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BOOK REVIEW

Convergence, contingency & morphospace

G. R. McGhee: Convergent evolution: limited forms most beautiful. MIT Press, Cambridge, MA, 2011

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Abstract George McGhee's book "Convergent Evolution: limited forms most beautiful" provides an extensive survey of biological convergence. This paper has two main aims. First, it examines the theoretical claims McGhee makes about convergent evolution—specifically criticizing his use of a total morphospace to understand contingency and his assumption that functional constraints are non-contingent. Second, it sketches a group of important conceptual challenges facing researchers interested in convergence.

Keywords Convergence · Contingency · Morphospace · Theoretical morphology

Introduction

All vultures are alike. Morphologically, they have featherless necks and heads for efficient carrion-gorging; they have acidic stomachs which protect from harmful bacteria which breed on putrefied remains; they are large; all have strong, hooked beaks adapted to tearing into carcasses. Behaviorally, they share a gregarious social organization, roosting in trees over night; they also engage in similar soaring behavior when scavenging. All vultures share a 'flying carrion-eater' niche.

These similarities are remarkable from a phylogenetic perspective. 'Vulture' is a paraphyletic clade, picking out (at least) two distinct ancestral groups. The 'old-world' vultures of Europe, Asia and Africa are from family *Accipitridae*, counting hawks and eagles as relatives. Vultures from North and South America are from family *Cathartidae*, most closely (though distantly) related to storks. Although these taxonomic groups are disputed (see Seibold and Helbig 1995; Wink 1995), it is clear

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that the common ancestor of all vultures lived millions of years ago, and lacked a vulture-like phenotype. This is just one example of *convergence*: a phenomenon which, according to George McGhee's book *Convergent Evolution: Limited Forms Most Beautiful* is "…. ubiquitous … in life and … occurs on all levels of evolution, from tiny organic molecules to entire ecosystems of species (xi)".

The repeated independent evolution of similar characteristics is an extremely important and under-investigated phenomenon and for this reason alone McGhee's book deserves attention. Convergence inspired the theory of evolution and often plays a role in informal defenses of it. After all, what else but natural selection could explain two different types of birds evolving into vultures? Moreover, surely convergences have something to tell us about the shape of life. That both stork-like birds and eagle-like birds evolved into vultures points to constraints on what stork-like and eagle-like birds can evolve into. The lack of attention paid to convergence is surprising. The most recent monograph on convergence was Conway-Morris's *Life's Solution*, back in 2003.

Most of McGhee's book (chapters 2 through 6) aims to establish the ubiquity of convergence. They are a long, yet absorbing, list of examples in animals (chapter 2), plants (3), ecosystems (4), developmental and molecular systems (5) and minds (6). Each convergent trait is discussed in reference to particular examples which are plotted in tables, including the taxonomic distribution of the lineages. Although *Convergent Evolution* is not encyclopedic, its rich summary of convergence is an important resource.

In addition to surveying, McGhee makes theoretical progress. Convergence is explained by two kinds of constraint: functional and developmental. Constraint is functional when natural selection restricts forms by shaping them to fulfill particular functions. There are only so many ways to successfully fly, and this restricts the possible morphologies of lineages adapted to that niche. By *developmental* constraint, McGhee refers to the role played by developmental systems in shaping phenotype evolution: "[t]he same forms have been produced by the repeated channeling of evolution along the same developmental trajectory (7)." A lineage's evolution is limited by the potentiality of their developmental system and the demands of natural selection. The ancestors of old-world and new-world vultures, then, shared developmental traits which enabled the evolution of vulture-like characters, and found themselves in selective environments conducive to those evolutionary pathways. Because many lineages have similar developmental systems, and find themselves under similar selective pressures, they converge on similar forms.

In chapters 7 and 8, McGhee discusses the predictability of evolution from the perspective of convergence. He employs the conceptual techniques of theoretical morphology to argue that, with some caveats, evolution is predictable in principle. Throughout the book functional constraint is presented as contingent on physical properties—so long as the world is 'earth-like' insofar as gravity, the atmosphere, and so on is held fixed, there are only so many ways of successfully fulfilling certain functions. It is these non-contingent functional constraints which drive McGhee's arguments for predictability. The thought is something like this: on alien worlds, at least those with similar physical properties as ours, we should expect to find large, winged creatures with bird-like morphology which flock in groups and feast on carrion.

This paper has two aims. First, I ask whether McGhee really has given us reason to see convergence as predictable. Theoretical morphology, at least as it is utilized in the book, does not appear to deliver the theoretical goods required to answer McGhee's question. I do think it has something more restricted to tell us about evolution's contingency. I also argue that the functional constraints McGhee discusses might indeed provide predictability, but that these are a very restricted class of constraints. Most functional constraints are not law-like, and so not predictable in McGhee's sense.

Second, I turn to problems with convergence more generally. Although McGhee is to be applauded for tackling convergence head-on, and for the empirical richness of his book, he underestimates the conceptual and theoretical challenges convergence faces. With this in mind, I summarize what I see as the main issues in this area—not with a disheartening aim, but rather in the hope of demonstrating the fertility and theoretical richness of convergence.

Contingency & convergence

For McGhee, the "… critical question in the analysis of convergent evolution… (251)" concerns evolution's predictability. This harks back to Gould's oft-discussed 'replaying the tape of life' thought experiment (Gould 1989). Gould argued that evolutionary pathways are highly contingent. The survival of lineages depends on chancy factors—which bodyplans from the Cambrian explosion survived; the timing of impact events which cause mass extinctions. Due to this chanciness, we should not expect to see the same history replayed, were we to rewind the tape. McGhee argues that convergence in fact shows that life is predictable. He employs some theoretical machinery for this, and points to certain non-contingent functional constraints. In this section I discuss first that machinery, and second those constraints.

McGhee has done much to develop and popularize the field of *theoretical morphology* (McGhee 1999). Theoretical morphology examines organismic form from the perspective of a 'morphospace'. A morphospace is an n-dimensional space, where each dimension represents some feature of a trait. The morphospace is generated a priori from the dimensions. By comparing the actual distribution of traits with a morphospace, biologists can examine the relationship between possible and actual form. The most well-known morphospaces are Raup's shell-models (Raup 1966). Raup generated a 'shell space' via three dimensions (the translation rate, expansion rate and the distance of the generating curve from the coiling axis). Actual forms were not uniformly distributed across that space, and much possible shell space was empty. This allowed Raup to ask why some shell designs are common and others non-existent.

In the seventh chapter McGhee tackles convergence and contingency via theoretical morphology. Take the morphospace of all possible forms. Subdivide these forms into **a**: those which are *functionally possible* and **b**: those which are *developmentally possible*, given the kind of developmental systems on earth. This gives us a group of interesting subsets. The intersection of **a** and **b** will contain all phenotypes on earth. The set including **b** but excluding **a** are those forms which could evolve on earth, if only they were functionally possible. The most interesting set, for McGhee, includes **a** but excludes **b**, for it is these forms which could evolve on other planets: the domain of alien developmental systems. He wants to know whether the breadth of this set is knowable (Fig. 1).

This is more extreme than Gould's question. Gould asked us to imagine what life might be like *on earth*, if we replayed prior to certain events. McGhee's set has a very different modal profile: he asks what would evolve if there were different 'genesis events'. Gould asks whether vultures would re-evolve as they have if certain events in the past were different, McGhee asks whether we should expect to find vultures on different planets; what life might be like if it were constrained by different developmental straightjackets (see Turner 2011 for an in-depth discussion of contingency in this context).

What does this have to do with convergence? McGhee takes it that the ubiquity of convergence proves that the space intersecting **a** and **b** (the earth-forms) is not infinite. If that is right, then an understanding of the rules governing that space would allow us to hypothetically predict its distribution.

This does not provide any obvious insight to the set b, however. The question of convergence in alternative life-worlds is important, but it is unclear what convergence *on earth* can tell us about that. After all, we have a sample size of one, so the projectibility of any claim is suspect (Sterelny 2005). It is far from obvious how this theoretical morphological approach sheds light on either convergence or life on other planets.

Taking the perspective of all possible forms, as McGhee does, might allow us to frame questions about other life-worlds, but it has important limitations. There is ambiguity about whether the space is theoretical or empirical. A *theoretical* morphospace is constructed a priori, while an empirical morphospace is constructed from data. This difference matters: the modal profile of a theoretical morphospace is more wide-scoped, while an empirical morphospace is grounded in the world.

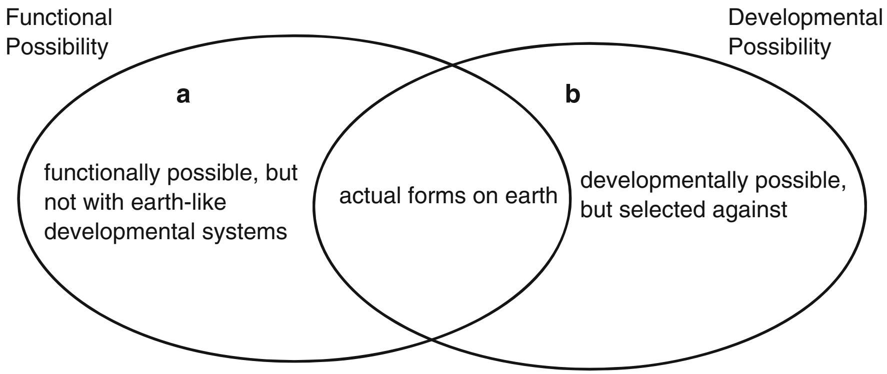

Fig. 1 Constraint in total morphospace

Moreover, a theoretical morphospace, as it relies on the intuitions of the modeler, is open to worries of mind dependence, while empirical morphospaces are worryingly sensitive to the selected data set (Maclaurin 2003).

McGhee's divisions look empirical in many ways, as he refers to convergence (which he has spent over two hundred pages providing examples of) as *telling us* something about the intersection of a and b. It looks like, in principle, we are supposed to construct the intersection by looking at empirical examples. But McGhee treats the intersection as theoretical: if it is to be used to contrast the evolution of lineages on other worlds, then it needs the kind of broad modal profile we gain from theoretical morphospaces.

> The set of existent forms of life on Earth… is a function of the functional constraint boundary and the developmental constraint boundary in the theoretical morphospace (McGhee 2011, 252).

Typically, such theoretical morphospaces are used to frame empirical investigation of the constraints the world imposes on possibility. It was examining the distribution of actual shells against his possibility-space that allowed Raup to theorize about constraints on shell evolution. If actual form is a *function* of the constraints, derived a priori from the dimensions of morphospace, then it cannot provide traction on those constraints. McGhee starts with the reasonable claim that convergence will be explained by a combination of functional and developmental constraint. With a dash of chance, something like this is surely right (although see Sansom 2003 for cautions about 'functional constraint'). However, the perspective of functional morphology does not help here. McGhee's morphospace divides into functional and developmental constraint without any clue as to *how* the divisions occur. Moreover, as the morphospace divisions *assume* that constraint explains convergence, takes the convergences as inputs, it is not clear what explanatory work it can do.

McGhee's morphospace helps us see clearly what we need to know to answer questions about alternative life: what is the nature of the set including a but not intersecting with b? But it does no more than that. Empirical investigations and abstract models of alternative developmental systems give us some insight, and McGhee summarizes these. However, at best the morphospace frames those enquiries.

And so, McGhee's use of morphospace provides some traction on an extreme version of Gould's contingency question. However, it does not seem that it can tell us anything about convergences on Earth, nor does it do more than frame investigations into alternative developmental systems and functional constraints. Having said this, it strikes me that theoretical morphospaces could play an important role in understanding convergence if they were restricted.

We can distinguish between a *local* and *total* morphospace (Maclaurin 2003). A local morphospace is bound by a small set of dimensions and captures a particular segment of life's form. Raup's shells, for instance, is a space of possible shells. Theoretically, Raup's dimensions would also fit into the totality of possible forms along all possible dimensions. Some of McGhee's difficulties arise from use of total morphospace. Perhaps more could be achieved by looking at local morphospaces, concerning themselves with particular morphologies and dimensions. Raup's shell-models provide traction on the functional and developmental constraints on shell evolution, in a quantified and flexible fashion. The approach gives us some grasp on how shells could have evolved differently. It is amenable to explaining *particular* convergences, as developmental and functional constraints can be discerned through a combination of mapping the actual distribution of traits into a local morphospace and empirical investigation. It may be that we could use a local morphospace to track aspects of vulture morphology, providing insight into which developmental and functional factors influenced the convergence.

In such local cases, the space is unambiguously theoretical; it explains particular convergences; and modal traction is provided (admittedly in a more limited form than McGhee might like). I leave this suggestion for further development (McGhee uses a local morphospace to explore questions of predictability in his 2007).

A central aspect of McGhee's views on the predictability of evolution concerns the nature of functional constraint. Throughout the book we are treated to constraints on biological function which appear non-contingent. This is problematic because McGhee does not consider cases of functional constraint which are relative to local selection pressure.

Some biological organization and behavior appears to be derivable from simple mathematical models. Flocking behavior, for instance, can be generated using a relatively small set of rules. It appears that some convergences are then explained by these 'mathematical facts': all lineages which flock, flock similarly in virtue of the nature of self-organizing groups (see Sumpter 2006). Something like this could be true of vulture-circling behavior as well. Other cases of convergence can be explained in relation to architectural, bioengineering, or even physical facts. Presumably the convergent similarities in vulture wing design (increased size for instance) is in part due to aerodynamic constraints. There are only so many ways to successfully design a wing using feathers, and this constrains any design using those materials.

And so for McGhee the space of functional possibility, in contrast to developmental space, is not relative to life as it has evolved on Earth, but rather to planets with similar physical properties as Earth. However, this is extremely problematic.

Consider McGhee's discussion of the set of forms which are developmentally possible but not functional (b excluding the intersection with a):

> Biologists over the ages have studied the many different mutant forms of life – two-headed snakes, three-legged frogs, and so on – that are lethal mutations… Developmental abnormalities like two-headed snakes and frogs with three hind legs instead of two are real and are also non-functional, in that they do not survive in the wild (251).

These cases are included in the set of the developmentally possible, but functionally impossible—they do not flourish on earth due to functional constraints. In virtue of what physical or geometric facts do frogs with extra legs not survive in the wild? They will be less efficient at hopping and will pay energy costs, but these can be mitigated. If there were strong enough sexual selection for three leggedness, the extra leg would be functional insofar as the frog's fitness would increase. The point is, much of what makes something functional in evolutionary terms is *not* physics or geometry, but is *relative to the selective environment*. Some domesticated animals would surely not function in the wild (some need our intervention to breed effectively, for instance), yet the morphological changes we have engendered in them have led to great success. Camouflage and mimicry are only functional in the presence of environments with things to camouflage in and organisms to mimic. The extremely energy expensive running behavior of cheetah is only functional in the context of an environment with fast things to chase. Frequency-dependent cases, such as group selection are highly problematic as their function depends on highly contingent facts about group-organization.

In short, the functional division of morphospace looks as relative as the developmental division, and this makes determining the nature of these sets much more difficult. The set of constraints which it seems McGhee *can* appeal to, those set by physical or geometric 'law', underdetermine form within the set. Yes, only a finite set of wings will successfully fly given some physical constraints, but there is *a lot* of room within that. Without knowing the more fine-grained constraints, the functional set is vague. McGhee's claims of predictability look more likely for constraints which are due to 'physical' facts like aerodynamics, but extremely unlikely for constraints which are due to 'biological' facts. Because of the nature of selection, attempts to find law-like regularities in regards to these facts will fail (c.f Rosenberg 2000). Perhaps the aerodynamic constraints on vultures lets us make some general claims about their wing-designs, and maybe their flocking behavior could be modeled computationally, but convergences like their roosting behavior or the chemical composition of their stomachs are only functional in virtue of biological facts. They are relative, and so not predictable in the sense McGhee desires.

Conceptual problems with convergence

Convergent Evolution is important for bringing together, in an accessible way, a large body of data regarding that phenomenon. It takes an admirably cladistic perspective (something which marred Conway Morris 2003). It also provides some interesting ways of thinking about convergence which, for all my reservation, has promise. There are conceptual problems with convergence which are far from decided, however. I finish by characterizing some of these issues.

Convergence and homology

There are real difficulties involved with pinning down a definition of convergence. McGhee's book, for instance, contains two substantively different accounts.

In the first chapter he provides a *taxic* definition of convergence, contrasting it with *homology*. By this definition, we identify convergent traits phylogenetically. Those traits which were present in the common ancestor of vultures (feathers, for instance) are homologous. Traits not present in their common ancestor (such as baldness) are convergent.

In chapter 7 McGhee provides a morphospatial definition of convergence whereby it occurs when there are overlaps in the space of forms which have drifted from divergent locations: "… when forms originally present in different regions of the morphospace evolve in such a way that they move to the same spatial region in the morphospace (247)." These definitions clash. Parallelisms, cases where traits have evolved independently from similar starting points (see below), count as convergent by the cladistic measure, but are not by the definition of chapter 7.

The taxic definition is extremely important due to its phylogenetic perspective, but is problematic because of homology's messiness. Brigandt and Griffiths (2007), for instance, point to three different concepts of homology. If convergence is supposed to contrast with homology, then homology's ambiguity is a problem.

Hall (2007) argues that homology and convergence ought to be viewed as a single graded concept. The thought behind this is owed to *deep homologies*: developmental switches involved in many apparently convergent traits. If retained developmental systems play lesser or greater roles in the evolution of similar traits, then it is tempting to think of traits as homologous to a lesser or greater extent. McGhee's response to deep homology is to admit an important role for developmental constraints in explaining convergence—another approach is to collapse the two concepts.

Future work on convergence, then, must unpick the relationship between conflicting definitions of convergence, and its relationship to homology.

Epistemic warrant

What are convergences evidence for? What do they give me leave to say? For McGhee, convergences tell us something about the space of possibility of the totality of life on earth. Conway Morris (2003) grants them even greater breadth, using them as evidence for claims about independent geneses of life. Currie (forthcoming) presents a much more restricted picture, claiming that (with certain caveats) convergences can be mustered to support adaptive models.

Everyone agrees convergences are evidence for something, but it is difficult to characterize just what. It seems right to say that the evolution of similar characteristics in new and old world vultures should count as evidence for claims about the adaptive benefits of those traits. However, whether it supports claims about vulture-like creatures on other worlds is doubtful.

Parallelism

In addition to a lack of clarity between convergence and homology, there is also confusion within convergence. Some convergences are *parallel*. A parallelism is supposed to be a special kind of convergence. Parallelisms have been defined as: convergences between closely related taxa; a convergent modification in the same ancestral trait (McGhee's definition); the independent evolution of the same trait from similar starting points; an internally constrained (as opposed to externally constrained) convergence. These definitions cross-cut, and all are problematic.

Those which appeal to close taxonomic relationships appear to be arbitrary. Those which appeal to ancestral traits are in danger of counting all convergences parallel. More sophisticated accounts point to the causal properties of the underlying developmental systems, but there is disagreement about whether we should take the difference as one in degree or kind (see Powell 2007, Currie forthcoming).

However we characterize them, parallelisms are important for McGhee's explanatory project. Parallel convergences owe much of their similarities to underlying homologies (they are probably due to developmental constraint), while non-parallel convergences are more likely to be due to similarities in selective environments. In Currie (forthcoming), parallelisms play an important role in determining epistemic warrant because by restricting ourselves to parallelisms we control for developmental noise in adaptive models. The convergences between old and new-world vultures may be parallel, and this may help us construct adaptive models restricted to particular clades.

A clear definition, and a clear account of parallelism's epistemic role, is still wanted.

Grain/shallowness

Not all vultures are alike. Old-world vultures, like their cousins the hawks, rely almost exclusively on eyesight and have distinctive anatomical features like the raptor's talons. New-world vultures locate food by scent and have a stork-like anatomical structure, including spindly legs. The Egyptian vulture uses tools: breaking open ostrich eggs with stones; new-world vultures keep cool by defecating on their legs; the African 'palm-nut' vulture is not even a scavenger, but is exclusively vegetarian.

It is a philosophical platitude that any two objects are infinitely similar and dissimilar. When discussing similarities like convergences, then, we must tell a story by which those particular similarities are *interesting*. The *grain problem* comes in several forms, the basic idea is the convergent similarities can (1) be generated simply by shifting grain and (2) are uninteresting. By 'uninteresting' I mean that the categories which the convergences point to have little explanatory merit.

Many of McGhee's examples leave me feeling uneasy. In chapter four, for instance, we find statements like:

> … there exist some animals, the carrion-eaters, who have converged on the saprophytic, necrophagous mode of life. The corpse-seeking carrion beetles and hyenas are very different-looking types of animals, one an arthropod and other a mammal, yet they are ecological equivalents (144)

Other examples of convergent ecotypes are "…eating-insects-on-the-wing… (140)" and "… eating wood-boring insects… (142)" I have deep reservations about these categories, especially in light of what McGhee thinks they tell us about prediction, and his claims of ubiquity. They are problematic because they are *coarse-grained* and *shallow*. The convergent similarities between hyenas and necrophagous beetles are at the level of ecological role, and the very heterodox nature of the category calls its projectibility into question. We can perhaps predict that, if there is a steady supply of decaying organic matter, something will evolve to eat it—but what makes that interesting? I also worry that McGhee loads the dice in favor of ubiquity: if all it takes to be convergent is to meet a category that broad and loose, then *of course* there is convergence everywhere.

These worries are not confined to ecological examples, either. Morphological convergence is also disappointingly coarse. McGhee presents three clusters of convergent swimming morphologies: *fusiform* (the standard dolphin/shark design), *eel-shaped* and *paddle-form appendages* (limbs evolved for paddling through the water) (see table 2.1). What kind of predictability or projectibility do we gain from these examples? I might expect, given an aquatic substance, to see animals swimming using designs which make them efficient swimmers. This might be true, but I'm not sure how remarkable it is (or whether I need to examine many cases of convergence to prove it). Moreover, the differences between a sea scorpion, sea turtle, and penguin are enormous—even if they all have paddles. This complaint is not so strong for molecular cases. Here it does look as if a case can be made that, given the sorts of developmental building blocks we are using, there is a relatively limited repertoire of options (although I am not versed enough in this field to make a judgment).

We can challenge the importance of convergent similarities by contrasting the explanatory potency of ancestry and niche. If I know an animal is a scavenger, all I know is that they eat flesh which they have not hunted (but I cannot distinguish between a vulture and a necophagous beetle). If I learn an animal is a bird, I immediately know much about it: it is feathered, bipedal, probably flies, is warm blooded, and lays eggs. On the face of it, homology is much more explanatory than convergence (Griffiths 1994). If convergent similarities do so little explanatory work, why should we be concerned with them?

Moreover, there is empirical reason to think that convergences are 'shallow'. As Griffiths has put it, "It is a truism in comparative biology that similarities due to analogy (shared selective function) are "shallow". The deeper you dig the more things diverge (Griffiths 2007, p. 216)." It is clear that claims about and based upon convergence need to be indexed to a descriptive level, but how to do this, the nature of the problem and the empirical adequacy of the shallowness claim is far from clear.

This presumably lays it on too thick. If anything, McGhee's book shows that there is a lot of convergence out there, and it is important. But we need to be much more careful about how we approach the phenomenon. Unpicking the conceptual issues with convergence would grant access to a wealth of empirical data important for both adaptive explanation and the predictability of life's path.

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