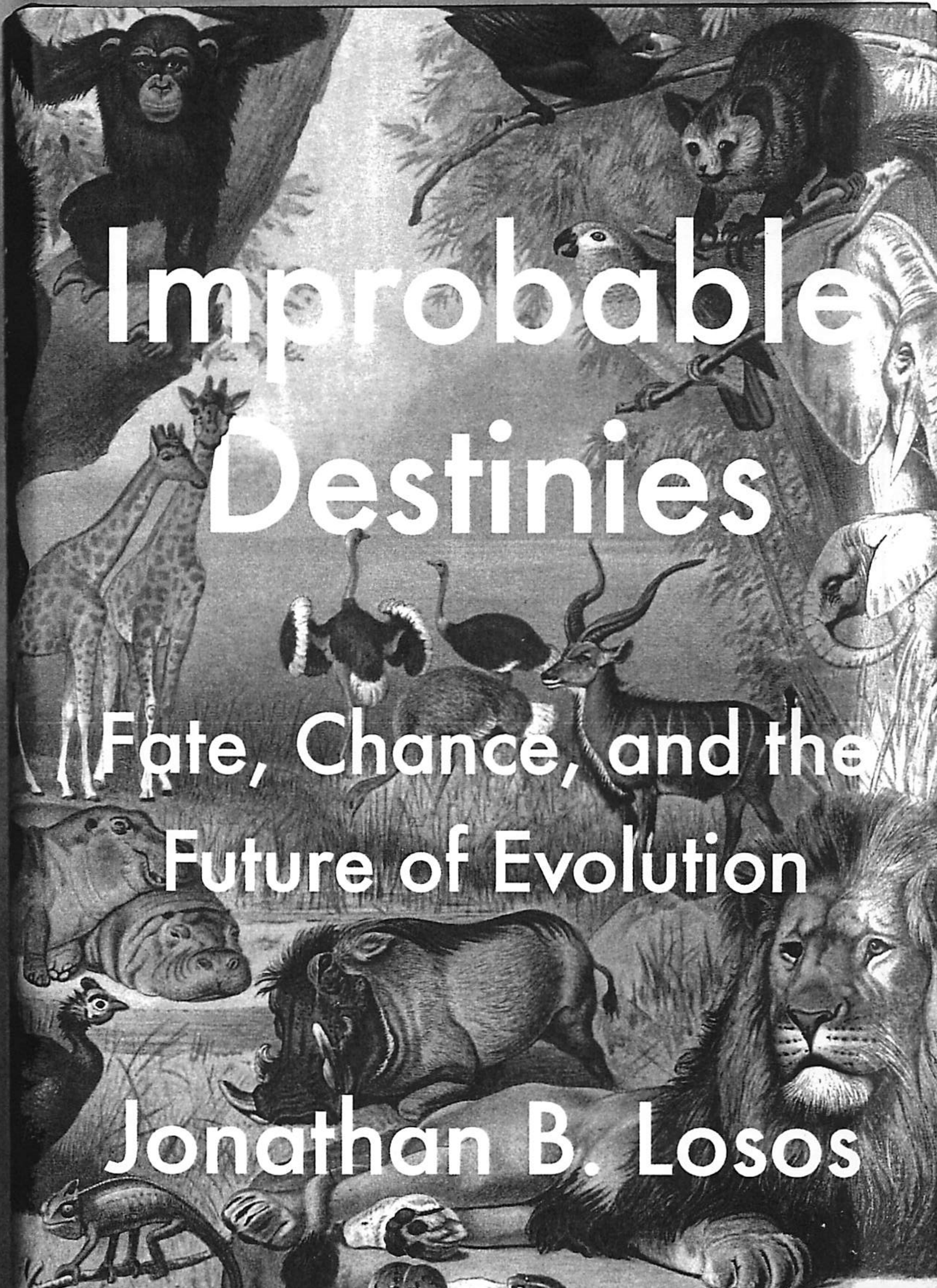

Improbable
Destinies
Fate, Chance, and the
Future of Evolution
Jonathan B. Losos

chapter one

Evolutionary Déjà Vu

Picture a whale swimming through the ocean: streamlined body, flippers, a small fin on the back, its tail undulating up and down. Given this piscine countenance, who could fault the ancient Greeks for thinking whales were a type of fish? That view persisted for millennia until Carl Linnaeus set things straight 250 years ago, recognizing the leviathans as mammals on account of their live birth, mammary glands, and other traits.* The Greeks had been tricked by convergent evolution.

We've come a long way since pre-Linnaean scientists. We certainly know a lot more about evolution than they did, and our enhanced understanding of anatomy and the evolutionary relationships of species has identified countless cases of convergent evolution. Nonetheless, our list is far from complete. As new data from molecular biology floods in, we're discovering time and time again that we've been misled, just as

* We now know that not all mammals give birth to live young. Platypuses and echidnas—grouped together as monotreme mammals—lay eggs. The production of milk and possession of hair are the two most obvious features of all mammals (though some mammals, like whales, have just a few whiskers).

the Greeks were, and that species we thought similar due to inheritance from a common ancestor instead have independently converged upon the same traits.

Let me provide two recent examples. By some measures, sea snakes are among the most deadly serpents, the venom of some species, drop for drop, as lethal as that of any ophidian. Fortunately, most sea snakes rarely bite even when handled. Not so, however, for the beaked sea snake, which defends itself fiercely and accounts globally for ninety percent of sea snake–caused human fatalities. Named for the tip of its snout, which overhangs the lower jaw, the species can be very common locally and has an enormous geographic distribution, from the Gulf of Arabia to Sri Lanka, Southeast Asia, and down to Australia and New Guinea, making it one of the most widely distributed snake species in the world.

Or so it was thought. In 2013, a team of Sri Lankan, Indonesian, and Australian scientists reported that they had conducted routine genetic comparisons among populations of the species and had gotten a most decidedly non-routine result. Even though the populations exhibit only minor anatomical differences across the species' range, they were highly divergent genetically. In particular, Australian populations of the beaked sea snake were most genetically similar to other Australian sea snake species rather than to Asian populations of their own species; similarly, Asian beaked snake populations allied most closely with other Asian species. In other words, there is not one species of beaked sea snake, but two. And the traits that define the species, not only its beak, coloration, and general appearance, but also its nasty disposition, have evolved convergently, so much so that distant relatives on opposite sides of the Indian Ocean were considered to be members of the same species.

And now for an example more familiar to those who have never seen a sea snake. As a lad, I was pure of mind and body, late to take up

the joys of stimulants and debauchery. One day early in my adulthood, I was visiting with a friend. She offered me some tea. I was not a tea drinker, but I wanted to appear worldly and agreeable, so I accepted. Soon, I began to feel funny. My body was tingling, my hands shaking, my heart racing. I thought I might be having a heart attack. But, I reasoned, I was too young for that, plus coronaries weren't supposed to be so energizing. I can't remember exactly how I coolly queried my host, no doubt suavely admitting that I felt a little bit unusual, but she quickly explained that I was drinking a particularly invigorating brand of tea, the closest thing back then to Red Bull. Now as an adult, I get going in the morning with a cup of java, but I religiously avoid the stuff after four in the afternoon. Coffee any later than that and I'll be up all night.

Maybe you're different, but for me, life seems to involve continually relearning the same lessons. And so there I was, one recent night in the Pantanal of Brazil, tossing and turning, unable to drift off despite a hard day and a heavy meal. "Why can't I sleep?" I wondered, as my mind raced from one thought to the next. And then an epiphany. That unfamiliar, fruity soft drink at dinner. I was thirsty and had two cans. It was fizzy and vaguely tasted like apple juice. What was it?

Some quick-fingered sleuthing on the keyboard tracked down the name of the soda, Guaraná Antarctica, and what it is made from, the guaraná plant, a large-leafed climbing plant in the maple family that hails from the Amazon rainforest. And guess what guaraná seeds are loaded with. The same compound that is in coffee and tea, Pepsi and Mountain Dew, and the chocolate in Hostess Ding Dongs. A purine alkaloid, the chemical 1,3,7-trimethylpurine-2,6-dione. Molecular formula: $C_8H_{10}N_4O_2$.

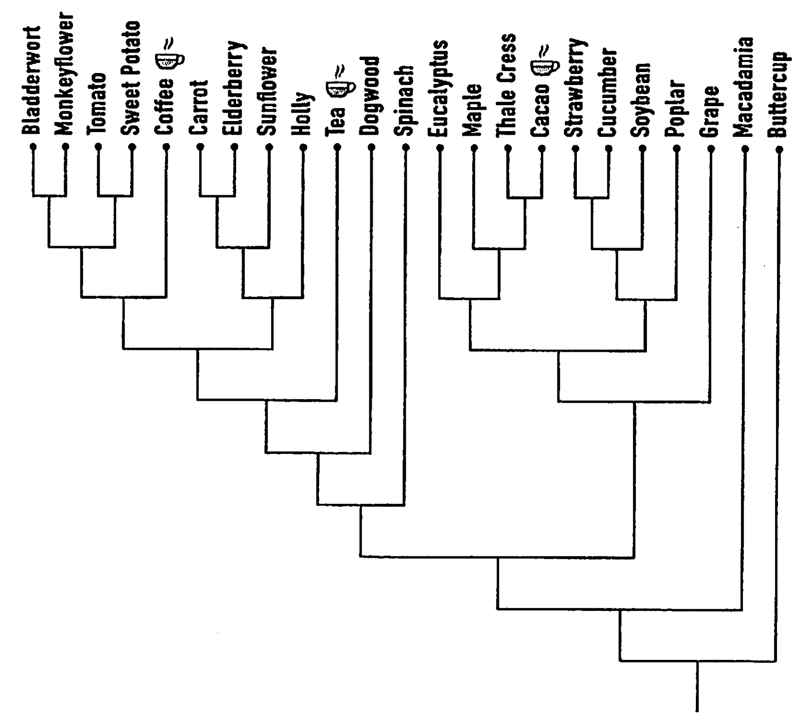
Caffeine.

Despite my awareness of its many delivery vehicles (Pepsi, tea, energy drinks), I had never given much thought to where the caffeine itself comes from. Coffee and tea come from eponymous plants; cola sodas, at least originally, came from the nut of the kola tree; chocolate from cacao; Guaraná Antarctica from the seeds of the guaraná plant (twice as caffeine-laden as coffee beans). All of these plants produce caffeine. And not different varieties, but the exact same molecule. Caffeine is caffeine, regardless of where it comes from. One molecule, many sources.

Because I'm an evolutionary biologist, my curiosity should have been piqued by the many different plants that produce caffeine, stimulating me to wonder whether these plants are all closely related or whether caffeine production has evolved convergently many times. But I was asleep on the job and the thought never occurred to me.

Fortunately, some more inquisitive botanists decided to investigate just this question. In a paper published in 2014, an international team of researchers used genetic data in a two-pronged approach to demonstrate that caffeine production has evolved independently in these plants. Prong one compared the DNA of many plant species to build an evolutionary tree of relationships among the caffeinaceous species (focusing only on three: coffee, tea, and cacao). Such evolutionary trees—"phylogeny" is the technical term—are like family genealogies. Closely related species occur near each other and can trace their ancestry to a recent common ancestor, just as brothers and sisters trace their lineage a short distance back to their parents. Distant relatives, like fourth cousins twice removed, occur on relatively distant branches of the phylogeny, and you have to work your way deeper down in the tree—further back in evolutionary time—to find their most recent common ancestor.

The team's phylogeny showed that coffee, tea, and cacao plants occur on different branches of the evolutionary tree—they are not closely related to each other. Rather, cacao is more closely related to maple and eucalyptus trees than it is to either tea or coffee. Similarly, coffee is de-



A phylogeny illustrating the evolutionary relationships of selected eudicot plants (plants with a specific type of pollen, constituting more than half of all plant species). Species that share a common ancestor are more closely related to each other than to species not descended from that ancestor. The steaming mugs represent species that produce caffeine. Because these three species are not closely related, the most likely interpretation is that caffeine evolved independently in each of the groups (an alternative possibility is that caffeine production was the ancestral state and was independently lost many, many times, but that scenario requires many more evolutionary changes and thus is less likely).

scended from an ancestor that also gave rise to potatoes and tomatoes, but not tea or cacao. Tea is on its own evolutionary branch, distant from all the other species in the study. Put another way, we have to go deep in the phylogeny, way back in evolutionary time, to find the ancestor that gave rise to tea, cacao, and coffee.

The fact that caffeine-producing species are not closely related indicates that the ability to make caffeine most likely evolved independently in the three types of plants. But the researchers dug deeper to test their caffeine convergence hypothesis by examining how the ability to produce caffeine has evolved. If species have independently evolved the ability to synthesize caffeine, then the actual biochemical way they do so may not be the same and examination of the DNA may reveal different routes to the same end. Conversely, if the species have inherited their caffeine-production abilities from their common ancestor, then we would expect them to make caffeine in the same way.

Caffeine is produced by transforming a precursor molecule called xanthosine into caffeine. This is accomplished by enzymes termed N-methyltransferases (for short, NMTs) that sequentially snip off parts of the xanthosine molecule and then add new bits. There are many types of NMTs in plants and they serve a variety of functions, so they did not originally evolve to produce caffeine. Rather, the evolution of caffeine-production capability resulted from evolutionary change in these pre-existing enzymes, altering them to transform xanthosine to caffeine.

By examining the genome of the different species, the researchers isolated the DNA of the different NMTs and discovered that the NMTs that were modified in coffee were different from the ones modified in tea and cacao. Thus, the evolutionary routes to caffeine production were different—convergence occurred through different evolutionary paths.

EVOLUTIONARY BIOLOGY is unlike many sciences in that its basic findings about the history of life cannot be derived from first principles. It is not a deductive science. You can't go to the chalkboard and derive the formula for a platypus. Rather, it is an inductive science in which general principles emerge from the accumulation of many case studies. These piles of research allow us to distinguish what occurs regularly from what happens only rarely. Put another way, evolution occurs in many different ways—just about anything plausible you can imagine has evolved somewhere at some time in some species. Given enough time, even the improbable will occur eventually. As the mathematician Ian Malcolm said in *Jurassic Park*, "Life finds a way." Thus, to understand the major patterns in the evolution of life, we ask not "What can happen?" but "What usually happens?"

And so it is with evolutionary convergence. The standard wisdom is that convergent evolution happens, but is not necessarily the expectation. Scientific papers routinely use words like "stunning," "striking," and "unexpected" to report its occurrence. News stories echo this sentiment, treating the publication of each additional example as if it were amazing and unanticipated.

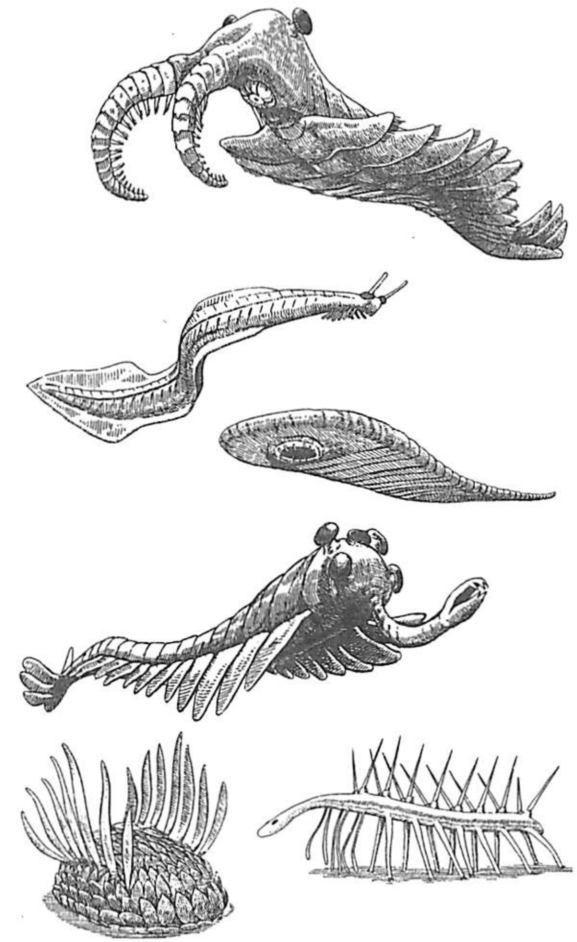
But all that is changing. In recent years, a cadre of scientists has taken the opposite view, arguing that convergence *is* the expectation, that it is pervasive, and that we should not be surprised to discover that multiple species, often distantly related, have evolved the same feature to adapt to similar environmental circumstances. From this perceived ubiquity, the scientists draw a broader conclusion: evolution is deterministic, driven by natural selection to repeatedly evolve the same adaptive solutions to problems posed by the environment. In this view, the contingencies of history play a minor role, their effects erased by the predictable push of natural selection.

AT THE FOREFRONT of this movement has been Simon Conway Morris. Mild-mannered and self-deprecating, the University of Cambridge paleontologist doesn't seem like the sort to rock the boat. But under this unassuming exterior lies a sharp-witted pugilist who has spearheaded a radical reconsideration of the role of replication in the evolutionary pageant.

That Conway Morris should be an evangelist for convergent evolution and a fierce critic of Stephen Jay Gould might at first be surprising. As a young whippersnapper at the University of Cambridge, he made a name for himself with his doctoral research on the bizarre animals of the fabled Burgess Shale geological formation of the Canadian Rockies. But that research focused on a phenomenon that was seemingly the antithesis of convergent evolution.

The Burgess Shale formed around 511 million years ago, during the Cambrian period, when animal life as we know it was just emerging. Before then, life-forms were simpler, usually more or less flat, and unfamiliar. How life transitioned from this alien world to the ancestors of today is still debated, but it happened quickly and prolifically, giving rise to the Cambrian Explosion, when most of life's familiar kinds of animals—mollusks, echinoderms, crustaceans, vertebrates—first appeared in the fossil record in a geologically short period of time.

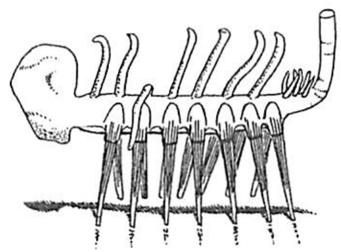
But it wasn't just the ancestors of today's fauna that appeared then. When the Burgess Shale fossils were first discovered in the early twentieth century by Charles Walcott, a paleontologist who was at that time the director of the Smithsonian Institution, they were all identified as belonging to well-known taxonomic groups—mollusks, crustaceans, worms, and so on. But when Conway Morris went back to reexamine the specimens a half century later, he found that many of these Cambrian species were paleontological weirdos, with no clear affinity to any recognized taxon (a taxon is an evolutionary group, such as fish or mollusks; multiple groups are taxa; the word "taxon" can apply to any evolutionary level, from species or genus to kingdom). Walcott, perhaps too distracted by administrative responsibilities or simply too narrow-minded to see them for what they were, had pigeonholed many of the Burgess Shale fossils into existing taxonomic categories despite their many oddities.



A sampling of the occupants of the Burgess Shale ecosystem 511 million years ago. From top to bottom: Anomalocaris, Pikaia, Odontogriphus, Opabinia, Wiwaxia *(left), and* Hallucigenia *(right).*

The term "weirdo" is not standard scientific parlance, but it gives a good sense of how peculiar they are. This realization came to Conway Morris as he painstakingly examined the tens of thousands of specimens collected by Walcott and residing in the musty drawers of the Smithsonian and other museums. Consider, for example, *Wiwaxia*, which looks like a pinecone lying on its side, lacquered in overlapping, oval-shaped plates. Add a flat bottom like a snail to glide along the seafloor and two rows of tall pointy spikes running down its back and you've got an animal similar to something out of a *Futurama* episode.

And then there's the creature Conway Morris christened *Hallucigenia*, referring "to the bizarre and dream-like appearance of the animal." "Cartoonish" is the word that comes to my mind. Conway Morris' reconstruction shows it to be a long, pencil-like tube with an ill-defined blob of a head at one end and a short, upturned, Scottish-terrier-style tail at the other. The tube body is festooned with seven pairs of pointy, unjointed stilts for legs, matched above by seven soft, squiggly tubes running down the back. At the back end, two rows of three short tubes sit side by side on the tail (assuming that part was the tail—Conway Morris admitted the possibility that he had the direction of the animal reversed such that what he thought was the head was actually the tail and vice versa—in his defense, the fossil was squashed flat and not of the highest quality).* In the paper announcing the species, Conway Morris put it simply, *Hallucigenia* "cannot readily be compared to any living or fossil animal."



Simon Conway Morris' original reconstruction of Hallucigenia

And these were not the only oddities—indeed, the Burgess Shale was inhabited by a veritable bestiary of the bizarre: *Opabinia*, whose five eyes and long, claw-tipped hose on the front of its head provoked an audience of scientists to burst into laughter when it was unveiled for the first time; *Anomalocaris*, various parts of which were originally described as three different species until scientists realized they were all part of the same animal; *Odontogriphus*, a long, flat, soft animal that resembled a floating Band-Aid with a circular mouth on the underside of the front end. And the list goes on and on.

* Thanks to new, better-preserved specimens, we now know that Conway Morris, through no fault of his own, reconstructed *Hallucigenia* upside down and backward. Those stilt-like legs were actually spines on the back, and the seven squiggly tubes on top were actually the legs, the second row of seven legs not detectable in the fossils he examined. In addition, better-preserved fossils showed the tail end to be the head and vice versa.

Stephen Jay Gould made the Burgess Shale oddballs famous in *Wonderful Life*. Subtitled *The Burgess Shale and the Nature of History*, the book was a detailed examination of the Burgess fossils and what they can tell us about evolution. And *Wiwaxia* and company weren't the only ones Gould made famous: the primary scientific hero of the book was none other than Simon Conway Morris, who had done so much to document how the Burgess Shale fauna was populated by so many unique life-forms so unlike anything previously known (Gould also lauded Conway Morris' doctoral advisor, Harry Whittington, and his fellow graduate student, now Yale professor, Derek Briggs).

In *Wonderful Life*, Gould dwelled on the outlandish anatomy of the Burgess Shale's inhabitants, arguing that the Cambrian fauna was the most diverse in Earth's history, pointing out the many anatomical forms that appeared and subsequently disappeared, nothing like them ever to be seen again. Gould speculated about why some of those ancient beasts survived and prospered, giving rise to today's diversity, while others perished. Were the survivors superior in some sense, destined to thrive, while the losers had evolved an inferior design? Or was it a matter of luck that some made it and others didn't? Gould concluded that there was no reason to believe that the survivors were necessarily adaptively superior to those that perished. Rather, it was happenstance, a lottery, that led some to survive and others to disappear. If life's narrative had been a little bit different, the tape replayed in a slightly different manner, he suggested, the world likely would be populated by a very different roster today.

Gould concluded *Wonderful Life* by focusing on one fossil in particular. *Pikaia* was a small animal that looked somewhat like a worm squished in a vise, vertically flattened and with no distinct head. This unprepossessing creature was the earliest known representative of the chordates, the evolutionary group containing vertebrate animals (that is, those with a backbone, like frogs, sharks, gorillas, and you and me).

In all respects, *Pikaia* was not a major Burgess player. Judged by the number of fossils discovered, it wasn't very abundant, and its size and shape were not very impressive. Amidst the great variety of species present then, a Cambrian observer would have been unlikely to pick out this species as a herald of great things to come. What if it was only a matter of luck that *Pikaia* survived while so many others died off? Replay the tape again, and *Pikaia* might not have made it. And if *Pikaia*'s line had perished, who would be ruling the world today? Not chordates, because we wouldn't be here.*

The argument for contingency was fashioned by Gould, but his lines of evidence, even some of his major supporting arguments, were pulled straight from the pages of Conway Morris' papers, as Gould repeatedly, exaltingly, emphasized.† Gould even suggested that for their accomplishments, Conway Morris and his two collaborators deserved a Nobel Prize in paleontology—if only there were such a thing.

But something funny happened on the way to Stockholm. Conway Morris, who had so emphasized the distinctiveness of so many of these fossils, came to see the world in a different light. Rather than dwelling

* Although still good for rhetorical effect, Gould's argument is diminished today by the fact that several other chordates have been discovered from the Burgess Shale and other similarly aged deposits. Consequently, even if *Pikaia* had perished, the entire chordate lineage would not have gone with it.

† For example, Conway Morris wrote, "If the clock was turned back so metazoan diversification was allowed to re-run across the Precambrian-Cambrian boundary, it seems possible that the successful bodyplans emerging from this initial burst of evolution may have included wiwaxiids rather than molluscs." And "a hypothetical observer in the Cambrian would presumably have had no means of predicting which of the early metazoans were destined for phylogenetic success as established bodyplans and which were doomed to extinction."

on the evolutionary uniqueness of so much of its fauna, Conway Morris concluded *The Crucible of Creation*, his own book about the Burgess Shale published in 1998, with a discussion of the importance and ubiquity of evolutionary convergence.

At face value, this reading of the rock record seems illogical—how do you go from celebrating the diversity of idiosyncratic, never-again-seen anatomies to seeing evidence for evolutionary replication everywhere? Conway Morris himself isn't sure, as he told me several years ago over lunch at St. John's College in Cambridge.

To some extent, he said, the explanation lies in new discoveries in the nearly three decades since *Wonderful Life*. Whereas a lot of the Burgess Shale species previously could not be associated with any known taxonomic group, newly unearthed fossils and detailed examinations have shown that many can now be assigned to recognized taxa. *Hallucigenia*, for example, appears to be related to modern-day velvet worms, an obscure, mostly tropical group of small animals that look like a cross between a centipede and a caterpillar; *Wiwaxia* is now thought by many to be related to mollusks.

So many of the Burgess Shale eccentrics are not so taxonomically iconoclastic after all. In addition, some analyses have compared the anatomical diversity of the Burgess Shale fossils to their modern counterparts, and have concluded—though this point is hotly contested—that the Burgess Shale fauna was no more diverse than living species are today.

These findings force a reconsideration of the Burgess Shale. Gould, following Conway Morris and his colleagues, had painted the Cambrian as a time of unparalleled anatomical diversity, occupied by a tremendous number of different types of organisms, most of which died out shortly thereafter. Ever since then, argued Gould, we have lived with a much-restricted range of anatomical design, all descended from the relatively few types that survived past the Cambrian.

Most researchers consider that the tide has turned on this viewpoint. The anatomical disparity was not so exceptional in the Cambrian, and the many forms that lived then do not represent failed evolutionary experiments that left no descendants today, but rather early relatives of today's surviving groups. Indeed, this was the thesis of Conway Morris' book, which in many respects was a sharply worded rejoinder to *Wonderful Life.*

Still, it's not clear why Conway Morris went from detailing Cambrian curiosities to cataloging convergence. The rescue of the Burgess species from taxonomic no-man's-land doesn't lessen their anatomical distinctiveness. Even if *Hallucigenia* is in the velvet worm lineage, for example, it is still anatomically unlike anything else that has ever evolved—these clarified phylogenetic relationships don't really make a case for convergent evolution.

One possible explanation for Conway Morris' about-face is that he was influenced by the direction the field was taking. In the mid-1980s, evolutionary biologists were increasingly employing the "comparative method," the idea that by comparing different taxa and looking for repeated patterns, one can find evidence for the operation of natural selection. Although this work was far from Conway Morris' research area, perhaps this emphasis on the importance of convergence shaped his thinking (although nothing he has said or written suggests this possibility).

We could also try our hand at psychoanalysis. Many are surprised at how critical Conway Morris has been of Gould, particularly given Gould's lionizing treatment of Conway Morris in *Wonderful Life.* One colleague proposed that Gould's views on the haphazard nature of evolution conflicted with Conway Morris' spiritual views. Another suggested that Conway Morris was embarrassed that Gould had publicly—in a best-seller!—trumpeted Conway Morris' earlier taxonomic views that subsequently had turned out to be mistaken. Whatever the cause of

his antipathy, Conway Morris may have been primed to find ways to oppose Gould. In our conversation, Conway Morris recalled reading *Bully for Brontosaurus*, a collection of Gould's essays, and noting a number of cases of convergence that Gould failed to remark upon. Perhaps this was all it took to get Conway Morris thinking about convergence's evolutionary significance.

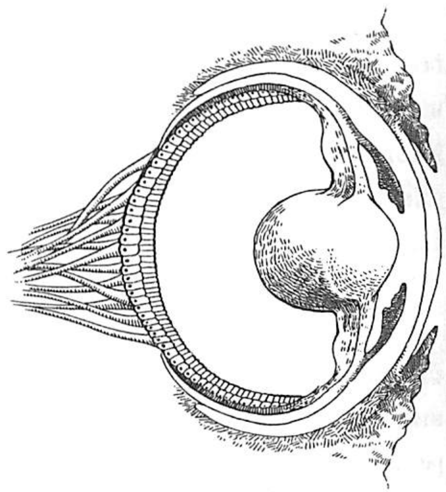
In any case, with the enthusiasm of a convert, Conway Morris has become the leading proponent of the view that convergent evolution is the dominant story behind life's diversity. "Evolutionary convergence is completely ubiquitous," he has said. "Wherever you look you see it." Consequently, he concludes, "Rerun the tape of life as often as you like, and the end result will be much the same."

UBIQUITY IS IN the eye of the beholder, but it would be hard to argue that convergence isn't common. In some cases, two species have independently evolved to be similar in one respect, such as the length of their tail, the color of their ears, the structure of their kidneys, even their mating dance. In more dramatic cases, species can be convergent in many different aspects of their phenotype, so much so that the two may appear to be indistinguishable, such as the two species of beaked sea snakes (the term "phenotype" refers to all the characteristics of an organism, everything from external anatomy to physiology to behavior).

Let's start by examining a few of the many different types of phenotypic traits that have evolved convergently. In recent years, scientists have identified convergence in almost any type of trait you might imagine. For example, many types of lizards have independently evolved flaps of skin under their necks that can be pulled out quickly like a semaphore to signal to mates or competitors; similarly, many birds have evolved colorful patches on their wings or breasts that are displayed prominently in social interactions. The natural world is full of examples of this sort: similar features, used in similar contexts, evolving multiple times in similar types of plants and animals.

Particularly impressive are traits that are convergent at an exquisitely detailed level, between species not at all closely related, from different parts of the tree of life. Here's a classic example: check out the eyeball pictured below.

If you remember your anatomy from whenever you learned it in school, that's a pretty typical peeper: could be a cow, or a human, or a cat, or even a lizard—the eyeballs of most vertebrates are pretty similar in basic structure. But that's no vertebrate's orb—that one belongs to an octopus! That's right—octopuses have eyeballs that are nearly identical to yours and mine, even though our most recent shared ancestor, which swam the Earth more than 550 million years ago, had no eyes to speak of.*



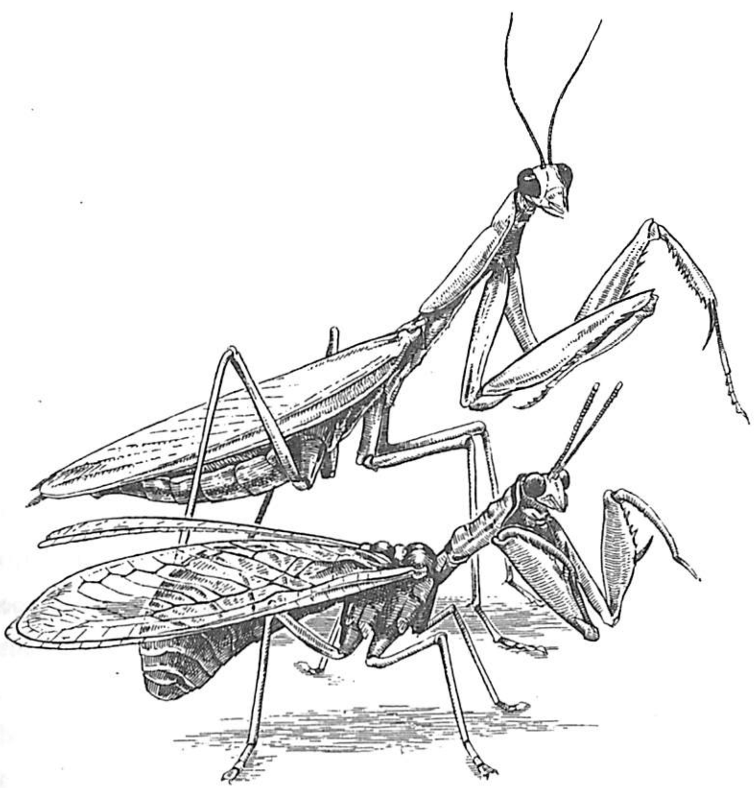
Octopus eyeball

Or how about this one? Everyone knows praying mantises: big bug eyes, long neck, arms folded in prayer. But they're not actually as de-

* In fact, in some ways the octopus eyeball is better than yours or mine. In vertebrate eyes, the nerves attach to the front end of each of the retina's photoreceptors within the eye itself, meaning not only that light has to pass through the nerves to get to the receptors, but also that when the nerves bundle together to exit the eyeball, they create a photoreceptor-free area in the retina, creating our famous blind spot. By contrast, the design of the octopus eyeball is much more sensible, with the nerves attached to the back end of the photoreceptors, where they neither impede incoming light nor cause a visual obstruction when they exit out of the back of the eyeball. If, in fact, evolution did not occur and life was created by an intelligent designer, that designer apparently practiced on us before creating the better-designed eye of the octopus.

vout as they appear—their supplicating posture in reality is a mousetrap primed to fire, its lightning-quick strike snagging prey between its spine-encrusted forearm segments (as if we could catch lunch by quickly rotating our hands downward, pinning something between the palm of our hands and our forearms . . . if our palms were covered with spines and half as long as our forearms).

But mantises aren't the only quick-draw artists in town. There's another type of insect called a mantidfly, which has nearly identical forearms for capturing prey with the same Superman-fast action. And the similarity doesn't end there—the mantidfly's long neck and bulging



Praying mantis (top) and mantidfly (bottom) eyes are so similar that its front half is a virtual mantis carbon copy, even though the two insects are separated by hundreds of millions of years of insect evolution (by contrast, the back half of the mantidfly looks more like that of its close relative, the lacewing).

Convergent evolution isn't limited to anatomy, of course. Species can converge in any attribute of their biology, from genes to behavior. There are many such examples, but some of my favorites come from the lowly ants and termites.

Most people assume that ants and termites must be closely related because you call the exterminator if you have a problem with either one, and also because they look alike. But if you pull out a magnifying glass for a closer look, you'll discover that, other than being standard insects with a head, a thorax, an abdomen, and six legs, they really don't look very similar at all. They also aren't at all closely related. Ants' nearest kin are wasps and bees; termites belong to—of all things—the cockroach family.

Despite their phylogenetic distance, the social structure of ants and termites is remarkably similar. Ant societies are characterized by a sophisticated division of labor: a queen (or sometimes queens) that lays countless thousands of eggs; tiny males whose only purpose in life is to mate with virgin queens; and a variety of worker types, all female, each with bodies well-tuned to the job they perform—caring for young, fighting off intruders, collecting food, and so on.

The social structure of termites is very similar. Termites, too, live in colonies numbering dozens to millions of individuals. As with ants, one or a few females do all the egg laying and a variety of worker types perform the main tasks necessary for colony maintenance. Both ants and termites use liquid food passed from one individual to another to regulate the type of worker a developing female becomes, and both communicate through the use of chemical signals, called pheromones;

for example, pheromone trails are laid down to lead foragers to food and to recruit soldiers to battle.

Among the most amazing convergences between termites and ants (and also, in this case, some beetles) is the construction of underground fungus gardens. These insects invented agriculture tens of millions of years before we did! Although there are some differences between the farming practices of these different insects, the general plan is pretty much the same. Underground in a termite mound or ant nest, the insects bring in and plant fungus that is allowed to grow and then is harvested and eaten. The ant and termite workers carefully tend the garden, removing waste products, controlling pests, and eliminating other competing fungi species (they specialize on a particular fungal crop, treating the others as weeds). They even use antibiotics grown from bacteria housed in specialized regions on their body or in their guts to combat invading bacterial pests (ants use the same bacteria that we have used to produce the antibiotic streptomycin).

As this brief collection of examples suggests, convergent traits abound in the natural world. But it wasn't until 2003 that Conway Morris proposed that convergence is the dominant pattern in the biological world, rather than just a curiosity. His magnum opus, *Life's Solution: Inevitable Humans in a Lonely Universe*, offered 332 pages (plus 115 pages of endnotes) chockful of an extraordinary diversity of case studies of convergence from throughout life's expanse. Eight years later, George McGhee wrote a similar book, *Convergent Evolution: Limited Forms Most Beautiful*, slimmer than Conway Morris' book at 277 pages, but, if anything, even more jam-packed with examples. Even as I was drafting this chapter in 2015, a third tome appeared, Conway Morris' second offering, *The Runes of Evolution: How the Universe Became Self-Aware*, with another 303 pages of mostly new examples (and 158 pages of endnotes).

The net effect of these books is to overwhelm the reader with the breadth, depth, and sheer commonness of convergent evolution. It's everywhere! Think of just about any trait, and it's evolved multiple times, sometimes in distantly related organisms. Says Conway Morris, "Show me anything which has only evolved once and I'll . . . jump up and say 'no, I can give you another example.'"

For instance, McGhee notes that animals have evolved a variety of types of body armor to ward off predators. Turtles wear an impregnable fortress into which they retreat at times of duress, and functionally similar castles of bone evolved in a type of dinosaur (*Ankylosaurus*) and glyptodonts, a Volkswagen-sized extinct armadillo. Instead of a covering of bone, some animals enwrap themselves in sharp spines for defense. I've already mentioned the two independently derived types of porcupines; their approach is mirrored by echidnas (the only other egg-laying mammals beside the platypus, sometimes called "spiny anteaters"), hedgehogs, and hedgehog tenrecs from Madagascar, the latter two so similar in appearance that Richard Dawkins wondered why he even bothered to commission separate drawings for his book *Climbing Mount Improbable.*

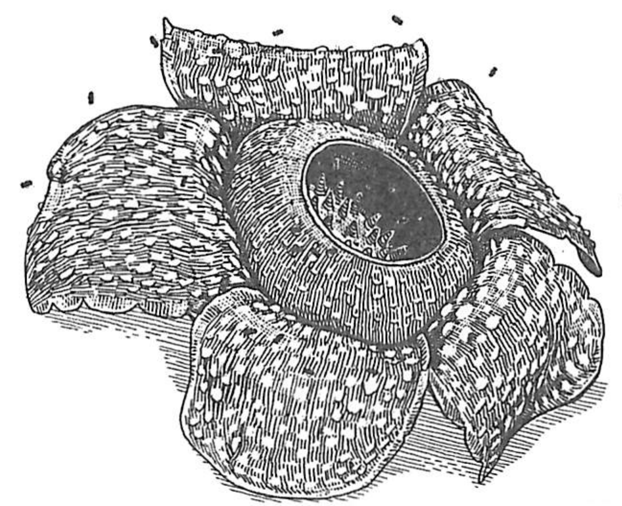
Finally, although we think of armor as a physical defense to deter predators, noxious toxins in the skin can serve the same purpose. Such chemical defenses have evolved in nudibranchs (a type of marine mollusk akin to slugs); many types of beetles, butterflies, and other insects; pufferfish; frogs; salamanders; and a type of bird, the hooded pitohui, among many others.

Similarly, we mammals may be proud of our ability to give birth to live young (platypus and echidna excepted), but McGhee reports that live birth has evolved more than one hundred times in just lizards and snakes, not to mention repeatedly in fish, amphibians, sea stars, insects, and many other groups. Convergence extends even to the placenta—the structure that transmits oxygen and nutrients from mother to

embryo—which has evolved many times in both fish and lizards; in fact, the placenta of one lizard species is strikingly similar to that of some mammals.

And convergence isn't limited to the animal kingdom. To cite just one botanical example from McGhee's book, many plants rely on animals to transport their pollen from donor to recipient (pollen is the plant equivalent of sperm). To do so, the plants need to attract their pollinators. In the case of hummingbirds, bright red apparently is irresistible. As a result, at least eighteen different types of hummingbird-pollinated plants have evolved bright red flowers.

Other plants, mostly in the Old World, have taken a different approach to procuring pollination services. Some species of flies and beetles lay their eggs in decomposing carcasses, and a number of plants—the corpse lily, the carrion flower, the Zulu giant carrion plant, among others—produce an odor that smells like rotting meat. The insects are fooled and come poking around looking for a site to lay their eggs,



The corpse flower from Sumatra and Borneo is the largest flower in the world (yes, those are petals!). It attracts insects by emitting a smell similar to decaying flesh.

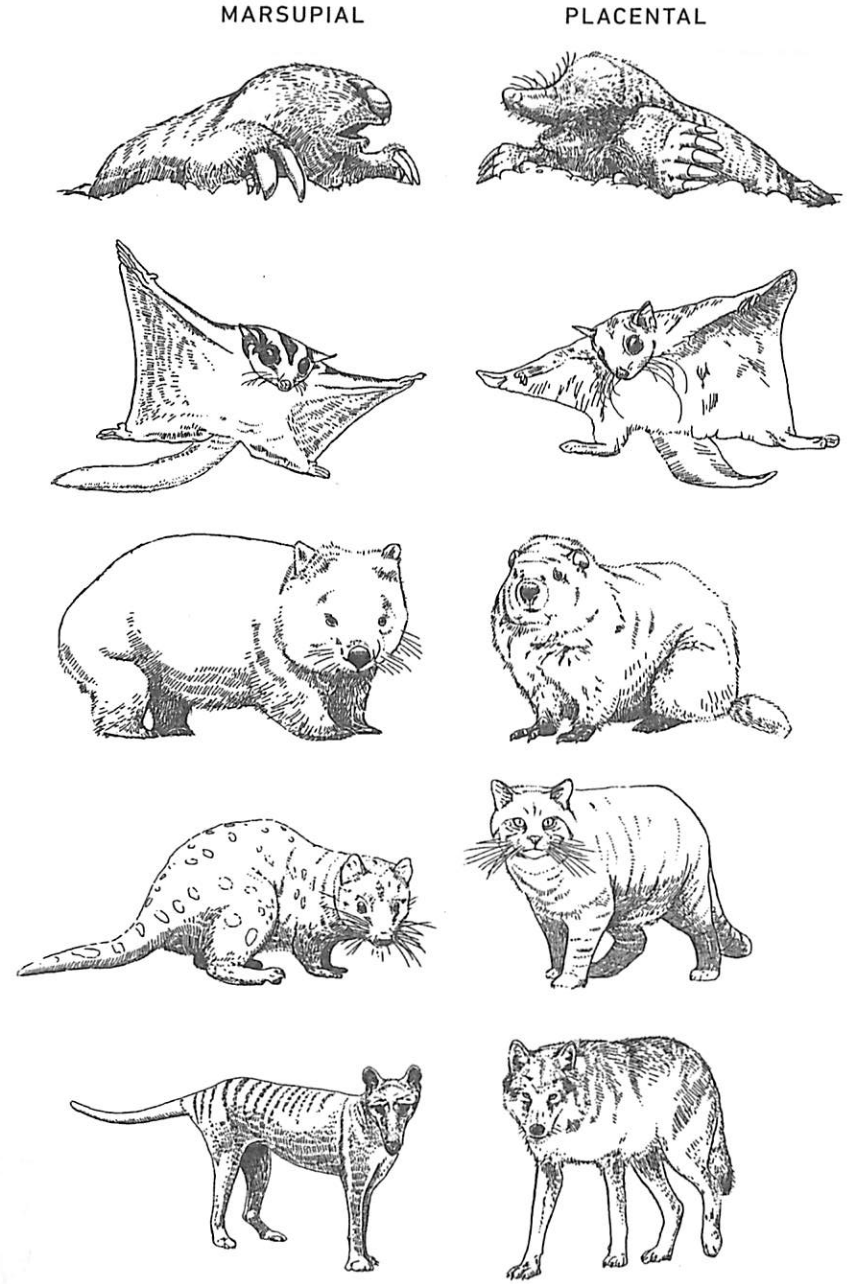
picking up and depositing pollen as they do so. Seven different types of plants have evolved such odoriferous ways.

CONVERGENCE OF PARTICULAR TRAITS is fascinating, but most textbooks illustrate convergent evolution with examples of entire organisms that appear convergent. The iconic comparison is dolphins, sharks, and ichthyosaurs, all streamlined marine predators with flippers for forelimbs, a dorsal fin, a pointy snout, and a powerful propulsive tail capable of high-speed pursuit of their aquatic prey.

The other common textbook example comes from that upside-down land, Australia, where everything seems to be a little bit different. And at the top of the list are the mammals. I've already talked about Australia's penchant for evolutionary one-offs—the platypus, koala, and kangaroo leading the way. But there's another side of the coin. Much of the remainder of Australia's mammalian fauna is convergent with mammals elsewhere in the world.

After the dinosaurs perished, we mammals took over. In most of the world, it was the placenta-bearing mammals (the placentals) that grabbed the brass ring. Not in Australia, however. There it was the mammals that raise their young in external pouches—the marsupials—that reigned supreme. Despite this different evolutionary ancestry, the two mammal radiations produced many species that fill the same ecological niches in the same way.

Textbook writers like to line up Australian marsupials with their placental doppelgängers from elsewhere. Moles, flying squirrels, groundhogs—some of the parallels are so precise that if the marsupial form showed up in your North American backyard, you wouldn't think twice. I'm partial to the quoll, which not only looks and acts like a cat, but is said to make a good house pet. But perhaps the best example—and certainly the most poignant—is the thylacine. A top carnivore with



Australian marsupials and their convergent placental counterparts (from top to bottom): marsupial mole–mole; sugar glider–flying squirrel; wombat–groundhog; quoll–wild cat; thylacine–wolf great resemblance to a wolf, I could easily see one of these creatures taking home Best in Show at Westminster, narrow snout and stiff tail notwithstanding. Decide for yourself on the doggishness of this species: go to YouTube and search for "thylacine"—you'll find a series of black-and-white videos of these animals wagging their tails, gnawing on a bone, jumping up and down, looking all the world like Buster, the family pet. Sadly, the thylacine is extinct, wiped out by Tasmanian ranchers a century ago—the eighty-year-old video footage shows some of the last individuals of the species.

Evolutionary copycats occur throughout the natural world. New World and Old World vultures are convergently ugly in their shared mortician's countenance. Australia's death adder is a member of the cobra family, but in appearance—and venom composition—it is a close match to the distantly related puff adder, a member of the viper family from Africa. Eel-like bodies have evolved not only in many types of fish, but also multiple times in aquatic amphibians and reptiles. Dry areas of Africa are covered with tough-skinned plants with sharp spines and no leaves, but they're euphorbs (members of the Euphorbiaceae), rather than the cacti of the New World.

This evolutionary emulation even crosses biological kingdoms. For example, tapeworms are members of the aptly named flatworm phylum that lives in the guts of vertebrates—including, maybe, you—and can grow up to thirty feet long, maybe even longer. At the front end, they have hooks and suckers that allow them to attach to the intestinal wall. In the neck region, they produce segments that contain embryos and have small projections thought to aid in nutrient absorption. New segments are produced toward the front of this region of the body, so that older segments are continually pushed to the rear end. Eventually, as the segment gets to the back end of the animal, the embryos are released or the entire segment breaks off into the intestinal void, and then you poop them out. If the tapeworm is lucky, you were doing your business in the great outdoors, and the embryos may find their way into their juvenile-phase host, an herbivore such as a grazing cow, in which they grow and develop. And if that cow is in turn eaten by a predator—such as you—without being cooked enough, then you've got a new intimate friend and the cycle begins again.

Although possibly spoiling your appetite, there's nothing particularly exceptional about this lifestyle—many other internal parasites live life similarly. What is unusual in this case is the story of dinoflagellates in the genus *Haplozoon*. Most dinoflagellates drift in the ocean, and many are photosynthetic (that is, they harness the Sun's energy to grow). But not *Haplozoon*. Despite being composed of only one cell, these organisms—which parasitize marine worms—have a body organization and life cycle paralleling that of tapeworms. For attachment to the intestinal wall, they have a sucker and hooks on the front end; for reproduction, they have egg-producing segments with small projections that originate mid-body and move posteriorly as new segments develop, eventually breaking off the end of the body, whence, just as with tapeworms, they are excreted out of the worm's body and set adrift to find their next host. What makes this case of convergence remarkable is that dinoflagellates last shared a common ancestor with tapeworms and other animals perhaps a billion years ago.

THE LIST OF EXAMPLES of convergent evolution is long and exotic, reaching into all corners of the biological world. But we really don't need to stray that far to see convergence—our own species provides many examples.

Homo sapiens emerged from Africa only 100,000 years ago, but in that short period we conquered the world, traveling and adapting to all four corners. And, in doing so, populations in different regions have occupied similar habitats—high on mountains in the Himalayas and the Andes, far to the north on several continents, in scorching deserts wherever they are found. The stage was set for convergence, and natural selection didn't disappoint.

The adaptive significance of variation in skin color among human populations has long been debated, but the field seems to be moving to a consensus that skin color reflects a balance between two factors. On the one hand, darker color, produced by a high melanin content in the skin, protects against ultraviolet radiation, which is particularly intense in equatorial regions. On the other hand, UV rays are important to the production of vitamin D. At high latitudes, where sunlight is less intense, lighter skin is favored to enhance the penetration of the vitamin-boosting UV rays.

Our species originated in Africa, which straddles the equator. As a result, the first humans likely were dark-skinned. This conclusion makes sense when viewed on a phylogeny; the branches that come off near the bottom of the evolutionary tree are the dark-skinned people of Africa. Higher in the tree, emerging from the African populations, are lighter-skinned populations from Europe and Asia. These phylogenetic relationships leave little doubt that dark color is the ancestral condition in humans, from which lighter color evolved.

Geneticists have discovered the changes responsible for skin color and it turns out that the light coloration of people of Asian descent results from different mutations than those causing light color in Europeans. These genetic differences strongly suggest that light skin color evolved independently—convergently—in different populations as they colonized northern areas.* In turn, the ancestors of the aboriginal people of Australia arrived Down Under about fifty thousand years ago,

* The pattern of convergence extends to our nearest relatives, the Neanderthals, who also lived in northern areas and evolved light color by means of a mutation not found in any *Homo sapiens* population.

descended from presumably light-skinned Asians. Their dark coloration, thus, is convergent with the similar shade of African populations.

Another case of convergence among human populations involves the ability of adults to drink milk. One of the defining traits of mammals is the production of mother's milk to nourish their growing offspring. To digest it, young mammals produce an enzyme, lactase, which breaks down lactose, a sugar that is an important constituent of milk. Once a growing mammal is weaned, however, the gene that produces lactase shuts down because the enzyme is no longer needed. This occurs in most human populations, as well as in all other species of mammals. Cats, for example, are not adapted to drink milk, contrary to common wisdom. Feed an adult cat milk and it will have digestive upset, usually ending in diarrhea. The same is true for adults in most human populations—sixty-five percent of the adult human population is lactose-intolerant, and for them, drinking milk is an unpleasant experience.

The other third of the human population is more fortunate. How is it that those individuals, uniquely in the mammalian world, are able to continue drinking milk after weaning? Cows provide the answer.

Within the last few thousand years, human populations in disparate parts of the world—East Africa, the Middle East, northern Europe—began herding cattle. Why ranching occurred in those areas and not others is a subject of debate among anthropologists, but it is clear that these people took up cow-tending independently of each other.

With cows came a ready source of milk. To take advantage of this bounty, natural selection quickly found a solution, favoring genetic changes that kept the lactase gene turned on throughout life, rather than shutting off at an early age. Those of you who enjoy a cool glass of milk—as well as milk shakes, ice cream, and cottage cheese—can thank your cattle-herding ancestors for endowing you with the genetic machinery to do so. Although several human populations convergently evolved the same adaptive solution, genetic analysis reveals that they didn't do it in exactly the same way. Rather, different mutations—each with the same effect of keeping the lactase gene switched on—evolved in the different populations.

We humans aren't the only species in which multiple populations adapt in the same way. In fact, such within-species convergence is quite common: populations of the oldfield mouse have repeatedly evolved light-colored fur after colonizing dazzlingly white sand dunes; many populations of the Mexican tetra (a relative of the fish species familiar to aquarium keepers) have moved into underground caves and lost both their pigment and their eyes; many populations of the rough-skinned newt have evolved high levels of tetrodotoxin (the toxin found in blowfish and fugu) as a defense against their predator, the common garter snake; in turn, in many places garter snake populations have evolved physiological resistance to this toxin. I could go on and on. When closely related populations are exposed to the same selective environment, they tend to adapt in the same way.

SO FAR, I've talked about convergence between two species living in similar environments. This is an idea with deep historical roots. Darwin spoke of it in several places in *On the Origin of Species,* and evolutionary biologists have discussed it ever since. As I've detailed, the idea, though old, has blossomed in recent years as we've come to realize that convergence is much more common than we had appreciated.

Some related ideas, however, are more recent, with shallower tendrils burrowing back only a few decades. Darwin's idea focuses on a single selective factor and how multiple species evolve in the same way, but why should convergence be limited to one set of species adapting to the same environmental challenge? We know that in any given

place, a wide variety of species exist, each adapted to its own ecological niche. If two places are very similar, might not natural selection produce an entire ensemble of convergent types, each adaptive form in one place paralleled by its convergent counterpart in the other? This is a much newer idea in evolutionary biology, one that has only been explored relatively recently. And much of this exploration has occurred on islands.