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BOOK REVIEW

There is Grandeur in This View of Life: The Bio-Philosophical Implications of Convergent Evolution

George McGhee: Convergent Evolution: Limited Forms Most Beautiful MIT Press, 2011, hardcover, 322 pp

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Interest in the evolutionary theoretical implications of convergent evolution has surged over the last decade, in part due to accessible monographs (such as Conway Morris 2003) that have drawn attention to this important and under-investigated evolutionary phenomenon. Just how ubiquitous is convergent evolution in the history of life, and what does the frequency of convergence tell us about the constraints on macroevolution as it has unfolded on Earth and as it might do in other nooks and crannies of the habitable universe?

Convergent Evolution: Limited Forms Most Beautiful is an exceedingly well-researched, lucidly written, and wonderfully synthetic review of convergent evolution research, making a strong case for the ubiquity of convergent evolution at all levels of the biological hierarchy. McGhee has compiled an impressive evidence base to be mined by future researchers, and the book is brimming with fascinating and underappreciated examples, some of which are of great evolutionary significance. Unlike existing monographs on the topic, *Convergent Evolution* is illustrated with clear, accessible figures and makes extensive use of cladograms that underscore the phylogenetic distance bridged by convergent events. It is now arguably the definitive empirical source for any biologist or non-specialist interested in the phenomenon of convergent evolution. However, like similar works before it, McGhee's exposition is somewhat less effective on the theoretical and philosophical fronts. Before canvassing our major criticisms of the book, we will provide a brief summary of each chapter.

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In the first chapter, McGhee introduces the phenomenon of convergent evolution and offers a terse treatment of definitional problems surrounding the concept of homoplasy. This crucial introductory chapter contains far less conceptual and methodological meat than one might expect of a work in theoretical biology. For instance, it fails to even gesture at problems confronting modern cladistics and phylogenetic inference, the contested nature of the homology concept, and philosophical debates over how we might distinguish between different types of convergent evolution. Like Conway Morris before him, McGhee treats parallel evolution, both in this chapter and throughout the book, as "simply a type of convergent evolution" (p. 7), without considering its deeper theoretical significance. On McGhee's proffered definition, "parallelism" refers to homoplasy that is produced from the same ancestral character or through cooptation of the same genetic-developmental resources, such as deep homologs. There are a host of empirical, methodological and conceptual problems that confront attempts to delineate parallelism in these ways, which McGhee fails to consider; these range from conceptions of sameness, to the level-relative nature of homology judgments, to the lack of total homology in the gene networks that are developmentally responsible for parallelism in closely related groups (for discussions of these and other problems, see e.g., Currie 2013; Pearce 2012; Powell 2012; Ramsey and Peterson 2012; Arendt and Reznick 2007). Furthermore, by characterizing both parallel and convergent events as *independently* derived outcomes, McGhee glosses over the theoretical importance of this distinction and its implications for our understanding of constraints on the shape of complex multicellular life (more on this below).

Chapter 2 is a tour de force of convergent evolution in animals, including (inter alia) swimming, flying, walking, burrowing and other locomotory morphologies, sensory modalities, teeth, beaks and claws, poison injection systems, digestive capabilities, defensive structures, reproductive strategies, and so on. This is easily the strongest chapter in the book, making a powerful case for the ubiquity and importance of convergence in animal evolution. Importantly, here and throughout the book, McGhee also considers intriguing instances of non-convergence, such as the lack of snake-like morphologies in mammals and the absence of mole-like excavator morphologies in reptiles. The chapter also takes developmental constraints seriously (though not seriously enough—see discussion below), explaining why 'centaur-like' forms (possessing four legs and two arms) cannot evolve within the confines of the four-limbed vertebrate body plan, but have evolved, repeatedly, in insects (namely, with respect to iterated 'mantis' forms). In contrast, McGhee shows that external physical constraints may explain why, for example, no predator has ever evolved eyes that can resolve the infrared range of the electromagnetic spectrum despite the obvious fitness advantages such an adaptation would confer.

Chapter 3 reviews convergences within the plant clade. Featuring the exceptional work of the biologist Karl Niklas and others, McGhee argues that convergence along multiple parameters on tree and leaf morphologies, water transport and root systems, and other structures has occurred repeatedly due to functional constraints imposed by the physical laws. McGhee argues, convincingly, that in both animals and plants, convergent reproductive strategies dwarf quintessential cases of morphological convergence—as is the case, for example, with viviparity in animals, and heterospory, seed and seed-dispersal systems in plants. It is important to note that many of the key convergences in plants hinge on the existence of animal pollinators and animal seed dispersal mechanisms. Plant-animal coevolutionary interaction appears to add layers of contingency to the evolution of certain iterated plant morphologies, as well as to the evolution of particular ecotypes (discussed in the next chapter), which the author fails to consider.

Chapter 4 sets out in search of a "periodic table of niches," focusing on the iterated evolution of ecotypes (such as insectivore, nectarivore, carnivore, omnivore, herbivore, chase predator, ambush predator, etc.), and ecomorphs (such as 'vulture', 'lion', 'ungulate' and 'mole'). McGhee takes convergence in ecomorphology, such as the strikingly similar faunas that evolved in parallel between marsupial and placental mammals, as evidence that "these [specialized] ecological roles exist in the absence of either placental or marsupial mammals and, since the placentals were not present in Australia, the marsupials independently discovered them in their own separate evolution" (p. 160). This conclusion is problematic because it fails to consider how contingent mammalian (and more broadly tetrapodian) body plans constrain and underwrite iterated ecological evolution. The discussion of pre-existing niches would also have benefited from connecting up with the wider theoretical literature on organism-niche codetermination, in particular with Richard Lewontin's well-known critique of so-called 'lock-and-key' models of ecological evolution. These quibbles aside, perhaps the most significant problem with this chapter—one that is symptomatic of an overarching impediment to the convergence project—is that it lumps plausible candidates for universal niches (such as broadly defined ecotypes) together with arguably more contingent iterated outcomes, such as ecomorphs that hinge on the tetrapodian body plan. For instance, the generalization "there will never evolve a sessile herbivore for sessile plants" seems to be far stronger (i.e., more widely applicable) than the claim "there will evolve a lion ecomorph," due to the sheer number contingencies that arguably underlie the evolution of mammalian and more broadly tetrapodian developmental architecture. We discuss this lumping problem in greater detail below.

Chapter 5 offers a preliminary examination of convergent evolution at the lowest scales in the biological hierarchy, from nucleic and amino acids to proteins. Among the most intriguing examples are the convergent evolutions of identical nucleotide substitutions producing similar sensitivities to light, of antifreeze protein molecules in cold-water fishes, and of enzymes that catalyze the first step in sugar metabolism. Homoplasy research is typically focused on the macromorphology of animals and plants, and thus McGhee's attention to convergence at the microscopic scale is much welcome. Nevertheless, his overarching analysis of convergence remains macromorphocentric, considering only a handful of examples of convergence in prokaryotes and never even mentioning archea. Thus, convergent evolution among single-celled organisms remains an important and under-investigated area that is ripe for future research.

Chapter 6 is, in our opinion, the weakest chapter in the book. It is sold as a review of convergent *minds* when in actuality it details convergence in *behaviors*. Prominent examples in the chapter include the "farming phenotype" arrived at by both ants (first) and humans (more recently), and "tool use" across vertebrate and even in some insect groups. These behavioral traits are clearly not underpinned by similar mental/cognitive mechanisms in the groups that have converged on them. It is well established in ethology that similar behaviors can be produced by fundamentally different mental activities and cognitive processes, a point overlooked by McGhee when he argues "animals with radically different brains have evolved the same architectural behaviors. Those analogous behaviors thus reflect analogous mental activities and cognitive strategies taking place in independent lineages, which is convergent mental evolution" (p. 221). McGhee thus makes the fallacious leap from "same behavior" to "same underlying mental/cognitive processes." Yet few would be sympathetic, for example, to McGhee's claim (p. 227) that the "agricultural minds" of ants and humans are the subject of cognitive convergence. The same is true for the mental mechanisms underlying herding behavior and pack hunting among various vertebrate clades. Nor is it clear that the loosely analogous phenotypes referred to in this chapter, such as "farming", "tool use", and "architectural behavior," are genuine natural kinds or even sufficiently similar traits to be properly classified as cases of convergence (though the impressive suite of independently derived agricultural features may suggest that this trait can be satisfactorily delineated). Although there is some discussion of convergent metacognition—among the few genuinely 'mental' elements of the chapter—McGhee curiously omits recent work on cephalopod cognition, which is without question the most robust example of sophisticated cognitive convergence that we know of, given that mollusks and vertebrates share an essentially brainless common ancestor in the base of the Cambrian.

It is not until Chapter 7 that the heavy philosophical lifting begins. Here, McGhee provides a theoretical framework and a series of useful figures for conceiving of the realm of the biologically possible, and for illustrating the interaction between internal (developmental) and external (functional) constraints that shape morphospace occupation (see Fig. 1). This chapter would have benefited, however, from closer contact with the astrobiological literature on possible life (c.f. Schulze-Makuch and Irwin 2012), as well as the philosophical literature on constraints in biology (c.f. Amundson 1994; Sansom 2003).

We finally come to the 'philosophical' implications of convergent evolution in the eponymous final chapter of the book. Disappointingly, it fails to wade into any major conceptual or methodological problems in the philosophy of biology that pertain to the present project. Instead, it proceeds to consider the implications of the radical evolutionary contingency thesis (and its antithesis) for our ability to find meaning in the universe and for the plausibility of theism. Frustratingly, McGhee presents a buffet of views on these matters without ever taking a clear stand or adjudicating their respective plausibilities. He does, however, in concluding the book, inveigh against what we believe to be an uncharitable caricature of the opposing Gouldian view of life, which we discuss in more detail below.

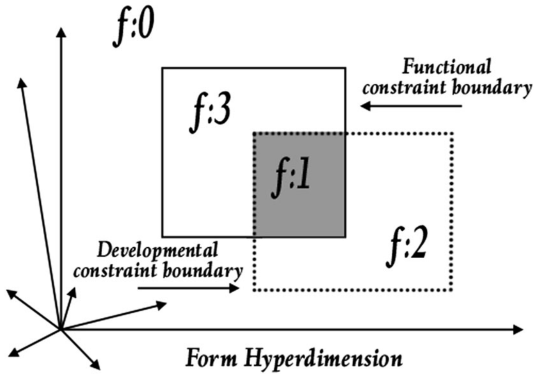

Fig. 1 Adapted from Figure 7.4 (p. 249). f:0 is the set of biological forms that are non-functional and cannot be developed by life on Earth. f:1 is the set of biological forms that are functional and can be developed by life on Earth. f:2 is the set of biological forms that are nonfunctional but could be developed by life on Earth. Finally, f:3 is the set of biological forms that are functional but cannot be developed by life on Earth

This brings us to overarching concerns with the book. *Convergent Evolution*'s greatest asset—its massive inventory of exemplar convergent events in the history of life—is also its greatest flaw. Like other recent attempts to establish the empirical and theoretical importance of homoplasy, McGhee's monograph is guilty of 'lumping' disparate convergent phenomenon into a single basket and proclaiming the ubiquity of the phenomenon. In effect, it treats all instances of homoplasy as if they are of comparable theoretical import, nomic necessity, and counterfactual robustness. Yet some proffered examples of convergence are the basis of far stronger generalizations than others, and McGhee offers no principled way of determining the relative significance of convergent outcomes. For instance, he lists nine examples of plants that have evolved vessels to transport water, and over twice as many examples of convergence in flowers that facilitate beetle pollination—but surely we would expect vessels to evolve earlier, more frequently, and more consistently in any given evolutionary system than features that are contingent on beetle pollination. In this respect at least, the whole is *less* than the sum of its parts, permitting uncharitable opponents to seize on the weakest cases in arguing against the law-like implications of convergence. In our own future work on this topic, we aim to develop a typology of convergence that breaks down the heterogeneous reference class of convergent events in accordance with the robustness of the generalizations they can plausibly support. McGhee's review will no doubt serve as a critical empirical resource for this conceptual project.

A second major problem with the book is that it fails to seriously engage with, and systematically mischaracterizes, Stephen Jay Gould's (1989) "radical contingency thesis." Gould's controversial, thought-provoking thesis is arguably the major motivation for recent work on convergent evolution, and yet it is not introduced until the very end of the book and then only briefly discussed (p. 266). And even there, it is considered only in relation to finding meaning in the universe. Like others before him, McGhee touts the ubiquity of convergent evolution as a rebuke of Gould's claim that the overarching shape of life is deeply historically contingent. The problem, however, is that McGhee's analysis never actually comes into contact with the core claims of Gould's thesis. It would have been helpful if McGhee had used the diagram from chapter 7 to contrast his view of life with that of

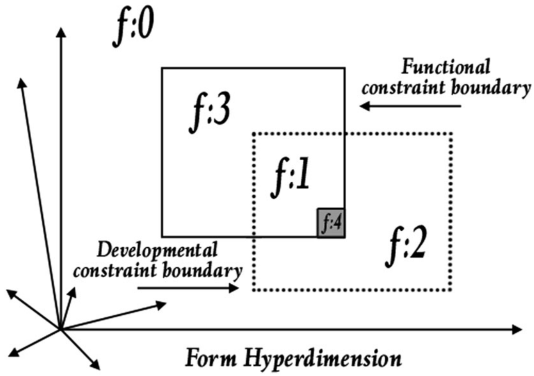

Fig. 2 In this modified version of Fig. 1, f:4 is introduced to represent Stephen J. Gould's radical contingency thesis, which holds that the actualized set of biological forms are but a small fraction of the set of functional, Earth-possible morphologies

Gould, perhaps by drawing smaller boundaries around the space of forms that are functional, developmentally possible, and actual (see Fig. 2). Instead, McGhee refutes a series of claims that Gould did not hold, and with which Gould would be unlikely to disagree.

For instance, McGhee arrives at the following two main conclusions (p. 271). "First, the view that the evolutionary process is nonrepeating (nonergotic) is demonstrably false." Nobody, and certainly not Gould, would hold such a blatantly false view, and thus McGhee dismantles a straw man in a way that obscures the genuine debate—which is really about the extent to which internal developmental constraints (including the broad parameters of animal body plans) are responsible for much or even most of the morphological reiteration. Contrary to McGhee, there is room within the Gouldian view of life, with its emphasis on internally constrained parallelism, for a great deal of reiteration and predictability (for a discussion, see Powell 2012). Second, the view that evolution is entirely historically contingent, and thus unpredictable (and nonrepeating), is demonstrably false." Let us set aside the problematic slide between epistemic issues (e.g., predictability) and metaphysical ones (e.g., the robustness of macroevolutionary pattern across changes in initial conditions). The trouble with this second conclusion is that once again, it is addressed to a straw man. Occasional rhetorical flourish aside, neither Gould nor any other contingency theorist could possibly hold that *all* of evolution is historically contingent. The convergence/contingency debate is clearly a relative significance dispute, and it should be characterized as such.

In addition, we must be clear about two things here. The first relates to the way in which the concept of repeatability is being used in these disputes. Precisely what *degree* of repeatability are we contemplating? McGhee is right that convergent evolution is often indicative of functional constraint. But the key point of contention between convergence proponents and contingency proponents is whether functional constraints transcend the entrenched development of any particular lineage. Some instances of convergence, especially interphyletic and interkingdom convergence, do seem to contradict the Gouldian narrative, while other instances of homoplasy do not (and could even be seen to bolster the Gouldian view). What we need to develop, therefore, is a systematic way of distinguishing between these sorts of cases. Second, we must be clear about the *explanandum*. If we are asking whether there is a high probability that teeth or the fusiform shape or the cambered wing foil would evolve in any given replay of complex multicellular life, then perhaps the amassed evidence of convergence points to an affirmative answer. If we are asking, instead, whether there is a high probability that dolphinoids would evolve in any given replay of complex multicellular life, then the amassed data on convergence is far weaker. Since we only see dolphinoid convergence *within* the vertebrate body plan, this tells us little about the robustness of such outcomes across the whole of complex multicellular life on Earth or as it might evolve on Earth-like worlds. So Gould's claims about the contingent survival and developmental entrenchment of a 'fortunate' subset of actual (and possible) Cambrian body plans are never directly addressed in the book.

A final regrettable aspect of the book is that it fails to connect up with virtually any literature in the philosophy of science, including a sophisticated body of work on biological laws, homology, phylogenetic inference, constraint, evolutionary progress, niche construction, fine-tuning arguments, and so on, all of which would have enriched the theoretical discussion.

In sum, *Convergent Evolution* is a seminal piece of synthetic empirical work that belongs on every biologist's shelf. It falls short, however, when it comes to addressing important philosophical dimensions of the convergent evolution debate. It is only by developing concepts and methods for carving up the vast set of iterated evolutionary events that McGhee and others have admirably compiled that we will understand the full bio-philosophical implications of convergent evolution.

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