

6 The Entanglement Problem

Science fiction has long been the stomping ground of grand thought experiments—a vehicle for imagining radically different biological, social, and technological worlds. Contemplating the properties of intelligent life on other planets has been a mainstay of this philosophical enterprise. Rarely, though, have depictions of extraterrestrial life broken free of our anthropocentric, and more broadly, vertebrate-centric framing of evolution. Science fiction has given us an endless parade of alien humanoids, some to copulate with (à la Captain James T. Kirk in *Star Trek*) and others to punch out (à la Captain Steven Hiller in *Independence Day*). In so doing, it has reinforced in the public mind the notion that macroevolution proceeds inexorably from “monad to man,” to borrow the title of a searching book on progressivist narratives in evolutionary theory by historian of ideas Michael Ruse.¹ Few cinematic and literary works aim to disabuse us of the notion that life begins with simple microbes and reliably culminates in the grandiose complexity of humanlike bodies, minds, and societies. Works of “hard science fiction,” such as the *Three Body Problem* trilogy by Liu Cixin, paint a similar “ascent-like” picture of technological evolution, which is assumed to proceed in a replicable series of stages.

Nevertheless, there are simply no good reasons for thinking that there is a law-like connection between the evolution of distinctively hominin or even vertebrate morphology on the one hand and the emergence of sophisticated forms of intelligence on the other. We know from our own example that the vertebrate body plan is *amenable* to intelligence, but we have no reason to project this body-mind trait cluster out into the universe or onto alternative deep histories of life on Earth. In fact, as we shall see in part II, the independent evolution of complex brains and cognition in several invertebrate body plans counsels against projecting the vertebrate body-mind cluster onto other life worlds. Proponents of the search for extraterrestrial intelligence (SETI), such as Carl Sagan and Milan Ćirković, as well as contingency theorists like Stephen

Jay Gould, are quick to acknowledge that complex forms of cognition could be instantiated in any number of theoretically possible body plans.

And yet there is a predilection to bundle morphological and cognitive traits together and to conceive of the entire “humanoid package” as a replicable evolutionary outcome. This “bundling problem,” as we shall see, extends well beyond the humanoid fallacy and is merely one symptom, or perhaps cause, of the broader failure to disentangle radically contingent features of the living world from robustly replicable ones. Finding a solution to this “entanglement problem” is the holy grail of astrobiology, and I am under no illusions that it will be solved here. The aim of this chapter is more modest. In what follows, we will elaborate on the bundling and entanglement problems, consider how convergence data might bear on them, and then go on to sketch some potential avenues for making progress on these issues.

1. The Bundling Problem

The “entanglement problem,” as I understand it here, refers to the great challenge of picking apart biological properties that are likely to be robust features of the evolutionary process from those that are likely to be radically contingent. The “bundling problem” contributes to, but is distinct from, the entanglement problem, in that bundling implicates specific cognitive biases or foibles of human psychology that motivate fallacious extrapolation from earthly evolutionary outcomes.

1.1 Cognitive Biases, Essentialism, and the Humanoid Epidemic

Before Darwin, theories of species were aligned with folk biological tendencies to essentialize the living world. In the Aristotelian tradition that dominated biology for centuries, species were conceived as immutable bundles of “essential” properties, with patterns of variation in morphology and behavior explained by these inner essences. On the Aristotelian view, variation within species is the result of environmental interference with a developmental process that would otherwise produce the essential characteristics of species. Work in cognitive psychology shows that humans are natural Aristotelians when it comes to thinking about biological species.² This explains why human minds are so resistant to the concepts of “population thinking,”³ “lineage thinking,”⁴ and “interactive development”⁵ that are central to modern biological thought. The Modern Synthesis (Darwinian theory + Mendelian genetics) and the New Synthesis (Modern Synthesis + developmental biology) have exploded the assumptions and explanations of bioessentialism, which has been extinct in the life sciences for some time.

Yet a certain “evolutionary essentialism” still lingers, not only in the humanoid-dominated worlds of science fiction, but also in the annals of biological thought. There is a tendency among some researchers to view bundles of traits as co-occurring nonaccidentally, akin to the nomic clustering of properties in atomic elements. Complex bundles of traits that characterize familiar evolutionary outcomes, such as “vertebrates” or “mammals” or “hominins” (in quotes to denote nonhistorical kinds), are viewed as replicable features of the evolutionary process. This “neo-evolutionary essentialism” is defended or at least intimated in the work of Simon Conway Morris and George McGhee (discussed in chapter 4). This evolutionary essentialism is “neo” in that it is consistent with our modern understanding of evolutionary mechanisms like blind variation and natural selection, though as we saw in earlier chapters it is not adequately accounted for by these mechanisms.

The new evolutionary essentialism continues to find expression in the science fiction of our post-Darwinian world, which has widely (though not uniformly) continued to depict intelligent extraterrestrials as distinctively humanoid in form—as if the trait of higher intelligence is nomologically linked to a suite of hominin-like traits to which it is tethered by some unseen law. The humanoid cluster includes such traits as bipedalism, stereoscopic vision, prehensile hands, expanded cranium, and the broader tetrapodean and vertebrate body plans. This is best exemplified, perhaps, in films from *E.T.: The Extra-Terrestrial* and *Close Encounters of the Third Kind* to the recently expanded *Star Trek* and *Star Wars* universes.

The standing humanoid epidemic in science fiction is not due solely to the limitations of imagination or to the pragmatic demands of cinema. Nor can it be chalked up to an ignorance of the disparate body plans in which terrestrial intelligence has arisen. Rather, there is a predilection to infer from what did happen in evolution to what had to happen,⁶ and this tendency is underwritten by the bundling bias. This predilection is properly characterized as a “bias” because, as we shall now see, it can lead to faulty inductions when traits co-occur accidentally.

1.2 From Humanoids to Heptapods

Ironically, the phenomenon of bundling is best illustrated by attempts to *avoid* the humanoid fallacy. Depictions of intelligent extraterrestrial life in books and films have been increasingly informed by evolutionary theory and animal cognition science, commendably avoiding the humanoid fallacy. In so doing, however, they have still fallen prey to the bundling bias. The depiction of aliens in the recent film *Arrival* (2016) nicely illustrates both the theoretical advances that have been made on this front, as well as the obstacles that bundling and

entanglement continue to pose to imagining the nature of intelligent life on other worlds.

The burgeoning field of animal cognition has begun to reveal complex cognitive mechanisms that have converged in distant animal lineages. Cognitive convergence has been demonstrated not only across mammals (such as between cetaceans and primates) and in vertebrates more broadly (such as between mammals and birds), but also between vertebrates and invertebrates (the topic of chapters 9–10). The movie *Arrival* was clearly influenced by some of this work, in particular research on coleoid cephalopod mollusks, whose extant forms include octopuses, squid, and cuttlefish. For reasons that will be explored in part II, coleoids are rightfully considered intelligent aliens on Earth: complex problem solvers with convergently evolved brains, the architecture of which is truly the stuff of science fiction.

The intelligent extraterrestrials portrayed in *Arrival* are called “heptapods” (Greek for “seven foot”). As their name suggests, heptapods have seven appendages, rather than eight like octopods (octopuses) or ten like decapods (squid and cuttlefish). But apart from this negligible modification, heptapods are, anatomically speaking, unmistakable coleoids. They boast several characters in the cluster of traits that are diagnostic of the coleoid clade: sucker-lined tentacles, jet-stream propulsion, camera-type eyes, and ink sacs from which they inexplicably squander a great deal of biosynthesis writing cryptic messages to humans (see figure 6.1).

The writers of *Arrival* deserve credit for declining to provide yet another vector for the cosmic humanoid epidemic, picking out a genuinely alien mind among us as a model for the evolution of extraterrestrial intelligence. For all its improvements, however, *Arrival* makes the same bundling error that gives rise to countless iterations of the humanoid. It lumps accidental traits with evolutionarily robust ones, and it treats the cluster as a single, law-like package, prompting a new bundle: the “cephalopod.”

The cephalopod bundle is just as fallacious as the humanoid bundle and for exactly the same reasons. The error in each case is to entangle what are plausibly robust, interconnected outcomes of the evolutionary process, such as complex brains, cognition, and eyes (part II argues for law-like linkages among of these features), with accidental features of animal body plans, such as hominin-style bipedalism or coleoid-style jet propulsion. The portrayal of intelligent “insectoids,” which have also cropped up from time to time in science fiction, emanates from the same bundling fallacy. In essence, what the standing humanoid epidemic and the incipient cephalopod outbreak in science fiction depict is not the plausible result of extraterrestrial histories of life, but *alternative histories of the shape of life as we know it on Earth*—a worthwhile, but very different, philosophical pursuit.

**Figure 6.1**

Heptapods from the film *Arrival* (2016) represent a new but equally fallacious bundling of traits that make up the “coleoid,” including sucker-lined tentacles, jet-stream propulsion, and ink sacs. Images from <https://alienfandom.com> and <https://www.dailymail.com>, respectively.

There is an interesting parallel between the fallacy of bundling and the cross-cultural proclivity to postulate supernatural beings—or what cognitive scientists of religion call “minimally counterintuitive agents” (MCAs). MCAs are postulated beings whose ontology is on the whole familiar, but which also exhibit some properties that breach intuitive expectations for how entities in that familiar ontological domain will look or behave (such as a tree that talks).⁷ In his impassioned defense of reason in *The Demon-Haunted World*, Carl Sagan remarks on the nonaccidental parallels between supernaturalism and folk depictions of alien visitations.⁸ Despite more than a century-and-a-half of evolution and cognition research, the portrayal of extraterrestrials has achieved little more than a naturalized version of supernaturalism: there but for the point of an ear or a supernumerary tentacle (and a spaceship) goes intelligent life as we know it.

If any features of life have cosmic projectibility, then some of these features will be present on Earth. But which aspects, if any, among the complex outcomes of earthly evolution are the cosmically projectible ones? Calling out the bundling problem is only the first step, for it leaves us with the even more daunting problem of disentanglement.

2. Disentanglement

We can potentially make progress on the entanglement problem by consulting patterns of convergent evolution. However, convergence data will be unable to serve this evidentiary role so long as (1) they remain causally unparsed and

(2) the research questions to which they are put remain underspecified. Building on recent work that I have done with the philosopher of biology Carlos Mariscal,⁹ I will discuss three ways of analyzing biological iterations that help to clarify their evidentiary relevance to the contingency debate. By focusing on the intersection of specificity, independence, and scope, we can identify iterations that are *structurally detailed* (rather than functionally disembodied), *modally robust* (rather than of shallow replicability), and *widely distributed in the living cosmos* (rather than vanishingly rare in the universe).

2.1 The Specificity of Iterations

Whether a given evolutionary outcome is radically contingent or robustly replicable will depend, first and foremost, on how the outcome is described. Functional properties that are characterized in vague terms and not tied to any specific structures will tend to be modally robust, though they will achieve this deep replicability at the price of being scientifically uninteresting. For instance, very generic phenomena like metabolism, thermoregulation, propulsion, mimicry, predation, and predator evasion are likely to be cosmically projectible properties of life, but not of the sort that undermine the radical contingency thesis (RCT). Universal generalizations on the basis of specific iterations, such as ant mimicry, would be interesting but probably false, whereas cosmic projections of mimicry *simpliciter* would be true, but uninformative. Disembodied functions are of little use in making predictions about the evolution of specific phenotypes so long as there is an unmanageably large disjunction of configurations that can realize the same function. The more specific iterations are, the more they undercut Gould's claim that contingency dominates at the level of details "that have always defined the guts and soul of biology."¹⁰

2.1.1 Specifying the Specificity at Stake. A key point of weakness in the critique from convergence (CFC), discussed in chapter 4, is that it is unclear about the levels of specificity at stake in the contingency debate. Take, for instance, McGhee's formulation of the following regularity: "If any large, fast-swimming organisms exist in the oceans of Jupiter's moon Europa ... I predict with confidence that they will have streamlined, fusiform bodies; that is, they will look very similar to a porpoise, an ichthyosaur, a swordfish, or a shark."¹¹ The ambiguity here lies with the phrase "look very similar." If McGhee is making the weaker, less interesting claim that fast-moving aquatic extraterrestrial "animals" will tend to assume fusiform shapes, then, as we saw in chapter 4, Gould would be unlikely to disagree. If, on the other hand, McGhee is making the stronger and more interesting claim that such organisms will tend to resemble sharks or porpoises in more detailed features *beyond their generic fusiform morphology*, then McGhee's claims will have outstripped the evidence. Squid

have tapered spindle shapes but in all other respects (save for their camera eye) bear little resemblance to a shark or a porpoise. Because we only see “dolphinoid” convergence within the vertebrate body plan (i.e., in Mesozoic marine reptiles, cetaceans, and to a lesser degree fish), this tells us little about the evolutionary robustness of these specific outcomes across the whole of multicellular life. Given vertebrate body plan parameters, there may be only a subset of modifications that can achieve a fully aquatic lifeway, and thus dolphinoid iterations may amount to Gouldian repetitions.

Other robustly replicable outcomes may or may not lie at the level of granular detail that is at issue in the contingency debate. For instance, the filter-feeding apparatus of the wading flamingo is remarkably similar to that of the pelagic baleen whale,¹² suggesting that the structure of macroscopic filter feeding—which involves the passing of water through entrapment surfaces to simultaneously ensnare numerous prey items that are too small to be foraged individually—may be highly externally constrained (see figure 6.2).

Similar filter-feeding apparatuses have evolved in living invertebrates, and a grill-like facial structure for sieving plankton has been found among suspension-feeding anomalocarids in the Cambrian.¹³ Physical constraints that determine the shape of suspension-feeding morphologies—such as the relation between the mesh size of the capture device and minimum prey size—allow for reliable predictions about morphology and ecology across disparate body plans. In all other respects, however, the outcome bundles that comprise whales, flamingos, and anomalocarids exhibit few convergent features.

This focus on specificity helps to avoid cross talk and bring out key points of disagreement in the contingency debate. Recall Gould’s claim that universal generalizations about form and function do not speak to the details that fascinate biologists. Without weighing in on subjective matters of fascination, we can interpret the RCT as claiming that only *very generic* evolutionary iterations will be deeply modally robust, whereas we can interpret the robust replicability thesis (RRT) as contending that patterns of convergence support the existence of evolutionarily robust outcomes with *high levels of specificity*.

What makes one trait more specific than another? Generally speaking, we can say that one trait is more specific than another when it occupies a higher position in a nested multiple realization base of function. For example, blubber is more specific than insulation, which in turn is more specific than thermoregulation; vision is more specific than image formation, which in turn is more specific than sensory modality. Likewise, the antifreeze protein AFP type II is a molecule with a highly specific structure that has evolved several times for

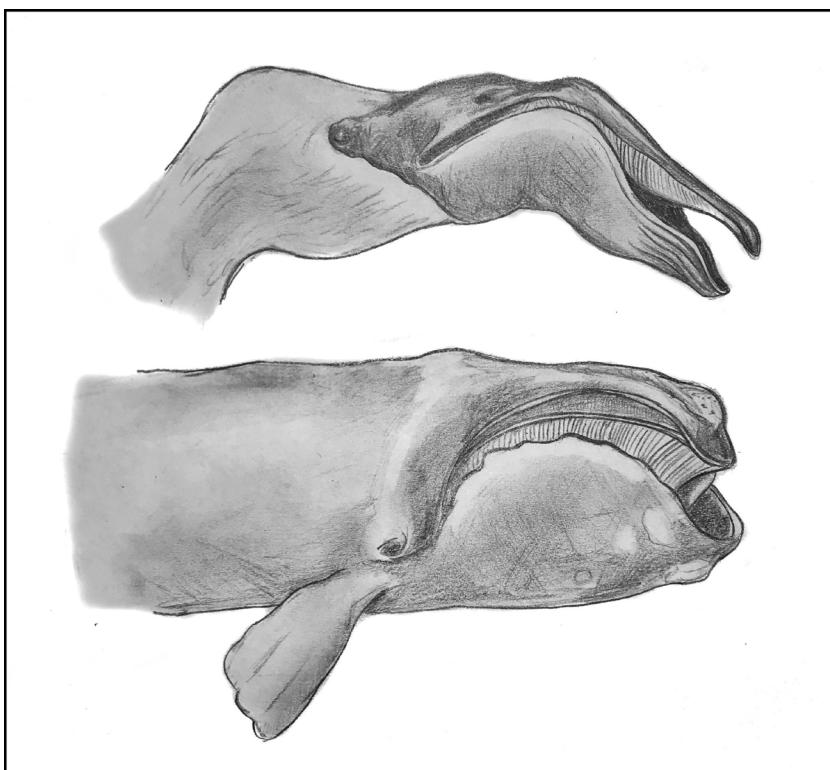


Figure 6.2

Filter-feeding morphologies of the lesser flamingo and right whale, respectively, which include a curved jaw to increase the surface area of the sieve, a narrow upper jaw and robust lower jaw, and a thick fleshy tongue. Redrawn from A. Feduccia, *The Origin and Evolution of Birds* (Yale University Press, 1999).

lowering the freezing temperature to prevent cell rupture. Because many proteins have ice-binding properties, “antifreeze” is a multiply-realizable function that has been achieved via selection on different genes and mechanisms in groups as disparate as animals, plants, fungi, and prokaryotes.¹⁴

All else being equal, the more generically an iteration is described, the “wider” its multiple realizability base, and hence the greater its modal robustness. Consider a sensory modality like hearing. The tympanal organ or “ear” in insects is a vibrating, drumlike structure that detects pressure waves generated by sound and converts acoustic energy into mechanical energy; it has evolved more than twenty times in the bodies, wings, and legs of various insect groups.¹⁵ A structurally similar “ear” has evolved in vertebrates using completely different developmental machinery. However, if “hearing” is defined

more broadly to include not only drumlike structures but any adaption to detect nanoscale vibrations and to transduce these stimuli into neuronal impulses that generate adaptive behavior, then the trait will be less specific but far more evolutionarily robust. Jumping spiders, for example, have long, sensitive hairs on their legs and bodies that activate auditory neurons, allowing them to “hear” predator or prey movements including airborne sounds at up to 3 meters (or 600 spider body lengths).¹⁶ Similarly, pinnipeds (seals, sea lions, and walruses) have highly innervated whiskers that are used to detect fluid motion left behind by fish trails when foraging in low light.¹⁷ Such vibrotactile adaptations could constitute “hearing” on very broad definitions. Likewise, the mechanosensory hair cells of the “lateral line” system in fish resemble those of the vertebrate inner ear. Bioacoustics in green plants, which initiate chemical defenses in response to vibrations caused by leaf chewing, may also meet broad definitions of “hearing.”¹⁸

Generality, however, comes with a cost—two costs, in fact. First, as previously noted, the more generic the iterations, the less scientifically interesting they are, and the less they undercut the RCT. Compare the following three predictions:

1. Some marine-dwelling animals will evolve a subcutaneous layer of adipose-like tissue in order to conserve heat.
2. Some marine-dwelling animals will evolve a covering in order to conserve heat.
3. Some marine-dwelling animals will evolve adaptations in order to maintain viable internal temperatures.

The first description is highly specific; the second is less specific but still might admit of a limited set of realizations; the third, though by far the most evolutionarily robust of the three, is so vague that it might be realized by an indefinite number of structural, behavioral, and physiological configurations ranging from metabolic and insulatory functions to habitat choice and seasonal migration. Such generic regularities admit of no useful predictions in the abstract, and it is implausible to think that they would undermine the RCT.

Second, although massive multiple realizability can underwrite the modal robustness of functions, it also undercuts the law-like replicability of specific forms.¹⁹ The more generically a functional outcome is described, the less reason there is to think that its realizations will be restricted to a small number of structural possibilities that could be the basis of a manageable set of laws. Establishing very generic laws of function would be little more than a pyrrhic nomological victory.

A final dimension of specificity relates to “hierarchical depth.” It is widely acknowledged that convergence is level-relative: A structure can be convergent at the level of morphology while being homologous at the level of tissues, at the level of proteins that compose tissues, and/or at the level of genes that code for proteins that compose tissues. Alternatively, a trait can be convergent on all these levels simultaneously. Jeanine Donley and colleagues, for example, show that the convergence between tuna (teleosts) and lamnid sharks (e.g., makos) extends well beyond their fusiform shape to the details of mechanical design and muscle dynamics that underpin their shared force-transmission system.²⁰

One might think that the “deeper” a convergence goes, the more it speaks to the power of selection to guide form toward certain evolutionary attractors, and hence the more decisively it contradicts the RCT. The fact that some iterations are more than “skin deep” is important. But if hierarchically deep convergence is due in part to shared developmental constraints operating at multiple levels simultaneously (as may be the case in teleost and lamnid fishes), then it will not be evidence of truly robust replicability. For this reason, hierarchical depth does not in itself have any clear-cut implications for the contingency or robustness of a given iteration.

Imagine that on some alien world creatures evolved that near-perfectly resembled human beings in gross morphological, cognitive, and behavioral respects. The implications of such a stunning replication for the RCT would not be undercut if we were to learn that these humanoids and their minds were constructed out of an entirely different molecular substrate. To the contrary, such multiple realizability would show just how cosmically accessible, and hence widespread, the humanoid outcome is. The point of this exercise is simply to show that whether an iteration occurs on multiple levels does not determine its evidentiary relevance to the RCT.

2.1.2 Macroevolutionary Bait and Switch. The level of specificity with which evolutionary outcomes are described can also affect one’s reading of faunal turnovers, a key plank in Gould’s bulwark of contingency (as discussed in chapter 2). During these transformative successions, lineages that were long subordinate are able to survive and thrive in the wake of a mass extinction perturbation, radiating into the empty niches vacated by previously dominant groups. Bats and birds filled the niches of recently extinct pterosaurs, whales and sharks filled the niches opened up by the extinction of the mosasaurs (pictured on this book’s cover), late Cretaceous mosasaurs filled the vacated niches of other Mesozoic marine reptiles like pliosaurs and ichthyosaurs, and so on.

RRT proponents handle the dynamics of extinction and faunal turnover by arguing, in essence, that certain evolutionary outcomes are “overdetermined”

in the sense that surviving lineages will tend to repopulate the emptied attractors in morphospace. At the extreme end of the macroevolutionary overdetermination view is the notion that deep replays will reproduce what Jonathan Losos, in a book published during the writing of this one, refers to as evolutionary “doppelgängers.”²¹ Losos contemplates that perhaps, following Conway Morris (but assigning more tentative credences), had the nonavian dinosaurs remained safe in their niches, the world today would be populated by humanoid doppelgängers of dinosaurian origin; or, if the dinosaurs did go extinct in the familiar way, then perhaps some other mammalian lineage would have evolved a humanoid doppelgänger.

The evidence weighs against this possibility, but we will reserve a discussion of the human(oid) case for the final chapter of this book. The general point is that describing the repopulation of niches in faunal turnovers as “iterations” runs the risk of a macroevolutionary bait and switch. In most cases, the regions of morphospace that are filled by successor lineages bear only superficial similarities to those of their predecessors. Sea lions are not all that similar in their ecomorphospace occupation to plesiosaurs, and wolves are not very similar to dromaeosaurs, even if these lineages occupy similar respective niches and share some generic morphofunctional specializations for common lifeways.

Other faunal turnovers in which morphospace repopulation is impressively specific may turn out to be Gouldian repetitions. Take the striking patterns of iteration within successive placental mammal faunas throughout the Cenozoic (discussed in more detail below). The reason why saber-toothed, mole-like, horse-like, shrew-like, hippo-like, cat-like, and wolf-like niches exist is because they represent local adaptive attractors or optimums within a mammalian body plan interacting with recurring selective environments. Local mammalian optima are illustrated by the mesonychians—a predatory group of even-toed ungulates that have been referred to as “wolves on hooves.” The mesonychians emerged not long after the dinosaur extinction and were the first major mammalian predators on Earth. The “wolf” ecomorph may be a global optimum for mammals that transcends Linnaean order-level body plans, but it is a local optimum from the standpoint of tetrapods more broadly. A similar point could be made about morphological convergence in large theropod dinosaurs such as tyrannosaurids, allosaurids, and ceratosaurs, all of which were working within same theropodian ground plan.

As fewer developmental parameters are shared, however, the similarities between iterations become increasingly attenuated. Bison are only minimally reminiscent of the ceratopsian dinosaurs (such as the iconic triceratops) that crowded the plains of North America 65 million years ago, even if they occupy a similar niche and share some features and behaviors thanks to a conserved

tetrapodian body plan. This raises a further issue about the nature of niches themselves: it is misleading to say that “successor lineages evolve to fill the niches that are vacated by their predecessors.” For this assumes that niches are wholly external to evolving lineages and simply waiting in the world to be filled—an assumption that the phenomenon of Gouldian repetition calls into question.

2.2 The Independence of Iterations

As we saw in the last chapter, many iterations do not meet the validity conditions for natural experiments in convergent evolution because they fail to satisfy the “independence” criterion. The reason why many iterations fail to satisfy the independence criterion is that although natural experiments in convergence are isolated in space and time, they often begin from highly similar developmental starting points that “load the evolutionary dice,” as it were, toward particular iterative outcomes. Such iterations are consistent with, and perhaps even corroborative of, the Gouldian view of life. How should we analyze the independence dimension?

2.2.1 A Two-Pronged Analysis. The independence of iterations can be assessed using a two-pronged analysis. First, it should aim to identify *causally specific developmental homologs* that are involved in the production of an iteration. Second, it should aim to identify features of the broader body plan that delimit the space of locally optimal solutions *even where no specific developmental homologs underwrite a given iteration*. Chapter 5 considered some of the conceptual and methodological challenges that confront these analyses and argued that these challenges must be overcome if convergence is to serve as evidence in the contingency debate.

Generally speaking, we can say that a small number of highly independent evolutionary repetitions offers stronger evidence against the RCT (and in favor of deep replicability) than does a large number of nonindependent repetitions. By the same token, iterations with a narrow phylogenetic distribution (e.g., iterations limited to taxa at or below the Linnaean class-level) are more likely to be nonindependent iterations (i.e., Gouldian repetitions) than they are to be cases of true convergence. This is because iterations among closely related taxa are more likely to deploy homologous, causally specific developmental machinery. Even where iterations among closely related taxa are produced by different developmental machinery, they will often ensue from conserved body plan parameters that are, for all we know, radically contingent.

On the other hand, if an iteration has a wide phylogenetic distribution, such as “viviparity” (the development of embryos within the body of the female), this indicates that an evolutionary outcome may transcend the peculiar body

plan parameters of particular lineages. Other iterated traits with high levels of specificity are found in clades as developmentally disparate as plants and animals. An example is urticating hair, barbed bristles connected to cells that produce poisonous or acrid fluids, which are designed to break off and lodge in the skin of predators. Convergences across plants and animals—which represent two distinct origins of complex multicellularity—hints at cosmic-grade projectibility.

2.3 The Scope of Iterations

Iterative regularities also vary with respect to their “scope,” or the ubiquity of the conditions under which they obtain. If convergent regularities are limited by conditions that are astronomically uncommon in the universe, then these regularities will have a very narrow scope, even if they emerge in a “law-like” way wherever these conditions obtain. We might distinguish between two broad types of limiting conditions: (1) “external” factors, which include features of both the abiotic and biotic environments, and (2) “internal” factors relating to the evolvability of the trait in question. Some external limiting conditions, like the presence of light or water or the existence of a continental crust that supports a terrestrial habitable zone, are likely to be common among life worlds and thus do little to restrict the scope of convergent regularities. Others, like the presence of particular coevolving lineages or specific internal developmental parameters, may be exceedingly rare among life worlds. Because we are not currently capable of identifying all the limiting conditions that underpin a given iteration, our pragmatic aim in assessing scope should be to identify the most restrictive limiting conditions.

For example, some iterations, such as the pollination syndromes discussed earlier, depend on the existence of both the angiosperm flowering platform and morphologically specific pollinator lineages, two very narrow limiting conditions that undermine the cosmic projectibility of these iterations. Contrast this with, say, convergence in vessels to transport water, which evolved many fewer times than pollinating morphology but which, given the invariant physics of aqueous chemistry, are likely to be universally projectible. Likewise, conditions for the evolution of the fusiform shape include active locomotion in a fluid environment and the internal structure necessary to maintain a sturdy, macroscopic shape, conditions that are probably widespread in environments that are conducive to the evolution of animal-grade multicellularity.

Developmental constraints that restrict the scope of convergent regularities are perhaps the most important class of internal limiting conditions, for two reasons. First, they explain why Gouldian repetitions are neither projectible to other life worlds nor stable across deep replays of the tape of life on the Earth.

Second, cast in in their positive role as facilitators of innovation, developmental constraints explain why many patterns of iteration exist in the first place and how they underwrite impressive degrees of replicability across “shallower” rewinds of life’s tape.

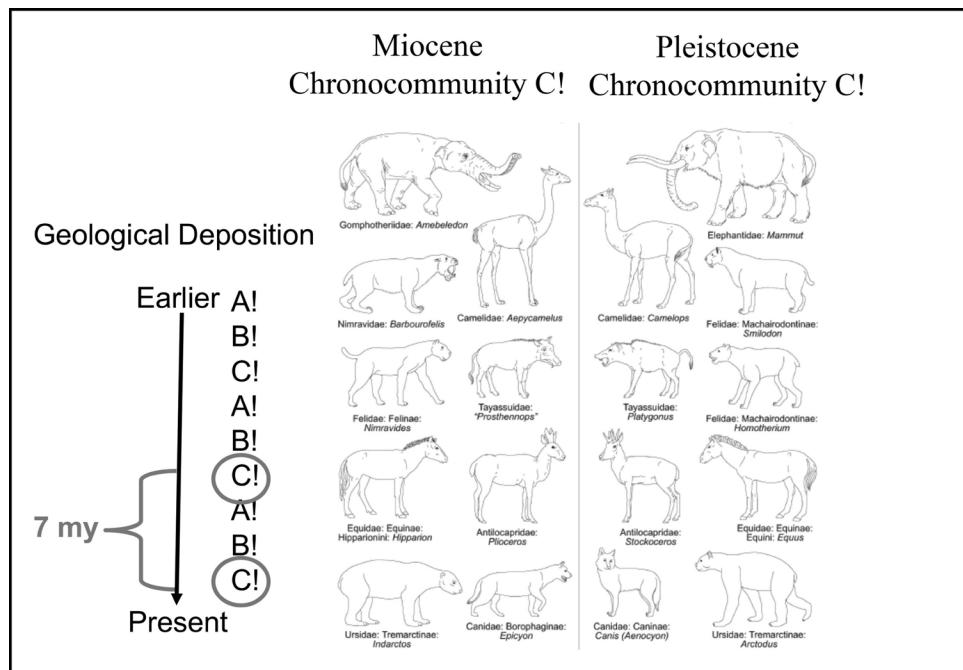
2.3.1 Replay Depth. We saw in the early chapters of this book that Gould’s Cambrian thought experiment presupposes the existence of multicellular animal life, and asks how the tape of animal life would unfurl were it played again. If an iteration hinges on the origin of radically contingent developmental parameters, then it will be stable across rewinds no “deeper” than the emergence and crystallization of those developmental parameters. In the case of iterations confined to lower level taxa, this stability will tend to be shallow; in the case of iterations between higher level taxa within-phyla, it will be moderate; and in the case of iterations across phyla or even the whole of multicellular life, the replay depth stability will be deeper still, verging on the cosmic.

Consider, for example, the striking set of convergences between marsupial and placental mammals, and within placentals, on a range of ecomorphologies throughout the Cenozoic (see figure 6.3).²² Given internal limiting conditions of the mammalian body plan and certain recurring ecological conditions, a range of specific mammalian forms may be highly replicable over a 55 million year period of evolution, even if they are not deeply robust features of vertebrate life on Earth, let alone of “animals” on other potential life worlds.

The same is true of the impressive convergences in aquatic bird morphology that occurred during the post-Cretaceous diversification of birds, including between penguins and auks (flightless relatives of puffins), gulls and albatrosses, grebes and loons, diving petrels and auklets, flamingos and herons—all cases that illustrate the adaptive optimization of a common bird platform to a diverse but finite range of ecological tasks (such as foot-propelled diving, fish capture, transoceanic flight, wading, and so on).²³ The iterative evolution of stickleback and *Anolis* ecomorphs, discussed in chapter 5, are indicative of replicability across even shallower rewinds of the tape of life. In contrast, the convergent evolution of (for instance) salinity tolerance across the archeal and bacterial prokaryotic domains reflects a far deeper replay depth stability (though it scores low on specificity). In sum, a key problem with the CFC is that it has failed to distinguish iterations of plausibly universal scope from those with a narrower set of limiting conditions.

2.4 Case Study: Image-Forming Eyes

Let us apply our analysis to an iterated regularity that appears to score highly along all three dimensions: the image-forming eye. The motivation for this particular example is not merely illustrative, however. The evolution of vision

**Figure 6.3**

Mammalian ecomorph assemblages (or “chronocommunities”) from the Miocene and Pleistocene, separated by millions of years of intervening time dominated by different faunal assemblages. Adapted from L. D. Martin and T. J. Meehan, “Extinction May Not Be Forever,” *Naturwissenschaften* 92 (2005): 1–19.

will take center stage in part II, where we explore the iterated evolution of cognitive complexity and its link to image-forming perception.

First, the image-forming eye earns a high score on specificity. It includes variations on two distinct configuration types—camera and compound—which reflect the two fundamental ways that optical components can be configured so as to produce spatial vision in organisms. The first involves adding more photoreceptors to a single apparatus (resulting in the single-chambered eye), while the second involves multiplying the apparatus itself (resulting in the compound eye). Each of these eye types are structurally specific, entailing particular cornea, lens, and retina configurations.

Second, image-forming eyes are likely to have a very broad scope given the universal laws of optics, the ubiquity of the light stimulus, the fact that light waves are generally shorter than the ecologically relevant objects that bend them (permitting the extraction of various types of information about those objects),

and the availability of substrates that can be readily coopted for optical functions. The wide range of crystallin proteins that have been used for lens transparency in diverse animal groups speaks to the availability of eye-friendly substrates.

Some of the molecular building blocks of eyes have been honed for globally optimal function. The photoreceptor pigment “rhodopsin,” for instance, is so beautifully optimized that it triggers an electrophysiological cascade in response to a single quantum of light. Moreover, eyes have arisen in many different parts of the body, including in animals without proper heads (see further discussion in chapter 7). As biologists Michael Land and Eric Nilsson put it in their seminal work on the evolution of eyes, the “enormous range of sizes, designs, and placement of eyes … gives a clear indication that eyes can evolve easily, recruiting whatever tissue is at hand, and become superbly optimized for the lifestyle of the bearer.”²⁴ In other words, both the external (ecological) and internal (evolvability) limiting conditions on eye evolution appear to be rather unconstrained.

Third, the weight of the evidence supports a high score on the independence dimension as well, although this issue is somewhat dicier. Each major eye type has arisen numerous times both within and between distant animal phyla, including vertebrates, mollusks, arthropods, annelids, and cnidarians.²⁵ Incredibly, a camera eye has even evolved in single-celled eukaryotes, where it has been sculpted by selection out of subcellular organelles, as will be discussed further in chapter 7 (see figure 6.4).²⁶

Complicating the independence score, however, are two factors—deep genetic homologs and cell-type homologies—that might lead one to the conclude that eyes are either monophyletic or at best Gouldian repetitions. First, as discussed in chapter 5, certain deeply conserved developmental mechanisms, such as *Pax6*, are implicated in all known cases of eye morphogenesis. Yet, as we saw there, this does not undermine the independence of the iterations in which *Pax6* is involved. The reason why independence is preserved in crucial cases of iterative eye evolution is that convergent eye-bearing phyla do not share causally specific developmental mechanisms that specify the gross morphological contours on which judgments of convergence are based. Nor do these converging lineages share other internal constraints that shape the specific parameters of eye evolution. Indeed, *Pax6* is present in echinoderms (e.g., sea urchins), even though this phylum does not have even the simplest eye. It is true that *Pax6* betrays the signature of history, for unlike rhodopsin it is not strongly functionally constrained. However, there is nothing to suggest that *Pax6* imposes limitations on eye evolution that would convert these stunning iterations into Gouldian repetitions.

Second, there is a growing consensus that the two cell types involved in photoreception—cilia (found in vertebrates, using c-opsin photopigments) and

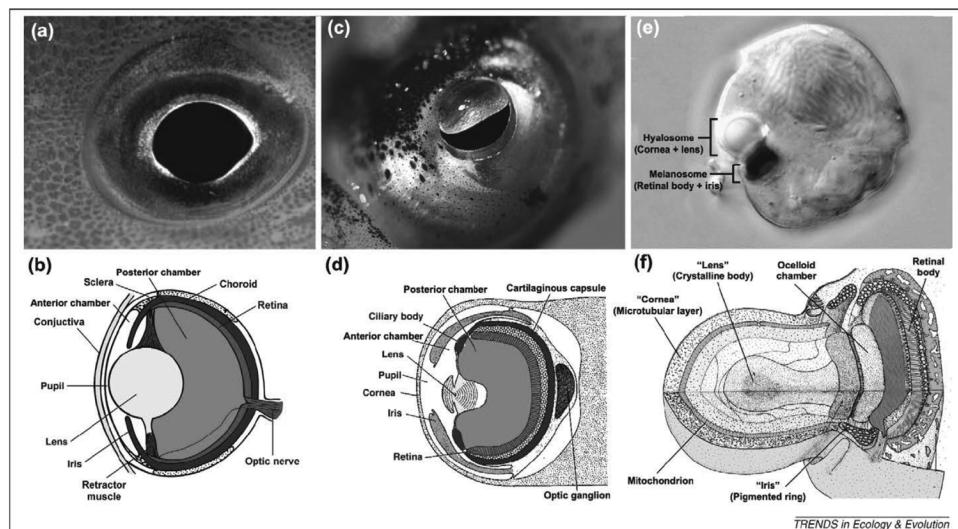
**Figure 6.4**

Photo and schematic pairs of the convergent multicellular camera eyes of (a and b) vertebrates and (c and d) cephalopod mollusks. (e and f) The subcellular camera eye of single-celled warnowiid dinoflagellates, composed of modified endosymbionts including a plastid (which forms the retina) and mitochondrion (which forms the cornea). From B. S. Leander, “Different Modes of Convergent Evolution Reflect Phylogenetic Distances: A Reply to Arendt and Reznick,” *Trends in Ecology & Evolution* 23, no. 9 (2008): 481–482.

modified microvilli (found in invertebrates, using r-opsin photopigments)—have a single origin. It turns out that some invertebrates have both types of photoreceptors, indicating that photoreceptor cells were present in the ancestor of all bilaterians;²⁷ in addition, there are structural homologies between these cell types that indicate they are “sister cells,”²⁸ with one having been derived from the other.²⁹ Nevertheless, as we shall see in chapter 9, the preponderance of the evidence suggests that the last common bilaterian ancestor did not have complex eyes (or a head or brain), even if it possessed *Pax6* and both types of photoreceptors.³⁰ If it is correct to characterize the last bilaterian ancestor as eyeless, then describing complex eyes as monophyletic (i.e., having a single origin), as some researchers have done, is misleading.³¹ For even if all eyes share some cell type homology, they would still be genuinely convergent at the level of macromorphology.

Furthermore, as with *Pax6*, there is no reason to think that conserved photoreception constrains the specific morphological parameters of eye evolution. The extent to which photoreceptor monophyly undercuts the evolutionary robustness of complex eye evolution depends on whether the origin of

photoreception is itself a radically contingent event. A singular origin is not in and of itself demonstrative of radical contingency: if an innovation like photoreception occurs early in the history of a clade (such as Eukaryota), we might very well expect it to be conserved over deep time and repeatedly deployed in diverse subclades.

At the very least, we can say that if photoreception is taken among the relevant initial conditions, then the evolution of complex eyes is a robustly replicable outcome. And with eyes come a slew of nomically linked properties that help to seal the place of the mind in the living universe. This is the story to be told in part II.

Contingency and Convergence

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