic trait. Since these mechanisms are the main reason that there is a fuzzy region between convergent and parallel evolution, Jablonski succeeds in making a sharp, operationally useful distinction. In this section, after presenting Jablonski's analysis, I will argue that his exclusion of developmental mechanisms means that his version of the distinction separates it from the questions about externalism that often motivate interest in convergence.

Traditionally, homoplastic traits are seen as convergent (i) if they appear in distantly related groups or (ii) if they are realized by distinct developmental mechanisms. Jablonski instead links convergent and parallel evolution to two distinct patterns of character state changes in a phylogenetic tree (Figure 1). Thus, whether a homoplastic trait is the result of convergence or parallelism depends only on tree topology. In convergent evolution, the same derived trait *Y* evolves from two different ancestral traits *X* and *Z* (Figure 1b), whereas in

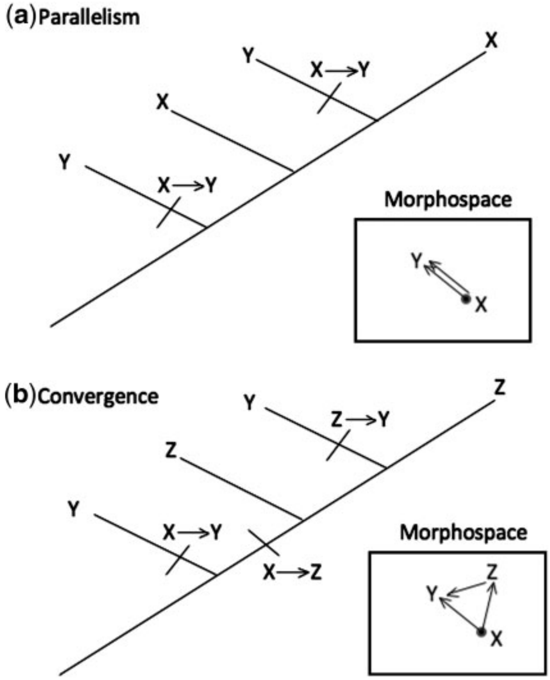

Figure 1. Jablonski on parallelism versus convergence. X, Y, and Z are different states of a character, i.e. traits. (**a**) X is the homologous ancestral trait, and there are two parallel transitions to Y, a homoplastic trait. (**b**) X is the ancestral trait, Z is a homologous derived trait, and there are two convergent transitions to Y, a homoplastic trait. From Jablonski ([forthcoming]).

parallel evolution, the same derived trait Y evolves twice from the same ancestral trait X (Figure 1a). The derived trait Y is homoplastic in each of the panels of Figure 1 because it is not shared by the most recent common ancestor; conversely, trait X in Figure 1a is homologous, as is trait Z in Figure 1b.[3] Robert Scotland ([2011], pp. 217–8) attributes this ‘ancestral state’ approach to Willi Hennig ([1966]) and Rupert Riedl ([1978]).

The classification reached using Jablonski’s method is often the same as that which results from consideration of taxonomic distance or developmental mechanisms. One of the most commonly discussed examples of parallelism is the evolution of similar traits in independent freshwater populations of the ancestrally marine three-spine stickleback, studied by Dolph Schluter, David Kingsley, and colleagues. Many different freshwater populations around the

---

[3] As noted by an anonymous referee, this depends on agreement about what counts as a trait in the first place. This point opens up a broader issue that cannot be addressed here. Suffice it to say that all accounts of homology and homoplasy depend on such agreement.

world have evolved a lower degree of lateral armor plating (Colosimo *et al.* [2005]). Although Colosimo *et al.* ([2005]) show that changes to a particular signaling pathway are responsible for the homoplastic changes in armor pattern, this fact is, in Jablonski's view, irrelevant to the classification of the case as parallelism rather than convergence.[4] All that matters is that the relationships between the populations possessing the trait in question correspond to those of Figure 1a. Let *X* in Figure 1a represents the high-plating phenotype and *Y* the low-plating phenotype: there have been multiple parallel transitions from *X* to *Y* in three-spine sticklebacks. This is parallel evolution by the other criteria as well: different three-spine stickleback populations are relatively closely related, and the trait in question is realized by the same developmental mechanisms.

However, there are cases in which the various accounts of the convergence–parallelism distinction arrive at divergent results. Freshwater populations of nine-spine sticklebacks have also independently evolved less lateral plating. Assuming that the high-plating phenotype is homologous between three- and nine-spine species, Jablonski's approach treats this case identically to the one considered in the previous paragraph: the low-plating state has evolved from the same ancestral state in several independent populations of two different species, and is thus an example of parallel evolution. The developmental criterion, however, classifies this case differently. Kingsley and colleagues have shown that the low-plating phenotype in nine-spine sticklebacks is a result of changes to a different chromosomal region than that involved in the three-spine case (Shapiro *et al.* [2009], p. 1143). Thus, although these authors treat the evolution of low-plating in different populations of three-spine sticklebacks as an example of parallel evolution, they treat the evolution of low-plating *between* three- and nine-spine sticklebacks as an example of convergent evolution (Shapiro *et al.* [2009], pp. 1143–4; cf. Colosimo *et al.* [2005]).[5]

This second stickleback case is counted as parallelism by Jablonski, but as convergence by the developmental approach. The reverse also occurs. Jablonski treats all cases in which similar phenotypic traits evolve from different phenotypic precursors as convergence, regardless of whether the two similar traits have similar developmental underpinnings. Thus, most homoplastic functional traits will be convergent by his definition, even though the

---

[4] 'Irrelevant' is perhaps too strong a word here. Jablonski's distinction is meant to be operational rather than dogmatic, and new developmental discoveries could change the structure of the relevant phylogenetic tree.

[5] Jablonski (personal communication) is committed to a multilevel approach to evolution. Thus he could view the three-spine/nine-spine trait as parallel at the phenotypic level, but convergent at the developmental level—with different tree topologies at different levels. See also Scotland ([2011]).

developmental conception treats such traits as parallel if they have the same developmental basis.

Jablonski's exclusively phenotypic approach intentionally excludes developmental information. This avoids two important problems faced by the developmental approach: first, even homologous traits can have different developmental underpinnings, and thus developmental information can be unreliable; second, it is unclear how much developmental overlap is required to classify a case as parallelism. I will discuss both of these problems in Section 4, where I defend a neo-Gouldian account of the distinction. The advantage of the latter account is that it makes the distinction relevant to Gould's eternal question about the dominance of internal or external factors in evolutionary history—i.e. the developmental distinction does more conceptual work than the topological distinction.

Why is this conceptual work important? As mentioned above, the ubiquity of homoplasy is often used as evidence for the externalist view, but this only holds if the homoplasy in question is convergent rather than parallel. In the three-spine stickleback case, which is an uncontroversial example of parallelism, there is an interaction between (i) external selection pressures altered by lake isolation and (ii) internal variation in a particular developmental mechanism. When the three- and nine-spine cases are compared, however, it looks like external selection pressures are dominant: they produce the same phenotype via different developmental mechanisms. By classifying cases in which the independent evolution of the same changes in homologous traits occurs via distinct developmental modifications as parallelism rather than convergence, a dogmatic application of Jablonski's method severs the connection between convergence and externalism.

Thus, a clear distinction is obtained only by sacrificing one of the most interesting aspects of evolutionary convergence—its relation to adaptation and selection. Even Richard Lewontin, arch-critic of adaptationism, links convergence to the power of selection:

> Adaptation is a real phenomenon. It is no accident that fish have fins, that seals and whales have flippers and flukes, that penguins have paddles and that even sea snakes have become laterally flattened. The problem of locomotion in aquatic environments is a real problem that has been solved by many totally unrelated evolutionary lines in much the same way. (Lewontin [1978], p. 230)

According to Lewontin, one of the most famous proponents of the importance of constraints in evolution (and thus certainly not an externalist), the aquatic environment has 'forced' the convergent evolution of flattened appendages for locomotion. This is a situation in which selection does seem all-powerful. The ideal distinction, of course, would capture the link between convergence and the *Allmacht* of selection while avoiding any gray area between parallel and convergent evolution. I will examine an attempt to provide such a distinction in the next section.

3 The Screening-Off Approach

Russell Powell's account of convergent evolution is explicitly connected to externalism—i.e. to 'the strong functionalist claim that selection is the predominant force behind macroevolutionary pattern' (Powell [2007], p. 568). Powell combines the traditional developmental approach with a notion of direct causal responsibility in an attempt to formulate a clear distinction between convergence and parallelism. In this section, I will argue that his analysis fails, primarily due to problems with the application of the screening-off criterion.

As mentioned above, the developmental approach to the convergence–parallelism distinction normally leads to a gray area: how much developmental overlap is required before a trait is counted as the result of parallel evolution? To circumvent this problem, Powell proposes that the relevant developmental generators must be 'directly causally responsible' for the structure in question: i.e. the relevant generators must be those from which the structure 'derives immediately' (Powell [2007], pp. 570–1). As a criterion for direct causal responsibility, Powell suggests Wesley Salmon's notion of screening-off, in which 'A screens off B from C iff $P(C|A,B) = P(C|A) \neq P(C|B)$' (cf. Salmon [1970], p. 199). That is, if the probability of C given A and B is the same as the probability of C given A alone, and this latter is not equal to the probability of C given B alone, then A is causally and explanatorily primary. Powell applies the same criterion to distinguish between convergence and parallelism:

> Proximal genetic cause P screens-off more distal cause D (e.g., a shared master control gene) of homoplastic trait T where the probability of T given P and D, is the same as the probability of T given P, and different from the probability of T given D. (Powell [2007], p. 571)

If P screens off D, T is the result of convergent evolution; if it does not, T is the result of parallel evolution. Powell operationalizes his criterion, arguing that if substitution experiments show that (a) $D + P \rightarrow T$, (b) $D^* + P \rightarrow T$, and (c) $D + P^* \rightarrow T^*$, then P screens off D with respect to the production of T and T is convergent (*ibid.*, p. 572).

There are two main problems with Powell's criterion: (i) its operationalization and (ii) its screening-off approach. First, one of Powell's proposed substitution experiments is not possible—a fact which he acknowledges, but of which he does not see the implications. Although Walter Gehring and colleagues have produced arthropod eyes (T) in arthropods when a chordate or molluscan 'master-control' gene (D^*) is substituted for the homologous arthropod gene (D), the reverse experiment—$D + P^* \rightarrow T^*$—has not been performed (Halder *et al.* [1995]; Tomarev *et al.* [1997]). In fact, it is hard to know how even to go about performing it, which is concealed by the false parallel that Powell draws between D and P—between an individual 'master--control' gene D and a whole network of downstream generators P. To substitute a whole suite of genes like P, one would essentially be required to build a developmental network from scratch. This first problem is in fact related to the second problem: even if phenotype screens off genotype with respect to selection (Brandon [1982]), it is not clear that a set of downstream genes can screen off a single upstream gene, given that both are involved in a complex network (see below).

Second, Powell's screening-off approach assumes (i) that more proximate causes are more causally and explanatorily relevant than more distal causes, and (ii) that we can easily distinguish between these two types of causes. Both of these assumptions are questionable, and Powell does not provide evidence in support of either of them. Given that Powell ([2007], p. 571) is employing 'Brandon's (1990) notion of "screening-off"', it is surprising that he does not refer to the criticisms of this notion by Elliott Sober and Christopher Hitchcock. As Hitchcock ([1997]) points out, the application of screening-off to the 'intermediate cause' case—Brandon's and Powell's focus—is much more problematic than its application to the 'common cause' case—Salmon's focus. Both Hitchcock and Elliott Sober ([1992], p. 149) argue that the screening-off criterion ignores the fact that 'greater explanatory power is often obtained by citing factors that are at some remove from the effect'.[6] Brandon and colleagues, responding to Sober, appeal to Salmon's later account of causality to argue that one can objectively identify those interactions that have major effects, and that one can explain an effect by appealing to its most proximate major cause. For example, the bat–ball interaction is the major cause of the ball's trajectory, and factors that follow this interaction can be treated as mere conditions (Brandon *et al.* [1994], p. 478). Hitchcock ([1997], pp. 525–6) has suggested in turn that the question of causal relevance can be treated pragmatically. Powell, because he does not provide a clear pragmatic or ontic solution to this difficulty, is in effect assuming that the proximal cause is always the most important interaction in a developmental network, without providing any argument for this claim.

Moreover, the screening-off approach assumes that we can identify the most proximate cause of the homoplastic trait in any given case. This 'chain-of-events' picture does not even begin to capture the complexities of

---

[6] Salmon ([1970], p. 219): 'a process leading up to a given event E consists of a series of events earlier than E, but such that later ones screen off earlier ones'. In later work, Salmon ([1984], pp. 44–5) admits that statistical relevance relations and screening-off cannot, by themselves, capture the relevant causal factors.

biological development. For instance, take the case of the bilaterian eye: much of the network of genes involved in eye formation is shared between arthropods and chordates. Thus, even though the eye itself is homoplastic, many of the underlying generators of the eye are homologous. It seems difficult if not impossible to determine which aspect of the partly homologous network behind eye formation in bilaterians is the most proximate cause of the eye, although this determination is required even to apply the screening-off criterion.[7] The basic problem is that screening-off is designed to handle chains of causes, not causal networks. If he wants to claim that causal networks, which invariably involve feedback, can be simply divided into proximal and distal causes, Powell owes us a further argument.

In a more recent paper, Powell ([forthcoming]) has sketched a proposed solution to the above problem. He abandons the screening-off approach, drawing instead on recent discussions of causation. As with Brandon's response to Sober, discussed above, what matters is figuring out how to privilege certain causes. Powell employs the idea of a 'specific difference maker', due to C. Kenneth Waters ([2007]). In Waters' example, DNA is a specific difference maker with respect to RNA because different changes to a DNA sequence cause different and specific changes in the corresponding RNA sequence (Waters [2007], p. 574). Powell argues that a particular case of homoplasy should count as parallelism only if the relevant developmental underpinnings are, at least in part, 'both homologous and causally specific'. According to Powell, this rules out many regulatory genes (including master-control genes) because they do not 'directly specify' traits, but simply determine whether or not they develop at all. This new account, though superior to the screening-off approach, still has its problems. For instance, if homologous *Pax* genes are always involved in the development of metazoan eyes, why should they be excluded from consideration just because they are not specific difference makers? As I argue below, this is a case about which biologists rightly hesitate. Nevertheless, Powell's new approach is clearly more consonant with the neo-Gouldian approach described in Section 4 below, in that it accepts that the boundaries between convergence and parallelism must remain fuzzy.

Powell's original distinction can be pithily stated: '*a homoplasy is a parallelism just in case a developmental homology is the proximate cause of the phenotypic similarity*' (Powell [2009], p. 397). Unlike Jablonski's account, Powell's is explicitly addressed to the problem of externalism and the contingency debate. However, Jablonski's analysis at least provides a defensible method for sorting between convergent and parallel evolution. Powell's

---

[7] For a complete list of the genes known to be involved in building a *Drosophila* eye, see (Brody [2008]). The developmental network behind the metazoan eye is enough to give nightmares to those philosophers who dream of orderly chains of causes.

attempt at a black-or-white distinction fails because the screening-off criterion cannot provide a clear measure of causal relevance in a developmental context. If neither of these accounts gives us what we need, where can we go from here? In the final section of the article, I will present a neo-Gouldian account of convergence that, although it does not produce a sharp distinction, still represents a clear and useful approach for biologists and philosophers.

4 The Neo-Gouldian Approach

Although this is not explicit in Powell's paper, his account of convergence and parallelism relies on Stephen Jay Gould's distinction between a 'realized structure' and an 'underlying generator'. According to Gould, parallelism is confusing because it shares aspects with both standard homology and convergence: it is like standard homology in that the underlying developmental generators are homologous, but unlike it in that the realized structure is not inherited; it is like convergence in that the realized structure is the result of selection, but unlike it in that the underlying generators are homologous (Gould [2002], p. 1078).[8] Gould's view is clarified in Table 1, below.

The first two rows in Table 1 represent cases of homology, and the latter two represent cases of homoplasy.[9] As the right-hand column of the table indicates, homology and homoplasy are distinguished by examining tree topology, i.e. phylogenetic patterns of character state changes, while parallelism and convergence are distinguished by assessing whether or not the developmental generators of a trait are homologous.

Thus, Gould uses an approach similar to Jablonski's for the homology–homoplasy distinction, but then uses a developmental approach for the convergence–parallelism distinction. In this last section of the article, I will defend a neo-Gouldian approach to the problem of convergent versus parallel evolution.

Before we can explore the advantages and disadvantages of this neo-Gouldian approach, however, we must briefly address the viability of the taxonomic distance approach. As Arendt and Reznick ([2008], p. 28) note, most biologists who use the terms 'convergent evolution' and 'parallel evolution' seem to depend on the taxonomic distinction: convergence is

---

[8] Brian Hall independently arrived at a similar distinction at around the same time as Gould (see Hall [2003], p. 412). Ehab Abouheif ([2008], p. 3) has argued, relatedly, that parallelism is 'a transition between truly homologous and truly convergent characters'.

[9] Although I will not deal with the problems of homology and novelty in this article, there is broad consensus that homologous structures are sometimes generated by different developmental mechanisms (Homology*), as indicated by the second row of Table 1 (e.g. the five-digit limb of tetrapods). For recent philosophical discussions of the problems of homology and novelty in biology, see the special issue on 'The Importance of Homology for Biology and Philosophy' of *Biology and Philosophy* (vol. 22, November 2007) and the symposium on 'Evolutionary Innovation and Novelties' in *Philosophy of Science* (vol. 75, December 2008, pp. 861–908).

Table 1. Homology versus parallelism versus convergence of a structure

	Underlying generator	**Same realized structure**
Homology	Homologous	Shared inheritance
Homology*	Non-homologous	Shared inheritance
Parallelism	Homologous	Natural selection
Convergence	Non-homologous	Natural selection

homoplasy in distantly related taxa, while parallelism is homoplasy in closely related taxa. They argue that this usage cannot be supported, as 'closely related organisms often evolve the same phenotype via different mechanisms and distantly related organisms often evolve the same phenotype via the same mechanisms' (*ibid.*, p. 27). Their argument is analogous to my criticism of Jablonski: it amounts to saying that the taxonomic distinction does not capture what we wanted it to capture, namely, the interplay of internal and external factors in evolution with externalism linked to convergence and constraints linked to parallelism. An obvious response to this argument is simply to take the neo-Gouldian approach: new discoveries by developmental biologists have shown that traits can evolve convergently in closely related groups and in parallel in distantly related groups. By assuming the importance of developmental mechanisms, Arendt and Reznick end up implicitly relying on something like the neo-Gouldian account.

Once they have discarded the taxonomic approach, however, Arendt and Reznick go on to criticize developmental approaches as well. They point out that because the production of a homoplastic trait 'involves a network of genes rather than a simple linear pathway', it is impossible to know how much 'homologyness' (Powell's term) is enough to classify a case of homoplasy as parallelism (*ibid.*, p. 30; Powell [2007], p. 570). Their conclusion is not very promising:

> [...] because phenotypes are often the product of multiple, interacting mechanisms, there will rarely be a clear distinction between 'same' and 'different' genetic pathways. Assigning such similarities to either parallelism or convergence is thus analogous to divining between shades of gray rather than discerning black from white. (Arendt and Reznick [2008], p. 30)

Finally, they suggest that all cases where similar phenotypes evolve independently should be called 'convergent evolution'.

How can we address their 'shades of gray' critique? A first step toward a response must rely on what the distinction is supposed to do. As we have seen, the distinction is connected to the power of selection: cases of convergence highlight the importance of selection, whereas cases of parallelism show that one must also consider constraints on variation. Distinctions, as H. P. Grice and P. F. Strawson ([1956], p. 141) noted long ago, can be rejected for a variety of reasons. Arendt and Reznick claim that the developmental approach to the convergence–parallelism distinction is not sharp enough—that there will be too many ambiguous cases. To defend the neo-Gouldian account of the distinction from this charge, one must show, to steal a line from Grice and Strawson (*ibid.*, p. 143), that if biologists and philosophers take up this account they will 'apply the term ["convergence"] to more or less the same cases, withhold it from more or less the same cases, and hesitate over more or less the same cases'.

Because the neo-Gouldian approach is developmental, we have already seen how it applies to the case of lateral armor plating in sticklebacks. Corresponding to the way Schluter, Kingsley, and colleagues have discussed the two cases, this approach classifies the independent evolution of the low-plating phenotype in different populations of three-spine sticklebacks as parallelism, as the phenotype has similar developmental underpinnings in all of these populations; conversely, it classifies the independent evolution of the low-plating phenotype in three- and nine-spine sticklebacks as convergence, as the phenotype has different developmental underpinnings in the two species (Colosimo *et al.* [2005]; Shapiro *et al.* [2009]).

Given results such as these, one might think there is at least a direct probabilistic relationship between taxonomic distance and homoplasy due to convergence. Arendt and Reznick ([2008]) dispute this, pointing to other work on sticklebacks showing that modifications to the *Pitx1* gene have led to pelvic reductions in both three- and nine-spine stickleback species, and even in manatees (Shapiro *et al.* [2006]). However, such cases are interesting precisely because they violate a *prima facie* plausible relationship between taxonomic distance and convergence: i.e. they are interesting because they are cases of parallel evolution where we expect convergent evolution. The converse type of case is interesting for the converse reason. For example, when two populations of the beach mouse *Peromyscus polionotus* independently evolve the same phenotype, the default assumption is that parallel evolution is responsible; thus, when the same phenotype turns out to be the result of different developmental modifications in the same species, i.e. when convergent rather than parallel evolution is discovered to be responsible, this is an interesting result (Hoekstra *et al.* [2006]). The neo-Gouldian account, by classifying the first of these cases as parallelism and the second as convergence, shows that each runs contrary to our expectations and is thus remarkable.

The evolution of pelvic reduction via *Pitx1* modification, presented as an example of parallel evolution in the previous paragraph, is now known to be the result of changes to a tissue-specific enhancer of *Pitx1* in the case of three-spine sticklebacks (Chan *et al.* [2010]). If different changes to the same gene region are found to be responsible for pelvic reduction in nine-spine sticklebacks or even manatees, does this still count as parallelism? Such cross-species cases do exist. For example, Hopi Hoekstra and colleagues demonstrate that light coloration in two different species of desert lizards is produced by modifications to the same gene. This appears to be a case of parallelism, but it turns out that the two different mutations affect different aspects of the gene's role; each of the mutations leads to the same light phenotype, but each has different additional effects as well (Rosenblum *et al.* [2010]).

In all of these examples—sticklebacks, mice, and lizards—the main point at issue is what counts as 'the same' or 'similar' developmental underpinnings: a change at the same locus? The same gene? The same gene region? The meaning of 'similar' here must be to some extent determined pragmatically, but my sense is that the same gene region is a good compromise. This choice also has the advantage of maintaining a connection to the broader conceptual issue of externalism: if a homoplastic trait always results from independent changes to the same gene region, then internal factors are playing an important role in the evolution of the trait. On this view, a case should be treated as parallelism even if different mutations are involved, as in the desert lizards case above.

Even if we settle on a particular meaning of 'similar', it is inevitable that we will hesitate over certain cases. A more strenuous test of the neo-Gouldian account is the evolution of eyes in multiple lineages. Eye evolution is a classic case of homoplasy, traditionally used as an example of convergent evolution. However, various 'deep' homologies associated with eye development have led some researchers to recategorize the repeated evolution of eyes in metazoans as parallel evolution (Shubin *et al.* [2009]). This is clearly a somewhat ambiguous case: all metazoan eye development involves *Pax* genes, and in some cases homologous cell types and cellular circuitry, suggesting parallel evolution; nevertheless, the developmental underpinnings of eyes in different metazoan groups are still quite different, suggesting convergent evolution. Thus, metazoan eye evolution really does seem to inhabit the gray area lamented by Arendt and Reznick—and this may be a problem with many complex homoplastic traits, the result of what Wake *et al.* ([2011], p. 1033) call a 'complex hierarchical evolutionary history'.

Despite this potential problem, Brian Leander ([2008a]), in a response to Arendt and Reznick ([2008]), shows that there are black and white edges of the gray area, even in the complicated case of eye evolution. Leander, who studies unicellular eukaryotes, points out that while metazoans diverged ~450 million years ago, other eukaryote lineages diverged ~950 million years ago; thus, one should expect most cases of homoplasy between the latter to be cases of convergence. He gives the photoreception apparatuses of warnowiid dinoflagellates (ocelloids) and metazoans (eyes) as an example, arguing that even if there is some small degree of developmental overlap between these two homoplastic eukaryote organs,

> [. . .] the structural modification of a cyanobacterial cell, and its associated subcellular systems, into a functioning ocelloid involves fundamentally different components and processes from those that led to the independent origins of multicellular eyes in vertebrates and cephalopods. (Leander [2008a], p. 482)[10]

The independent evolution of ocelloids in protists and eyes in animals is a stunning case of convergence: dinoflagellate ocelloids and bilaterian eyes are very similar in both structure and function, as Figure 2 shows. There are many other examples of convergent evolution between unicellular and multicellular eukaryotes: e.g. several traits of gastrotrichs and ciliates living in interstitial marine habitats (Rundell and Leander [2010], pp. 433–4).

Leander ([2008b], p. 60) calls cases of this sort 'ultimate convergence', which describes homoplastic characters 'consisting of very few, if any, homologous components (genetic or structural)'. Ultimate convergence requires low 'residual capacity', which is correlated with high 'phylogenetic distance' as shown by Figure 3. 'Residual capacity' refers to ancestral constraints and developmental homology. Thus, Leander's view of convergence is actually very similar to the neo-Gouldian account. Translating the terms in Figure 3, 'parallel convergence' is *parallelism*, 'ultimate convergence' is *convergence*, and 'proximal convergence' refers to cases that can be classified as either parallelism or convergence, depending on the amount of residual capacity.

More recently, several biologists have discussed Arendt and Reznick's paper, but have not substantially changed the argumentative terrain as described above. Jonathan Losos ([forthcoming]) follows Arendt and Reznick ([2008]) in claiming that 'actually delineating what constitutes the same pathway is extremely difficult', though he outlines an experimental approach to investigating trait variation that is consistent with the neo-Gouldian account. David Wake *et al.* ([2011]) and Robert Scotland ([2011]) both endorse a developmental distinction. Scotland ([2011]), p. 220), however, criticizes the neo-Gouldian version, arguing that it is not useful because we rarely have the necessary information about developmental underpinnings. We cannot, he argues, use phenotypic information as a proxy, as the developmental basis of homologous or homoplastic traits can change over time, even as

---

[10] Ocelloids are apparently derived from plastids, and thus from endosymbiotic cyanobacteria. For more on endosymbiosis in eukaryotes, see (Bhattacharya *et al.* [2004]).

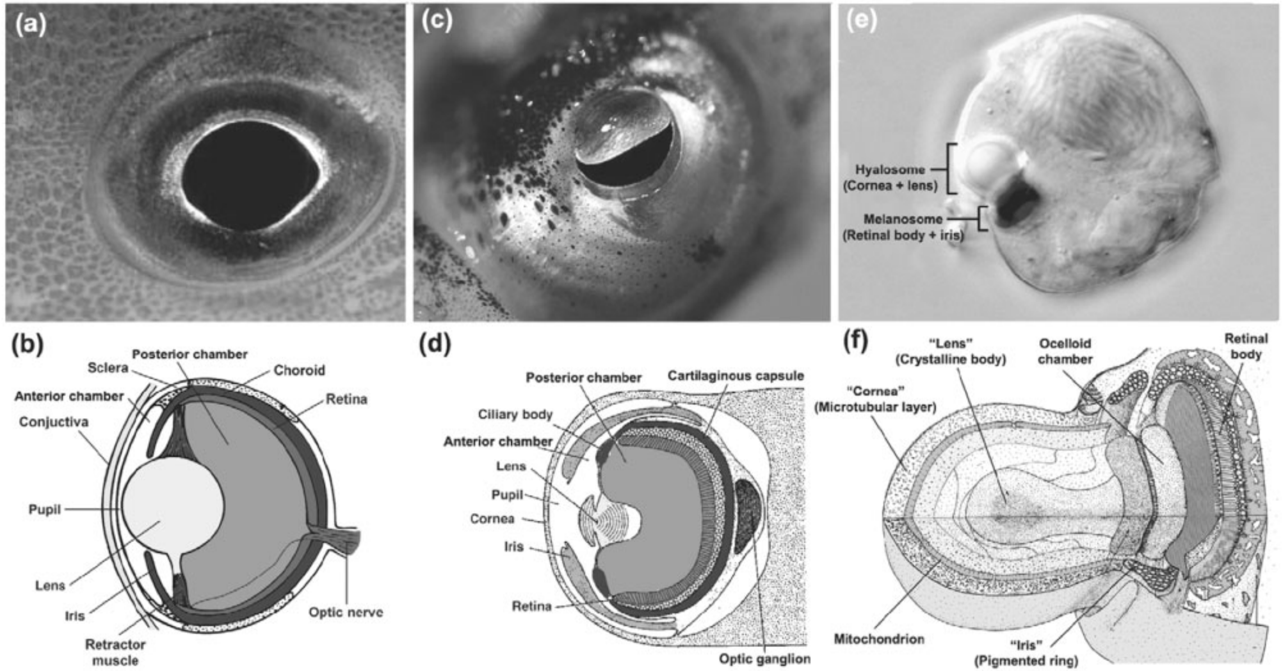

Figure 2. Anatomical structure of eyes and ocelloids. (**a**) The eye of a fish, and (**b**) the general structure of the vertebrate eye. (**c**) The eye of a squid, and (**d**) the general structure of the cephalopod eye. (**e**) The ocelloid of a warnowiid dinoflagellate, and (**f**) the general structure of the ocelloid. The ocelloid has analogs to the cornea, lens, and retina of the two bilaterian eyes. From Leander ([2008a]).

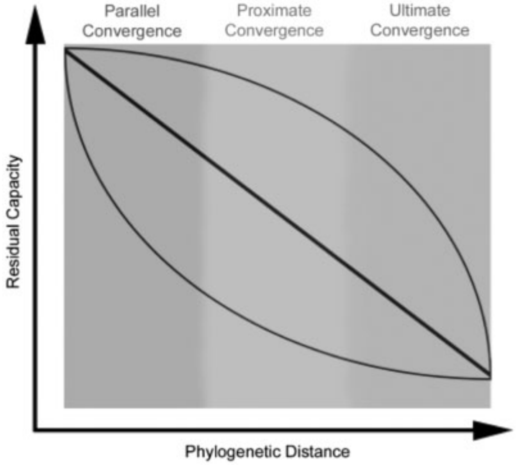

Figure 3. Leander's view of convergence. From Leander ([2008b]).

the traits remain similar. Thus, traits may appear to be convergent because of altered developmental mechanisms though they initially evolved in parallel via similar mechanisms. There is no real solution to this difficulty; however, the hope would be that the more developmental information we have about the organisms in question and their relatives, the less likely it is that we will be misled in this way.

Although Leander ([2008a, b]) and Arendt and Reznick ([2008]) disagree about the importance of taxonomic distance, they both want to use the term 'convergence' to refer to all cases of homoplasy—as does Losos ([forthcoming]). This move seems only to add confusion to an already complicated problem. The neo-Gouldian approach cannot remove the gray area between convergence and parallelism, but there are clear-cut cases of each, as we have seen. The existence of cases that are not easily classified as either convergent or parallel evolution, because they have some elements of both, does not mean that we must abandon the distinction. The externalist should still be able to argue, using widespread convergence as evidence, that selection is the dominant force in evolution. Those who resist externalism should be able to argue in turn that many putative cases of convergence are in fact cases of parallelism. These arguments inevitably focus on the nature and extent of developmental overlap, and what this overlap means for our understanding of evolutionary history. Therefore, we should not fear gray areas: the neo-Gouldian account is what makes possible a fruitful debate over externalism, the *Allmacht* of selection, and the role of development and contingency in evolution.

5 Conclusion

Disputes over externalism are far from over, as shown by the essays collected in Simon Conway Morris's *The Deep Structure of Biology* ([2008]). Indeed, according to Gould, the internal–external debate is eternal. One way into this debate is via the distinction between convergence and parallelism: widespread convergence that cannot be reinterpreted as parallelism suggests that selection is omnipotent, and constraints unimportant. Hence, it is helpful to have a good working distinction between convergence and parallelism. Jablonski ([forthcoming]) provides just such a distinction; however, because he classifies homoplasy directly derived from the same ancestral traits as parallelism, even if it arises from changes to different developmental mechanisms, he breaks the link between convergence and the *Allmacht* of selection. Powell ([2007]), on the other hand, keeps this link intact, but his screening-off criterion fails to provide a coherent account of direct developmental responsibility.

An approach derived from Gould ([2002]) accepts as inevitable the gray area that has arisen between convergence and parallelism in the wake of recent developmental discoveries. This neo-Gouldian account states that convergent traits are realized by non-homologous underlying generators, whereas parallel traits are realized by homologous underlying generators. Such an account captures the questions involved in recent work on homoplasy in sticklebacks, mice, and lizards, and also maintains the connection to questions about externalism in evolution. The independent evolution of eyes in different metazoan lineages is a challenging case, as it is not obviously convergence or parallelism. However, metazoan eyes and dinoflagellate ocelloids are a clear case of convergence—these homoplastic organs presumably share very few homologous developmental mechanisms.

One must specify what counts as the relevant underlying generators, and also what counts as developmental similarity, before one can classify a 'gray area' case as either convergence or parallelism. This need for specification, however, does not mean that the selection–constraint distinction or the convergence–parallelism distinction should be abandoned; after all, distinctions do not need to be razor sharp to be useful. Although revising the meaning of older biological terms often seems fruitless, as Wake ([1999]) emphasizes, such terms and distinctions can productively reframe new and existing biological research. With the neo-Gouldian account in hand, biologists and philosophers can continue to apply the terms 'convergence' and 'parallelism' to the same cases, withhold them from the same cases, and hesitate over the same cases. Such hesitation is a small price to pay for the conceptual work accomplished by the distinction between convergent and parallel evolution.

Acknowledgments

I thank David Jablonski, William Wimsatt, Robert Richards, Denis Walsh, Russell Powell, Chris Diteresi, Beckett Sterner, Bill Sterner, an anonymous referee, and the audience at the University of Toronto philosophy of biology workshop for comments on earlier drafts of this paper. Research for the paper was supported by a Neubauer Family Presidential Fellowship in the Humanities (University of Chicago), a doctoral fellowship from the Social Sciences and Humanities Research Council of Canada, and a Mellon Foundation Dissertation-Year Fellowship (University of Chicago).

University of Wisconsin-Madison
Department of Philosophy
Helen C. White Hall 5123
600 N. Park St., Madison, WI 53706
USA
trpearce@wisc.edu

References

Abouheif, E. [2008]: ‘Parallelism as the Pattern and Process of Mesoevolution’, *Evolution & Development*, **10**, pp. 3–5.

Arendt, J. and Reznick, D. [2008]: ‘Convergence and Parallelism Reconsidered: What Have We Learned about the Genetics of Adaptation?’, *Trends in Ecology & Evolution*, **23**, pp. 26–32.

Beatty, J. [1995]: ‘The Evolutionary Contingency Thesis’, in G. Wolters and J. G. Lennox (*eds*), 1995, *Concepts, Theories, and Rationality in the Biological Sciences*, Pittsburgh: University of Pittsburgh Press, pp. 45–82.

Beatty, J. [2006]: ‘Replaying Life’s Tape’, *Journal of Philosophy*, **93**, pp. 336–62.

Bhattacharya, D., Yoon, H. S. and Hackett, J. D. [2004]: ‘Photosynthetic Eukaryotes Unite: Endosymbiosis Connects the Dots’, *BioEssays*, **26**, pp. 50–60.

Brandon, R. N. [1982]: ‘The Levels of Selection’, in P. D. Asquith and T. Nickles (*eds*), *PSA 1982*, Volume 1, East Lansing, MI: Philosophy of Science Association, pp. 315–23.

Brandon, R. N. [unpublished]: ‘The ZFEL Explanation of Macro-Evolutionary Diversity’, *Philosophy of Biology @ Madison Workshop 2010*.

Brandon, R. N., Antonovics, J., Burian, R., Carson, S., Cooper, G., Davies, P. S., Horvath, C., Mishler, B. D., Richardson, R. C., Smith, K. and Thrall, P. [1994]: ‘Sober on Brandon on Screening-Off and the Levels of Selection’, *Philosophy of Science*, **61**, pp. 475–86.

Brody, T. B. [2008]: *The Interactive Fly: A Cyberspace Guide to Drosophila Development and Metazoan Evolution*; Available online <http://www.sdbonline.org/fly/aimain/1aahome.htm>.

Chan, Y. F., Marks, M. E., Jones, F. C., Villarreal, G., Shapiro, M. D., Brady, S. D., Southwick, A. M., Absher, D. M., Grimwood, J., Schmutz, J., Myers, R. M., Petrov, D., Jónsson, B., Schluter, D., Bell, M. A. and Kingsley, D. M. [2010]: 'Adaptive Evolution of Pelvic Reduction in Sticklebacks by Recurrent Deletion of a *Pitx1* Enhancer', *Science*, **327**, pp. 302–5.

Colosimo, P. F., Hosemann, K. E., Balabhadra, S., Villarreal, G., Dickson, M., Grimwood, J., Schmutz, J., Myers, R. M., Schluter, D. and Kingsley, D. M. [2005]: 'Widespread Parallel Evolution in Sticklebacks by Repeated Fixation of Ectodysplasin Alleles', *Science*, **307**, pp. 1928–33.

Godfrey-Smith, P. [1996]: *Complexity and the Function of Mind in Nature*, Cambridge: Cambridge University Press.

Gould, S. J. [1977]: 'Eternal Metaphors of Palaeontology', in A. Hallam (*ed.*), *Patterns of Evolution as Illustrated by the Fossil Record*, Amsterdam: Elsevier, pp. 1–26.

Gould, S. J. [1989]: *Wonderful Life: The Burgess Shale and the Nature of History*, New York: W. W. Norton.

Gould, S. J. [2002]: *The Structure of Evolutionary Theory*, Cambridge, MA: Harvard University Press.

Grice, H. P. and Strawson, P. F. [1956]: 'In Defense of a Dogma', *Philosophical Review*, **65**, pp. 141–58.

Halder, G., Callaerts, P. and Gehring, W. J. [1995]: 'Induction of Ectopic Eyes by Targeted Expression of the *eyeless* Gene in *Drosophila*', *Science*, **267**, pp. 1788–92.

Hall, B. K. [2003]: 'Descent with Modification: The Unity Underlying Homology and Homoplasy as Seen Through an Analysis of Development and Evolution', *Biological Reviews*, **78**, pp. 409–33.

Hennig, W. [1966]: *Phylogenetic Systematics*, Urbana, IL: University of Illinois Press.

Hitchcock, C. R. [1997]: 'Screening-Off and Visibility to Selection', *Biology & Philosophy*, **12**, pp. 521–9.

Hoekstra, H. E., Hirschmann, R. J., Bundey, R. A., Insel, P. A. and Crossland, J. P. [2006]: 'A Single Amino Acid Mutation Contributes to Adaptive Beach Mouse Color Pattern', *Science*, **313**, pp. 101–4.

Jablonski, D. [forthcoming]: *Macroevolution*, Chicago: University of Chicago Press.

Leander, B. S. [2008a]: 'Different Modes of Convergent Evolution Reflect Phylogenetic Distances: A Reply to Arendt and Reznick', *Trends in Ecology & Evolution*, **23**, pp. 481–2.

Leander, B. S. [2008b]: 'A Hierarchical View of Convergent Evolution in Microbial Eukaryotes', *Journal of Eukaryotic Microbiology*, **55**, pp. 59–68.

Lewontin, R. C. [1978]: 'Adaptation', *Scientific American*, **239**, pp. 213–30.

Losos, J. B. [forthcoming]: 'Convergence, Adaptation, and Constraint', *Evolution*.

Morris, S. C. [2008]: *The Deep Structure of Biology*, West Conshohocken, PA: Templeton Foundation Press.

Pearce, T. [2011]: 'Evolution and Constraints on Variation: Variant Specification and Range of Assessment', *Philosophy of Science*, **78**.

Powell, R. [2007]: 'Is Convergence More Than an Analogy? Homoplasy and its Implications for Macroevolutionary Predictability', *Biology & Philosophy*, **22**, pp. 565–78.

Powell, R. [2009]: 'Contingency and Convergence in Macroevolution: A Reply to John Beatty', *Journal of Philosophy*, **106**, pp. 390–403.

Powell, R. [forthcoming]: ‘Convergent Evolution and the Limits of Natural Selection’, *European Journal for the Philosophy of Science*.

Riedl, R. [1978]: *Order in Living Organisms: A Systems Analysis of Evolution*, New York: Wiley.

Rosenblum, E. B., Römpler, H., Schöneberg, T. and Hoekstra, H. E. [2010]: ‘Molecular and Functional Basis of Phenotypic Convergence in White Lizards at White Sands’, *Proceedings of the National Academy of Sciences of the United States of America*, **107**, pp. 2113–7.

Rundell, R. J. and Leander, B. S. [2010]: ‘Masters of Miniaturization: Convergent Evolution Among Interstitial Eukaryotes’, *BioEssays*, **32**, pp. 430–37.

Salmon, W. C. [1970]: ‘Statistical Explanation’, in Robert C. Colodny (*ed.*), *The Nature and Function of Scientific Theories: Essays in Contemporary Science and Philosophy*, Pittsburgh: University of Pittsburgh Press, pp. 173–231.

Salmon, W. C. [1984]: *Scientific Explanation and the Causal Structure of the World*, Princeton: Princeton University Press.

Scotland, R. W. [2011]: ‘What is Parallelism?, *Evolution & Development*, **13**, pp. 214–27.

Shapiro, M. D., Bell, M. A. and Kingsley, D. M. [2006]: ‘Parallel Genetic Origins of Pelvic Reduction in Vertebrates’, *Proceedings of the National Academy of Sciences of the United States of America*, **103**, pp. 13753–8.

Shapiro, M. D., Summers, B. R., Balabhadra, S., Aldenhoven, J. T., Miller, A. L., Cunningham, C. B., Bell, M. A. and Kingsley, D. M. [2009]: ‘The Genetic Architecture of Skeletal Convergence and Sex Determination in Ninespine Sticklebacks’, *Current Biology*, **19**, pp. 1140–5.

Shubin, N. H., Tabin, C. and Carroll, S. B. [2009]: ‘Deep Homology and the Origins of Evolutionary Novelty’, *Nature*, **457**, pp. 818–23.

Sober, E. [1992]: ‘Screening-Off and the Units of Selection’, *Philosophy of Science*, **59**, pp. 142–52.

Tomarev, S. I., Callaerts, P., Kos, L., Zinovieva, R., Halder, G., Gehring, W. J. and Piatigorsky, J. [1997]: ‘Squid Pax-6 and Eye Development’, *Proceedings of the National Academy of Sciences of the United States of America*, **94**, pp. 2421–6.

Wake, D. B. [1991]: ‘Homoplasy: The Result of Natural Selection, or Evidence of Design Limitations?’, *American Naturalist*, **138**, pp. 543–67.

Wake, D. B. [1999]: ‘Homoplasy, Homology and the Problem of “Sameness” in Biology’, in G. Bock and G. Cardew (*eds*), 1999, *Homology*, New York: Wiley, pp. 24–33.

Wake, D. B., Wake, M. H. and Specht, C. D. [2011]: ‘Homoplasy: From Detecting Pattern to Determining Process and Mechanism of Evolution’, *Science*, **331**, pp. 1032–5.

Waters, C. K. [2007]: ‘Causes that Make a Difference’, *Journal of Philosophy*, **104**, pp. 551–79.

Weismann, A. [1893]: ‘The All-Sufficiency of Natural Selection’, *Contemporary Review*, **64**, pp. 309–38, 596–610.