Convergent Evolution: Limited Forms Most Beautiful
by George R McGhee
reviewed by Kevin Padian

George McGhee is a paleobiologist and theoretical morphologist at Rutgers University who has long been interested in general problems in macroevolution, ranging from how organisms occupy space in morphology and in ecosystems to what has allowed certain kinds of organisms to survive mass extinctions. Here he turns his attention to one of the textbook staples of evolutionary biology, the concept of convergent evolution. I like this book for two main reasons. First, it’s a great compendium of information (there are dozens of tables in the book laying out examples of functional and ecological convergence in a huge range of animals, plants, ecosystems, and molecules). Second, it’s well written and a really stimulating read for graduates and undergraduates alike. A whole lot of term papers will find inspiration in this book.

If I were reviewing Convergent Evolution for an audience of paleontologists or other evolutionary biologists, I might take a different tack. But at NCSE, our focus is on evolution education, so my emphasis will be on how we can use this excellent book to teach about a pervasive and sometimes confusing concept. In fact, the concept is not really confusing, and McGhee lays things out very nicely, so the volume works as a great little sourcebook for further study.

To cut to the chase: yes, there is a nice five pages on the evolution of the eye (p 67–71), not only a tabulation of the many groups that have evolved some form of sight, but also a good phylogenetic sense of the progression of eye development and sophistication in various groups, and how these stages have evolved to convergent degrees in different taxa. Bottom line: maybe sixty independent times. The phylogenies have come far enough that our “intelligent design” friends are going to have an increasingly tough time making hay out of this hoary story, if they are honest about the state of research.

Particularly illuminating from the outset is the clarification between parallelism and convergence. Fifty years ago they were distinct if related terms. Parallelism denoted similar changes that evolved in closely related lineages, and convergence denoted the evolution of similar adaptations in very different lineages, often with quite different equipment. With the advent of pattern cladistics in the 1970s, more conservative phylogeneticists decided that anything that was not homologous was convergent, and therefore of no interest in constructing phylogenies (and therefore of no interest). But molecular genetics taught us the deep homology of many traits that showed morphological transformations in monophyletic lineages, and so revealed a stronger base of homology that often underlies the re-emergence of physical traits. The question, therefore, is not whether one can recognize convergence, but what actually is convergent and what is homologous about a given
feature or functional complex. In this way we can return a bit to the distinction between parallelism and convergence that we recognized half a century ago, but with an explanation from genetics of why the distinction is often quite useful. This distinction enriches the questions that we can ask about biology.

To me, a good example of parallelism is the reiteration of live birth in lepidosaurs, a condition that has happened over a hundred times, notably in complexes of very closely related species. There is even considerable work on the ecological factors that bring out this change, and some work on the genetic underpinnings. On the other hand, sometimes apparent parallelism is deceiving. In a case that McGhee does not mention, Michael Nachman, Hopi Hoekstra, and their colleagues have shown that southwestern mice that live on lava flow substrates have independently evolved darker coats that camouflage them from predators. The interesting thing is that different genes are coding for the dark color in different populations: melanin is commonly associated with a structural protein that is “easy” to evolve but can arise from different genetic sources, so here even in populations of the same species we cannot claim parallelism, but convergence.

There are macroevolutionary examples as well. Henry Fairfield Osborn (1857–1935) spent much of his long career working on fossil Proboscidea (elephants and their kin), and he was continually impressed by how often the same kinds of molar and tusk patterns evolved. In the early 1920s he had discerned 19 different parallel lines of proboscidean evolution, a number that grew over the years into the high 20s and finally to 39 distinct lineages! Recent research on the genes that underlie molar patterns, pioneered by Jukka Jernvall and other mammalian developmental paleontologists, are beginning to show how the expression and repression of some genes can account for such parallel patterns in mammal teeth, including the proliferation of these shapes in rodent molars.

The majority of the book comprises discussions of convergence at several levels and in several dimensions. The obvious functional-ecological convergences of structural adaptation are well covered but not belabored, and it is nice to see that both animals and plants are extensively treated. Moreover, it is not just single adaptive traits or ecological roles that are considered, but also roles within communities and comparisons of communities as a whole for their convergent properties. I am more comfortable when McGhee uses the term “ecological role” than when he slips into the use of “niche” (mainly following Eric Pianka), but this is because I was one of the last people to learn at least some ecology from G Evelyn Hutchinson, and so I accept the “niche” as a multi-dimensional trait peculiar to an individual species that another species can never wholly duplicate. McGhee creatively explores Pianka’s suggestion that there might be a “periodic table of niches” (I’d say ecological roles) that evolve repeatedly in communities, and this is one of the most enjoyable parts of the book. Still, as both Pianka and McGhee acknowledge, it can be easy to oversimplify or assume ecological roles for extinct critters that cannot be verified or that are merely showing superficial resemblances. Herbivorous dinosaurs such as duckbilled hadrosaurs have often been compared to ungulates (hoofed mammals), but they probably ate completely different plants, used their environments differently, and walked and fed much differently, to say nothing of their systems of growth and reproduction. Here we get into a perpetual conundrum. We paleobiologists who try to reconstruct physiology and ecology of our long-dead critters often exasperate our colleagues in physiology, ecology, and biomechanics, who spend their lives painstakingly measuring, recording, calculating, and analyzing the least
significant differences among their animals. They are constantly surprised and frustrated by how often their results don’t match their expectations. So, they complain, how can we “wee folk who dwell among the rocks” (as AS Romer called paleontologists) possibly say anything meaningful about animals who are completely extinct? It’s a humbling prospect indeed.

I found myself repeatedly amazed at the compass of McGhee’s study, which includes vertebrates, invertebrates, plants, microbes, individuals, ecosystems, and molecules. It takes an unusually broad and dedicated scholar to pull off a book like this one. And yet (because there is always an “and yet” in academia), I found some points that perplexed me in the treatments of critters with which I have at least a slight familiarity. These do not detract from the book in any important way; most merely involve a particular choice of words or an angle from which to view the problem.

First, the classic comparison of birds, bats and, pterosaurs as flying animals (p 17) works fine, but I have found that students make more sense of the problem if they are asked: what is homologous and what is convergent about these wings? All have homologous bones, muscles, nerves, and skin, and all of these are involved in the flight apparatus to some degree. But the airfoil is differently constructed in all three (bats with skin supported by four fingers, pterosaurs with skin trailing behind the bones of the arm and hyperelongated fourth finger, supported within by a network of collagenous fibrils, and birds with feathers). Feathers are likely homologous at some level (as mostly collagenous epidermal structures) to the hairy coverings found on the wings of bats and (surprisingly) pterosaurs, but they do not serve the same functions. And, of course, the common ancestors of these three groups did not fly, so the evolution of flight is manifestly convergent.

Another passage that needs clarification concerns ratite birds (p 147–154). The consensus based on molecular studies is that ratites (the ostrich, kiwi, cassowary, emu, and so on) are indeed monophyletic, but only if tinamous are included, and traditional “struthioniformes” (ostriches) comprise several paraphyletic basal stems to the group as a whole. Because tinamous are capable of at least weak flight, the loss of flight seems to have evolved several times; but this has no bearing on the monophyly of ratites. I would also suggest that the evolution of high growth rates (and therefore attendant high metabolic rates, often mislabeled “endothermy”) in pterosaurs and dinosaurs does not represent two independent events (p 79–80), but rather a common ancestry of those traits in basal Ornithodira (which we have been able to support by analysis of dinosaurian outgroups). And the paleoecological features of some extinct taxa are listed perhaps too confidently: the size and bizarre morphology of the alvarezsaurid forelimb do not strongly support an interpretation of ant-eating (p 144), which has never been adequately tested, and there is no evidence that the tall dorsal spines of three different dinosaurs in several different groups (and other taxa) supported webbing that somehow was used for thermoregulation (p 78–79). (The immediate relatives of these individual dinosaurs lack such specializations, but show no evidence of different ecological or physiological features.) Still, these ideas are in the literature, and they did not originate with McGhee, so it is reasonable for him to put them out there for further testing.

The final two chapters of the book provide the most food for thought. McGhee considers the role of evolutionary constraint in the production of convergence, and the question of
what has evolved versus what could (and couldn’t) evolve. Given the laws of physics alone, it is inevitable that (for example) swimming vertebrates would converge on a fusiform shape, and that running vertebrates would concentrate their limb muscles proximally, leaving mostly bony and sinewy distal parts. Given the constraints of the geometry of protein folding, only certain configurations can allow these molecules to function, and even slight departures are fatal. So, when Stephen Jay Gould, David Raup, and other paleobiologists have talked about “replaying the tape” of life—as with, for instance, what would have happened if Middle Cambrian chordates had become extinct and no vertebrates had ever evolved—just how different would many of the results have been?

But is there more than one question here? Physics may dictate to some extent what “can” evolve structurally and functionally (and as McGhee notes, there is a tremendous amount of unused morphospace out there). Chemistry may dictate to some extent what biomolecules “can” evolve structurally and functionally, too. So, it is intriguing to consider what would happen if chordates had evolved skeletons based on silica instead of calcium phosphate (recall that silica is the mineral basis of the skeletons of many microorganisms, sponges, and plants). But “replaying the tape” is more a phylogenetic question than an ecological one. To some extent the “what if?” question is a “contingency” one. Rejecting teleology as an evolutionary “goal” (a discussion that McGhee handles masterfully), perhaps it is just luck of the draw that the first chordates didn’t settle on silica for their skeletons. Otherwise we would all have glass jaws.

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