REVIEW

The predictability of evolution: glimpses into a post-Darwinian world

Simon Conway Morris

Abstract The very success of the Darwinian explanation, in not only demonstrating evolution from multiple lines of evidence but also in providing some plausible explanations, paradoxically seems to have served to have stifled explorations into other areas of investigation. The fact of evolution is now almost universally yoked to the assumption that its outcomes are random, trends are little more than drunkard's walks, and most evolutionary products are masterpieces of improvisation and far from perfect. But is this correct? Let us consider some alternatives. Is there evidence that evolution could in anyway be predictable? Can we identify alternative forms of biological organizations and if so how viable are they? Why are some molecules so extraordinarily versatile, while others can be spoken of as "molecules of choice"? How fortuitous are the major transitions in the history of life? What implications might this have for the Tree of Life? To what extent is evolutionary diversification constrained or facilitated by prior states? Are evolutionary outcomes merely sufficient or alternatively are they highly efficient, even superb? Here I argue that in sharp contradistinction to an orthodox Darwinian view, not only is evolution much more predictable than generally assumed but also investigation of its organizational substrates, including those of sensory systems, which indicates that it is possible to identify a predictability to the process and outcomes of evolution. If correct, the implications may be of some significance, not least in separating the unexceptional Darwinian mechanisms from underlying organizational principles, which may indicate evolutionary inevitabilities.

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Introduction

The study of evolution is riddled with paradoxes. By most accounts, Charles Darwin (1809–1882), despite his acute intelligence, was himself a modest individual. Nevertheless, he applauded the belligerent stance adopted by his friend T.H. Huxley in defense of the theory of descent with modification. Nor has the rancor subsided: Too much of modern day evolutionary discourse is dogged by a stridency that in other areas of science would be regarded as astonishing. To some extent, this is a reflection of the growing influence of so-called intelligent design. This combines the worst of all possible worlds, being non-science and flawed theology. Nevertheless, I suspect the problems go beyond "intelligent design." While the polarization of attitudes, most obviously between materialist ultra-evolutionists and theistic creationists, is at best unhelpful, it is also obvious that despite protests (especially from the former group) the issues are not restricted to scientific evidence but go much deeper to world pictures and ultimately metaphysics (even if nihilistic; see Giberson 2008). Creationists, of course, strongly dispute the evidence for evolution, but to equate them with flat-earthers is to miss the point. What, if anything, will serve to persuade creationists of the reality of evolution is impossible to say, but perhaps the opposing lobby might also care to re-examine its credentials. Am I alone in thinking that the insistence that

for all intents and purposes the study of evolution is complete, comprehensive, and unassailable reflects a closing of the scientific mind? Not that anybody (apart from the aforementioned creationists) disputes the truth of evolution, nor for that matter the primacy of the mechanistic formula of adaptation and natural selection (Darwin 1859). But that does not mean we have a complete explanation. Here I will try to explain why.

First we have no adequate definition of life. Michael Polanyi's seminal essay "Life's irreducible structure" (Polanyi 1968) still provides a bench-mark for discussion. Thus, while our intuitive sense of life being both self-organized and highly dynamic, and from which hierarchies, non-linearities and remarkable thermodynamic engines seemingly emerge effortlessly, goes some way to capture this seemingly evanescent—but in reality astonishingly robust—entity, we possess no underlying theory to delimit life. Drawing on both Polanyi and other luminaries such as Schrödinger, Prigogine, and Kauffman Peter Macklem's brief but compelling essay (Macklem 2008) captures the knife-edge-like existence of life as a physico-chemical state poised between vast regions of either crystalline immobility or chaotic flux. But in addition to this depiction, Macklem also stresses that if we could but understand the nature of emergences, not least consciousness, then we might be on the threshold of "the next biological revolution" (p. 1846). From this perspective alone to suggest that our understanding of evolution is complete is surely open to question.

This, to repeat, is not to question the Darwinian formulation, but simply to insist we are engaged in unfinished business. Nor would I for a moment wish to claim that I am a lone voice. Figures such as Brian Goodwin (1994) and Stuart Kauffman (1993) have evoked post-Darwinian scenarios to explain biological complexity. The approach here is somewhat different and less theoretical, but concludes with equal force that current explanations are incomplete. To support this view I will touch on only a handful of topics revolving around such topics as (a) the nature of the Tree of Life and the seductive notion of "twigs," (b) the improbability (or otherwise) of major transitions, (c) the question of molecules of choice, (d) inherent tendencies or innateness, (e) the identification of a predictability (possibly even a "logic") in biological systems, and (f) the limits to biological "engineering." To a considerable extent these are categories of convenience, by no means mutually exclusive, but collectively they talk to a wider program. In essence this review aims to demonstrate that contrary to almost all received "neo-Darwinian" wisdom the evolutionary destinations—say humans—are very far from being fortuitous, and by implication unpredictable. To the contrary, the evidence suggests that in reality rather than being an open-ended process evolution is deeply constrained. The number of options it can pursue is surprisingly few. That the view of fortuitousness is very

deeply embedded in the Darwin-based modern theory of biological evolution (e.g., Carroll 2000; Kutschera and Niklas 2004; Kutschera 2009) will be evident from even a cursory reading of the literature. Here I will expand upon just a single example to argue the contrary case.

The road less traveled?

Evolution is littered with its icons. Among the most intriguing are the bats, with our fascination in them largely revolving around their capacity for echolocation. Even so this sensory modality has evolved many times in other groups, notably in various mammals (e.g., Thomas et al. 2004) and also the birds (e.g., Griffin 1958). So too even though echolocation is taken to be the evolutionary hallmark of the bats, within this group itself convergence is also found. Thus, chiropteran echolocation may have evolved more than once (e.g., Eick et al. 2005), and so too there are striking instances of convergence in terms of various call types and the nature of the frequencies employed (e.g., Jones and Holderied 2007). Of these a particularly intriguing example revolves around the rhino-lophids (horse-shoe bats) and a New World mormoopid, specifically the Greater Mustached bat. In both animals the cochlea possesses an acoustic fovea to detect the very narrow frequencies of ultrasound, and as Gerhard Neuweiler remarks, this is "one of the most striking examples of convergent evolution" (Neuweiler 2003, p. 255). But in his analysis, Neuweiler seems to lose his Darwinian nerve when he also writes "It challenges our imagination to conceive evolutionary driving forces" that might lead to such an acoustic fovea. Indeed he goes on to wonder if this admittedly remarkable piece of bio-engineering might be the result of "an accidental non-functional mishap" (p. 255). But against this view of contingent accident, we need to note that not only is this acoustic fovea convergent but also that the convergences do not stop here but extend to the auditory cortex (Neuweiler 1990).

This initial example serves, therefore, to introduce some wider issues. Evidently there can be a tension in the identification of convergences, and this is also echoed in the almost invariable employment of adjectives with the connotation of surprise: "Remarkable," "striking," even "uncanny," and "stunning" are the regular linguistic currency that is employed. So too, convergences challenge the atomistic thinking typical of cladistic methodologies because emphasis on the former looks toward integrated complexes. Things seldom evolve in isolation but rather in the context of functional interdependence (with, of course, the potential for concerted convergence (e.g., Givnish et al. 2005) and ecomorphs (e.g., Losos et al. 1998)).

These remarks are clearly consistent with the "Darwinian program," that is an integral part of modern theory of biological evolution (Carroll 2000; Kutschera and Niklas 2004), not least in terms of adaptation. Nevertheless, the fit may not be entirely comfortable. This arises from another point of tension. That is, while an appeal to the accidental and other mishaps in the history of life is deemed to be consistent with the current Darwinian *zeitgeist*, epistemologically, this may lead to more problematic territory. In brief one can argue that the Darwinian mechanism lacks traction. By this I simply mean that the description of the mechanism is valid, but forecloses the investigation of predictability. If indeed every evolutionary product is fortuitous, then in one sense apart from noting that things change according to a given algorithm nothing is being explained at all. It is difficult to think of any other science that would regard such a formulation as particularly satisfactory. But in present-day evolutionary biology, this view remains pervasive. Unlike other sciences, so it appears, evolution has neither predictabilities nor any sense that it might depend on pre-existing substrates that could in one way or other determine possible outcomes.

Uncanny evolution?

I suggest, therefore, that within the "Darwinian framework" there exists a very interesting intellectual tension. This lies between the ostensibly fortuitous, a central tenet of the modern theory of biological evolution, as against the uncanny capacity for organisms to navigate to particular solutions. Innumerable such examples could be given, but consider just one instance. This example revolves around pollination strategies, and specifically the shift from bee to hummingbird pollination. In the case of the plants known as the penstemons, such a shift may have occurred in this group alone as many as twenty-one times (Wilson et al. 2007). Not only do the authors employ the word "attractor" but they also exclaim that "the number of origins of ornithophily is astonishing and indicates to us that the hummingbird pollination niche is *just waiting to be claimed* by plants with flowers like penstemons in a way that other pollination niches are not" (Wilson et al. 2007, p. 889; my emphasis). And what of the hummingbirds? So far as they and evolutionary convergences are concerned, this is only the tip of an evolutionary iceberg. Thus, convergences extend not only to the evolution of particular flower-types (Brown and Kodric-Brown 1979) and avian nectarivory (including the remarkable convergence between the meliphagids and Hawaiian honeycreepers (Fleischer et al. 2008)) but also beyond the birds to the insects and specifically the hawkmoths. Their similarity to hummingbirds famously fooled the naturalist Henry Bates (1892)
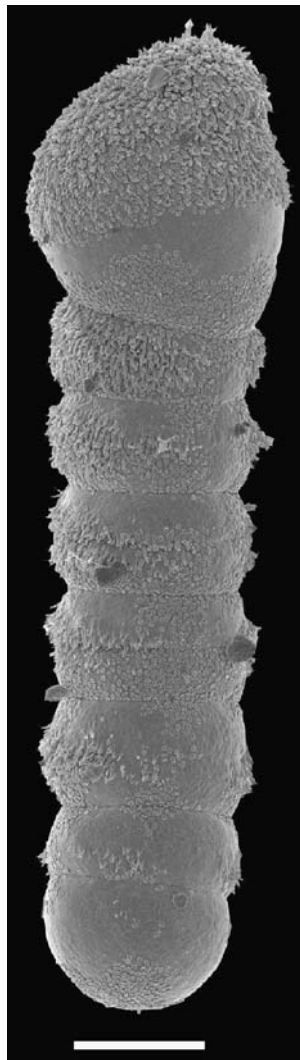
who as a collector sought the former, but routinely shot moths. This blunder is all the more excusable given that the convergences extend to physiological and metabolic identities (Welch et al. 2006). And this trail of convergences can be followed yet further, to the nectarivorous bats (e.g., Dickinson 2008; Welch et al. 2008).

Again, as is almost always the case, these convergences come with the customary adjectives of surprise. Michael Dickinson, for example, exclaims how the hovering flight of bat and moth are "uncannily similar" although he goes on to note how they are "united by the laws of physics" (Dickinson 2008, p. R470). Yet most biologists, I suspect, would still register a protest. Yes the convergences that revolve around nectarivory are striking, be they aerodynamic or metabolic (e.g., Suarez et al. 2009), but each clade is unique. Hawkmoths, hummingbirds, and nectarivorous bats are all convergent, but they are not identical. One might respond that perhaps it is time we addressed biological properties per se if we want to bring some order to evolution rather than reiterate for the umpteenth time the dry bones of the Darwinian formulation.

Trees and twigs

But the mold will be difficult to break. Who, after all, can fail to be impressed by the sheer diversity of life? It would be difficult to believe that the respective experts on dinoflagellates and tapeworms would have much to say to each other. Yet this case entails a striking intestinal convergence. Thus the dinoflagellate *Haplozoon praxillellae* (Fig. 1) adopts the form of a tapeworm to the extent of evolving attachment devices, strobili, and even a microtrichous surface (Rueckert and Leander 2008). So too in at least some cases diversification obviously occurs but it transpires to be ultimately local, whereas the convergences emerge as global (e.g., Westneat et al. 2005). Such a view, of course, is consistent with an evolutionary tree, but it is one with a decidedly peculiar shape. Again, perhaps an unforeseen tension is evident. Thus, for most biologists, what is arguably his most powerful piece of writing in the *Origin* is the depiction of the Tree of Life (Darwin 1859). No doubt there is a grandeur of this vision, but perhaps because in reality practically the entire tree is dead—in other words entombed in the fossil record—much emphasis is placed on the metaphor of twigs. Here surely is both the epitome of innumerable and remote evolutionary end-points, again with the half-articulated sense that this metaphorical Tree is blindly extending in any direction. Upon one such twig, humans are perched, supported by a slender series of branches, all now lifeless, that represent the local and entirely unimportant radiation of *Homo*. Thus, we encounter one of the central tropes of evolution. Humans are indeed

Fig. 1 The parasitic dinoflagellate *H. praxillellae*, an inhabitant of the intestine of a polychaete annelid and strikingly convergent on a tapeworm. Photograph courtesy of Brian Leander, University of British Columbia
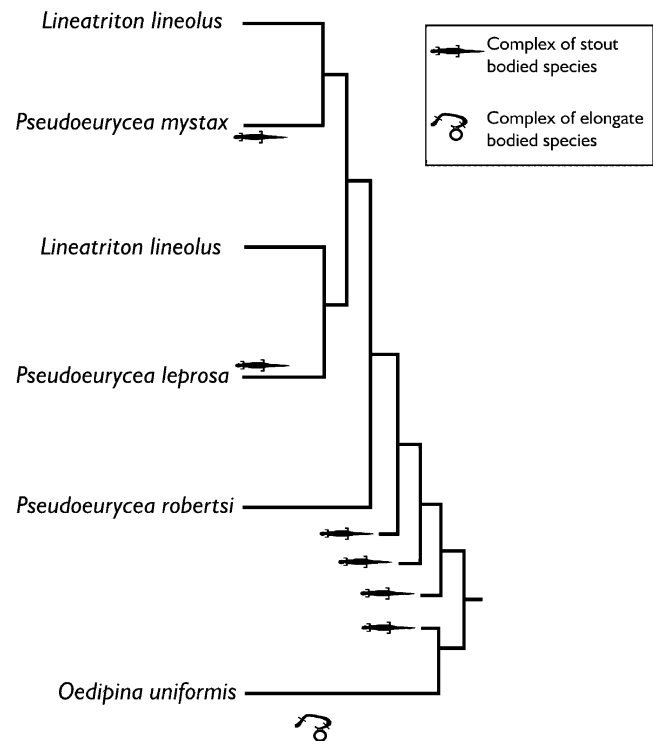

vertebrae are extended. It comes as no surprise to find two independent solutions to the same problem, and in passing we might note that only one other option exists, as exemplified in the Triassic reptile *Tanystropheus* which adds *and* elongates its neck vertebrae (see McNamara 1997, pp. 224–226). But in the case of *Lineatriton* (Fig. 2) molecular data show that this arrangement evolved at least twice (Parra-Olea and Wake 2001). In this case, therefore, convergence bites twice, both in terms of fossoriality and the manner in which body elongation is achieved. Yet Gabriela Parra-Olea and David Wake (2001) write "This is extraordinary because the morphology... is extreme in its degree of specialization... and [in *Lineatrion*] has been considered to be unique in the combination of characters" (p. 7889). Their astonishment is, however, short-lived because they then try to save the situation by remarking that this "'Lineatrion' phenomenon appears to be local and limited... [and] can *only* be considered [as] terminal twigs in the bolitoglossine radiation" (p. 7891, my emphasis). But what is there necessarily to prevent an indefinite regress of such biological solutions in the Tree of Life?

Consider, therefore, the other amphibian case, that of ranid frog ecomorphs in Madagascar and Asia (principally

"just another species": The irony that this species alone comprehends *any* metaphor escapes most observers, but seldom is irony (nor for that matter a philosophical competence; see e.g., Midgley 2003) a strong point of most biologists.

More importantly, however, is the characterization of twigs anything more than a tautology? Consider three particularly revealing examples, two taken from the amphibians, and the third from the birds. Thanks largely to the work by David Wake (e.g., Wake 1991) of all the amphibians arguably the salamanders have proved among the most instructive in terms of evolution. Of the various adaptive radiations, particularly striking are those of the plethodontids and not least those bolitoglossines where a shift to fossorial habits leads to major changes in body architecture in the form of elongation and limb reduction. In such taxa as *Oedipina* elongation is achieved by the "sensible" expedient of increasing the number of vertebrae in the trunk. Not so, however, in the related *Lineatriton*. Here the "giraffe solution" is employed whereby the

Fig. 2 Convergences of fossoriality among the Neotropical bolitoglossine salamanders whereby an elongated body and associated fossorial lifestyle have evolved independently from species with a stout body, but in addition separately in the fossorial species *Lineatriton lineolus*. Redrawn from Fig. 3 of Parra-Olea and Wake (PNAS 98:7888–7891; 2001), copyright (2001) National Academy of Sciences, USA, with their permission and the authors

India). Long thought to reflect a common ancestry on account of both adult and larval similarities, molecular data unequivocally demonstrate that these ecomorphs, adapted to such habitats as arboreal and fossorial, are convergent (Bossuyt and Milinkovich 2000). The one to one correspondences are very striking, but there is one obvious anomaly. Thus, while Madagascar boasts the poisonous mantellids (e.g., Chiari et al. 2004), no such counterpart occurs in Asia. Does the principle of convergence fail? No, because there are a series of impressive parallels between the mantellids and Neotropical dendrobatids, including aposematism (e.g., Vences et al. 2003) and alkaloid sequestration (e.g., Clark et al. 2005).

So by definition any evolutionary end-point is a "twig," but other than it was arrived at by a process of successive bifurcations, what does this tell us about the Tree itself, the grand topology of life? After all, if poisonous frogs in the form of the dendrobatids and mantellids, with their striking series of correspondences, emerged independently within the ranids, then how likely is this group, or the anurans, or the amphibians, or....? In other words, I suggest that the metaphor of the twig is misleading: Because evolution has an inevitable geometry, this does not preclude the possibility that the template of bifurcations is in one way or another restricted and is very far from occurring in "free space." In other words Darwinian evolution necessarily involves continued diversification, but what if the outcomes are subject to repeated channeling? It may then transpire that the tree has a quite specific structure, and one that it is far from a random exploration of biological space. From the two cases just considered, the bolitoglossines and ranids, this seems to be a legitimate conclusion. Does it, however, occur at any level?

In this regard, the birds may be informative. It is common knowledge that they are derived from theropod dinosaurs, as exemplified by *Archaeopteryx*. This story needs little introduction, although new discoveries (such as the legs also bearing feathers (Christiansen and Bonde 2004)) continue to be made. What is less well known is that within the theropods the "birds" evolved at least twice, and possibly three (Fig. 3), even four times. One such example is from the Upper Cretaceous (?Campanian) of Madagascar, in the form of *Rahonavis* (Foster et al. 1998a, b). While this co-exists with the true bird *Vorona* (Foster et al. 1996), this is a distinctive dromaeosaurid complete with a sickle-like claw on either foot (Makovicky et al. 2005; Senter 2007). A more basal dromaeosaurid, again of Cretaceous age, is the four-winged *Microraptor gui* (Xu et al. 2003), which although interpreted by some as capable of powered flight (Xu et al. 2005) is also reconstructed as a very efficient bi-plane glider (Chatterjee and Templin 2007; but see Hutchinson and Allen 2009).

Even more intriguing, however, are trace fossils from the Santo Domingo Formation of Argentina (Fig. 4). These are
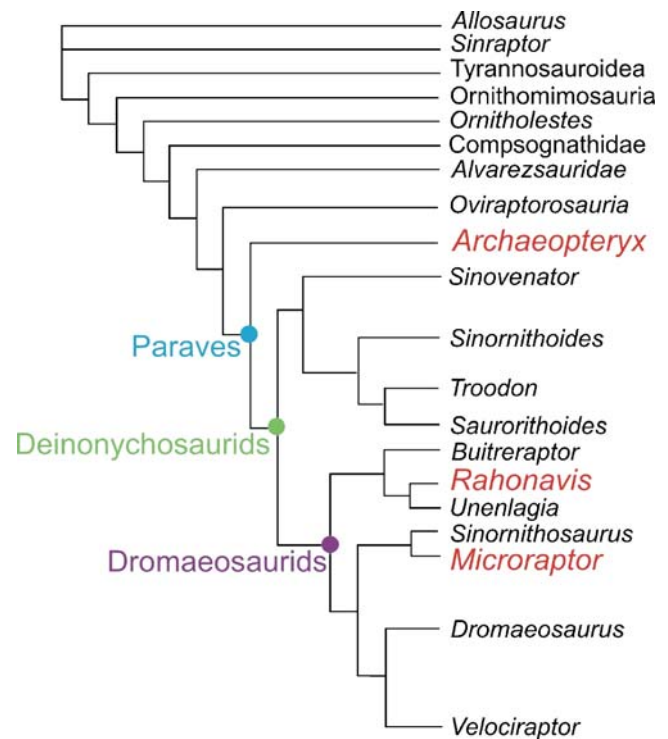
Fig. 3 Outline phylogeny of the theropod dinosaurs to demonstrate the independent evolution of flight in the Upper Jurassic *Archaeopteryx* and Upper Cretaceous *Rahonavis* and at least skilled gliding in the Lower Cretaceous *Microraptor*. Redrawn and simplified from Fig. 4 of Senter (2007), with permission of Cambridge University Press and the author

dated as late Triassic to early Jurassic, but they are remarkably bird-like. They include not only trackways but also evidence for alighting and even prod-marks, the latter recalling the behavior of modern shore-dwelling birds (de Valais and Melchor 2008; Genise et al. 2008). In this last case, it remains conjectural what group of reptiles was flying some 50 million years (Ma) ahead of *Archaeopteryx*, although yet another theropod is certainly plausible (Melchor et al. 2002). It also needs to be pointed out that so modern in appearance are these trackways that the proposed date of c. 200 Ma needs independent confirmation. The point, however, remains that independently several groups of theropods took to the air. The emergence of a "bird" seems, therefore, to be inevitable.

Trace fossil evidence suggests that the total diversity of theropods is under-determined (Li et al. 2008), and we should not be surprised if yet other clades had air-borne representatives. But such a prolixity of avian-like adaptations might at first sight be used to argue that while flight is polyphyletic in this group, it has no wider significance. Thus small size, a necessary pre-requisite for flight, evolved before any theropod took to the air (Turner et al. 2007a). As importantly, not only were large theropods quite incapable of flight evidently possess feathers (Turner et al. 2007b) but

Fig. 4 Trackways from Triassic sediments of Argentina, interpreted as being made by a flying theropod-like reptile, presumably convergent on the younger avialians. Photograph courtesy of Ricardo Melchor (Universidad Nacional de la Pampa, Argentina)

also various theropods show a variety of integumentary structures (e.g., Xu and Zhang 2005; Zhang et al. 2008), some of which are plausible intermediates to true feathers (e.g., Xu et al. 2009). So too early theropods showed features of both behavior and anatomy "necessary" for a subsequent avian existence (Milner et al. 2009).

Avian theropods are, therefore, pre-ordained, but in an evolutionary context how likely is a "feather" or a "theropod"? More than might be thought. First among the other major group of dinosaurs, the ornithischians, filamentous integumentary structures are also known (Zheng et al. 2009). Whether all such structures derive from a common ancestor or evolved independently remains conjectural, but in support of the latter view (see also Mayr et al. 2002) is the occurrence of feather-like appendages in reptiles yet more remote from either theropods or ornithischians, that is the diapsids (Voigt et al. 2009). More significant, however, is the recognition that among the major group of reptiles that preceded the dinosaurs, the archosaurs, there are a series of striking convergences with the former group (Molnar 2008). In this context, the most important are those archosaurs, which not only converge on the theropods, but to specific groups. This extends to even the level of the ornithomimosaurids (Nesbitt and Norell 2006; Nesbitt 2007), which are near-relatives of the paravialians (see Fig. 3). It is important to stress that at an earlier stage of investigations these taxa, now known to be archosaurs, had been assigned on the basis of morphological similarity to the dinosaurs. This, of course, has significant implications for the history of large reptiles in the Triassic, as well as the validity of identifications on the basis of fragmentary material. In other words archosaur and dinosaur may not always be easy to distinguish. But more importantly once again, we need to

enquire if something very like a theropod as a biological property appears to be highly probable, if not inevitable? If so, then could this principle apply to the archosaurs, the reptiles, and the vertebrates?

In conclusion, the emphasis on a vast Darwinian Tree with innumerable terminations (the twigs) has blinded us to the possibility that the points of bifurcation are much more determined than at first appears. Support for this view will emerge from other lines of enquiry, such as the nature of major transitions, the concept of innateness and inherency, and the problems with so-called deep homology. And it is the last mentioned topic to which I now turn.

Reading the runes: is there a case for deep homology?

I suspect that the great majority of biologists will be very uncomfortable with this argument of an indefinite regress. By this I mean that any time in the past the extremities of the Tree of Life necessarily are defined by the twigs, each of which will in the future either go extinct (most likely) or bifurcate (ignoring pseudoextinction or rampant "hybridization"). If, however, the principles identified above, whereby each and every cladogenesis (at any scale) results in convergences (or parallelisms), then it is difficult to avoid the conclusion that the structure of the Tree is much more deterministic than often thought. In other words the convergences are an inevitable result of the constraints of form and the strong likelihood (not least because of geographical separation) that the "experiment" will be run independently several times. In this way we are invited to consider a regress of evolutionary possibilities. Three lines of evidence can now be brought to bear. The first revolves around the identification of so-called deep homology, the notion that "complex regulatory circuitry inherited from a common ancestor" (Shubin et al. 2009, p. 818) underpins the evolutionary commonality of often morphological disparate structures. The other two are to some extent related. Thus it might seem perfectly reasonable to argue that almost by definition the higher taxonomic groups, approximately of phylum and kingdom rank, are monophyletic. There can, therefore, be no repeatability, and in any event by virtue of purported macroevolutionary processes these major transitions are by implication highly improbable. In the case of major transitions it could be argued an evolutionary breakthrough, and here instances such as the eukaryotic cell or language might come to mind, certainly has dramatic consequences but are themselves the products of fortuitous concatenations of events. From these various perspectives, therefore, one could argue that our biological "universe" is just one of an almost infinitely large number of alternative possibilities.

Whether this is quite the case will be addressed below, but consider first the claims of deep homology. In this formulation we have a homunculus-like argument with the evolutionary future "sealed" in a prior genetic arrangement. From this perspective, therefore, the repeated emergence of a complex novelty, say the camera eye, is not a convergence but at best a parallelism that draws on homologous genes. So far as the concept of deep homology is concerned there is only space to address in any detail one case, albeit of classic status, that of the eye (e.g., Kutschera and Niklas 2004). A *leit-motif* of this discussion has been the identification of the near-universal employment of regulatory transcription factors, most famously *Pax6* (and its equivalents such as *eyegone*, *eyeless* and *twin of eyeless*). In his overview of this topic, Gehring (2005) not only argued "for a monophyletic origin of the eye" (p. 171) but also even suggested that the metazoan eye was originally derived by the agency of lateral gene transfer (see also below) involving the symbiotic relationship between a dinoflagellate and a cnidarian. This proposal was inspired by the extraordinary ocelloid of some warnowiid dinoflagellates (e.g., Couillard 1984; Gómez 2008), a topic to which we return below. Nevertheless, this comparison and proposed origin is highly questionable. This is both because of the apparent absence of the appropriate regulatory genes in even the protistans closest to the metazoans, that is the choanoflagellates (King and JGI Sequencing Group 2008), as well as the fact that the warnowiid ocelloid is derived from a chloroplast (Greuet 1987) and so has no obvious link to any part of the metazoan eye.

Even so the role of key regulatory genes, including not only *Pax6* (and its orthologues) but also genes such as *Six* (and its equivalents such as *eyes absent* and *sine oculis*) and *Dachshund*, appear to provide powerful arguments in favor of eye monophyly. Similar remarks could apply equally to the identification of common cellular circuitries. But only at first sight; the reality is much more complicated. First, in the case of the remarkable camera eye of the cubozoans (Fig. 5; Nilsson et al. 2005; Garm et al. 2007) the key regulatory gene is indeed a *Pax* gene (Kozmik et al. 2003). As Plaza et al. (2003) demonstrate, however, there is no simple relationship between this gene (termed *PaxB*) and *Pax6* (which is not found in cnidarians). Indeed another cnidarian gene, referred to as *PaxC*, appears to have the closer evolutionary link to *Pax6*, but in these primitive metazoans, perhaps oddly, it plays no part in eye development. Given this evolutionary connection between *PaxC* and *Pax6*, it is not so surprising that the former gene can be ectopically employed in eye development in the fly, but to add to the confusion so can *PaxB* (Matus et al. 2007).

Of equal significance is that while various regulatory genes are indeed employed in eye development, both the families of genes and more importantly their interactions far

Fig. 5 The eye complex of a cubozoan jellyfish. Photograph courtesy of Anders Garm (University of Lund, Sweden)

pre-date the evolution of eyes (Hoshiyama et al. 2007). Thus among the most primitive metazoans that lack not only eyes but even a nervous system, a *Pax* gene occurs in both the sponges (Hoshiyama et al. 1998) and placozoans (Hadrys et al. 2005). Equally importantly another gene of key importance in eye development, *sine oculis*, occurs in the sponges (Bebenek et al. 2004). Hoshiyama et al. (1998) draw the reasonable conclusion that the *Pax* genes have adopted multiple roles. As the discoverers of *sine oculis* in sponges also remark this occurrence "would appear to raise as many questions as it answers" (Bebenek et al. 2004, p. 348), but they also stress that in various ways sponges are sensitive to light (e.g., Leys et al. 2002). So too in the case of the placozoans a possible association of what appears to be a primitive *Pax* gene with fiber cells, that might themselves be distant precursors of nerve and muscle cells (Hadrys et al. 2005), is an indication of how this evolutionary association might have arisen. It scarcely seems sensible, however, to argue that simply because a cell or tissue is in some ill-defined manner "ancestral" to the eye (as might be the case with these fiber cells), so the associated precursor gene is in turn equivalent to a *Pax6* (or *Six*) gene.

Since then these genes have never looked back. Even in groups that are drastically simplified, as in the mesozoans (which have dispensed not only with eyes but their entire nervous system), *Pax6* (and other genes) nevertheless retain functionality (Aruga et al. 2007). More significantly in at least the mammalian eye, *Pax6* shows a quite remarkable versatility of interactions in numerous aspects of development in all three transparent tissues (cornea, lens, and retina). This leads Cverkl et al. (2004) to conclude how this gene "is interwoven into a delicate network of processes at multiple

genetic... and biochemical levels" (p. 838). Further evidence for the versatility of *Pax6* in the mammalian system is evident where it can serve either to promote or repress crystallin expression (Yang et al. 2004). So too in the case of the cubozoans the *PaxB* gene has been independently co-opted for the regulatory control of several crystallins (Kozmik et al. 2008a), and these proteins of course provide further evidence for convergence across animal eyes as a whole.

Nor, as is well known, are these classic regulatory genes restricted to eye development. Consider, for example, their employment in the mushroom bodies of insects (Kurusu et al. 2000). Here *eyeless* and *dachshund* are essential, as they are in eye development. But neither *sine oculis* nor *eyes absent* are expressed, while in contrast to the eye, the regulation of the former genes is independent of each other. As Kurusu et al. (2000) note, eyes and mushroom bodies employ "a distinct combinatorial code of regulatory genes and parallel cascades" (p. 2144). Of course, finding these genes in the context of mushroom bodies is not itself surprising given that the *Pax6* genes have major roles in olfactory and brain development (e.g., Andrews and Mastick 2003). So too in fly we see spermatocyte development employing *Six* genes (*eyes absent*, *sine oculis*; Fabrizio et al. 2003), while thorax subdivision looks to a *Pax6* gene (Aldaz et al. 2003). Nor is this a peculiarity of the insects because in the vertebrates the genetic cascade utilized in the fly eye finds employment for muscle development (Heanue et al. 1999). Such redeployments may be familiar (see also Rebay et al. 2005; Kumar 2009) but they remind us there is no "master template" for eyes (nor indeed for any other organ). Presumably no biologist would wish to argue that spermatocytes, thorax, and muscle are homologous because they employ the same genes. Obviously *Pax6* was derived from more primitive genes and so too has been redeployed in organ systems far removed from eyes. To regard this as any sort of "deep homology" is at best uninformative, and in reality a near tautology.

One might reasonably claim all that this indicates is the deployment of the genes from an "original function," but determining what this nebulous function actually was turns out to be far more elusive. As already indicated, *Pax* and *Six* genes are evolutionarily very ancient, and via a complex evolutionary history (e.g., Hadrys et al. 2005), they have evidently been very widely deployed. Thus to return to the case of the eye, to observe that there is a basic identity of cellular phototransduction processes (Koyanagi et al. 2008, but see Kozmik et al. 2008b) hardly serves as a demonstration of deep homology. This is for two reasons. First, the opsin cascade identified by Koyanagi et al. (2008) is only one component of the visual system. More importantly it leaves open the possibility that the system derives from a more primitive system involved with sensory transductions that have at best a tenuous connection to phototransduction.

An alternative, dare one say, more fruitful approach is the one adopted by Kozmik (2008; see also Jonasova and Kozmik 2008), who notes how care is required in "drawing homologies based solely on gene expression (molecular) data" (p. 336). Thus the conservation of developmental cascades of regulatory genes may appear to be striking but it always needs to be put in a wider context. Some aspects of this are reviewed above, but Kozmik's (2008) proposal is important because he suggests that given the basic function of any eye depends on the dual structure of a shielding pigment and a transduction protein (an opsin), so this bipartite necessity arrangement is directly correlated to the twin roles of the paired domain and homeodomain in the *Pax* gene. Given this intriguing possibility of a congruence between molecular architecture and the design specifications of the simplest type of eye, then to speak of this as a homology is almost trivial. So too the repeated emergence of complex eyes, in what Jonasova and Kozmik (2008) briskly identify as a "lens/corneal upgrade," re-affirms that complex eyes are, as long supposed, polyphyletic.

While the role(s) of *Pax6* and eye evolution exemplify the tension that exists between molecular architecture and expressed phenotypes, such questions that attempt to appeal to notions of deep homology are pervasive in evolutionary biology. What, for example, are we to make of the puzzling phenomenon known as sleep, not least in terms of cognitive competence? Intriguingly the striking similarities between birds and mammals, including slow wave sleep (SWS) and rapid eye movement, are evidently convergent (Low et al. 2008). In the case of the former mode of sleep, the presence not only of SWS but also of its homeostatic regulation in both birds and mammals may be linked to the evolution of large brains showing extensive interconnections that are a sine qua non for cognitive sophistication (Rattenborg et al. 2009). This is all the more important because of evidence that cognitive capacity in the two groups arose independently (e.g., Emery and Clayton 2004), but is based on strikingly dissimilar brain architecture (Jarvis et al. 2005).

But the capacity for sleep goes phylogenetically much deeper and proponents of deep homology might legitimately identify what appears to be the common genetic and cellular currency (e.g., Shaw et al. 2000) as evidence against convergence. But again caution may be required. First the striking similarities between sleep in mammals and the insects, notably the bees (e.g., Kaiser 1988; Eban-Rothschild and Bloch 2008) and fly (e.g., Nitz et al. 2002), involve species with cognitive capacitance and complex behaviors. So too when a possible example of sleep is identified in cnidarians (Seymour et al. 2004) the assumption that this points to phylogenetic antiquity needs to be balanced against the fact that the jellyfish in question are the extraordinary

cubozoans, behaviorally sophisticated (e.g., Lewis and Long 2005) and possessors of sophisticated camera eyes (Fig. 5; Nilsson et al. 2005). To speak of conserved mechanisms of sleep (e.g., Olofsson and de Bono 2008) begs, therefore, the same sorts of questions as are raised in considering the evolution of eyes. Moreover, while Allada and Siegel (2008) adopt a similar stance in support of a fundamental identity of sleep in animals, they also remind us that the biochemical antecedents may extend far deeper into the Tree of Life.

Major transitions: too big a hurdle for convergence?

It seems, therefore, that the concept of deep homology provides an orthodox Darwinian perspective, but in doing so may serve to elide some more interesting general principles of evolution. Two of these revolve around the questions of (a) whether there are particular major transitions in evolution that are in themselves demonstrably improbable or fortuitous and in a related vein (b) exactly how such transitions are achieved. Are they, for example, exemplars of rare macroevolutionary processes (an admittedly diffuse topic that could include species selection, punctuated equilibria, or gene transfer)? Both topics deserve book-length treatments, and here only an outline of the argument can be presented.

Ponder, for example, the origin of the eukaryotic cell, not least in terms of the topic of primary endosymbiosis (e.g., Kutschera and Niklas 2004, 2005). Suppose that this event is exactly the sort of evolutionary hurdle—a once-in-a-galaxy event—that would permanently derail the notion of evolution having any predictability. Without eukaryotes, multicellular complexity, including readers of *Naturwissenschaften*, is permanently precluded. While the hallmark of the eukaryotes are the endosymbiotically acquired mitochondria and chloroplasts, the fact that an ongoing endosymbiosis between an amoeba (*Paulinella*) and a cyanobacterium (phylogenetically remote from the ur-chloroplasts) not only provides a glimpse as to how this process may have occurred some 2 billion years ago (Marin et al. 2005; Nakayama and Ishida 2009) but also indicates that at least this aspect of eukaryogenesis is unlikely to be a fluke.

A priori, and perhaps one day to be confirmed on the discovery of an extraterrestrial biosphere, the evolution of a eukaryotic condition does not seem to be inherently a highly improbable step in the history of life (not least because in fact various bacteria possess many features otherwise thought to be typical of eukaryotes). Similar exercises can in principle be undertaken with respect to the origination of any major group. In each case I would suggest that the combination of inherency (notably in the availability of already evolved molecular systems) and

convergence (indicating the likelihood of a given biological solution) will indicate that any transition, however major, is far from fortuitous.

While it is reasonable to assume that major transitions are in the making today, for all practical purposes, the only direct method of inspecting such events is via the fossil record. Such evidence is necessarily highly sporadic because of the incompleteness of the fossil record and the general reliance on skeletal remains. Nevertheless I suggest that the few cases where sufficient information is available could be indicative of a universal pattern. It is also worth mentioning that just as evolutionary convergences engender repeated exclamations of surprise, so the literature documenting such emergences is redolent with similar adjectives that proclaim the observed patterns to be "puzzling," "bizarre," "unexpected," and "surprising." And as with convergences it is interesting to see how expectations, almost always drawing on the irreproachable methodology of cladistics and where homoplasies are regarded as at best a profound irritant, collide with how evolution appears actually to work.

As it happens, the origin of birds (Figs. 3 and 4) is instructive in this regard (Zhang et al. 2008), but perhaps of even greater interest is the fish-tetrapod transition. This entails, of course, a set of changes that in moving from water to land are at least as profound as those required for the conquest of the air. In the context of the origin of a tetrapod, while much material is fragmentary (e.g., Daeschler et al. 2009), a series of new discoveries, including remarkable cases of articulated material, means that the observed patterns of evolutionary diversification are at least moderately secure.

Concerning tetrapod origins, a convenient starting point lies within the Silurian osteichthyans, in as much as this group shows a fundamental divergence into the actinopterygians and the ancestral assemblage of sarcopterygians (which include the coelacanths and lungfish, but also the group that ultimately gave rise to the tetrapods). In the case of the osteichthyans, remarkable articulated material of *Guiyu oneiros* from south-west China (Zhu et al. 2009) reveals what transpires to be the *leit-motif* of such transitions, that is the unexpected mixture of anatomical features whereby primitive and derived are intermingled. Not only that, but this is combined with rampant parallelism, in this case between the actinopterygians and sarcopterygians.

Exactly the same, however, applies to the latter group where in their landmark paper Ahlberg and Johanson (1998) noted "Tetrapod-like character complexes evolved three times in parallel within the Tetrapodomorpha" (p. 792; Fig. 6). Of particular interest is a basal group, known as the rhizodonts. Here the pectoral fins have independently evolved a striking limb-like arrangement (Jeffery 2001; Johanson and Ahlberg 1998), and the jaws

Fig. 6 An outline of tetrapodo-morph phylogeny to indicate parallelisms in limb development among rhizodontids, tristichopterans, and crown-group tetrapods. Redrawn from Fig. 3c of Long et al. (2006), with permission of the Nature Publishing Group and the authors
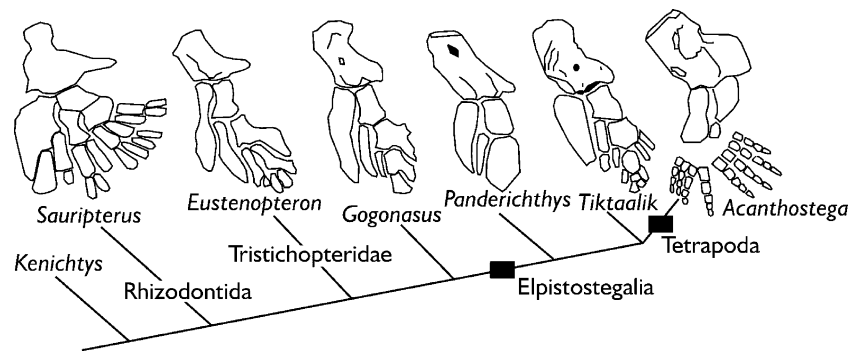
also show significant parallels (Brazeau 2005). And these principles, of repeated parallelisms and unexpected character combinations, apply at each level of divergence within the tetrapodomorphs. Thus we see further convergences between the tristichopterans (which includes the canonical *Eusthenopteron*) and the tetrapods (Snitting 2008); even in the most crownward group, we continue to encounter unexpected mixtures of characters (Alhberg et al. 2000; Long et al. 2006; Boisvert et al. 2008; Boisvert 2009).

From one perspective these parallelisms are, despite the recurrent expressions of surprise, exactly what one might expect. As many of these workers point out that the emergence of tetrapod-like forms is associated with a major change in ecology, from the primitive method of active swimming and suction feeding (the latter, of course, convergent, e.g., Deban and Olson 2003) to a lurking ambush predator. So too it is evident, although again unsurprisingly, that the degree of diversification has been considerable. Accordingly, many of the unexpected morphologies reflect hitherto "unsuspected" specializations, notably in limb design (Shubin et al. 2004).

Despite the momentous nature of the evolution of tetrapodomorphs, it is curious that the wider significance of the major advances in our documentation of this event seem to have provoked at best a muted response. Nevertheless, just as with birds, and in the light of repeated parallelisms, it is difficult to see how the evolution of a tetrapodomorph should in any way be unexpected, at least since the emergence of the jawed fish (which again invites a regress of enquiry ever deeper into the Tree of Life). Yet in the canonical world of current evolutionary research, such evidence is systematically side-lined. Nor is this at all surprising. First, like the eyes, the evolution of the limbs is cast into the context of deep homology (Shubin et al. 2009), with the implication that if somehow the relevant developmental genes had not been available then no tetrapods would have hoisted themselves out of the water. However, the objections raised in the case of the eye are likely to apply with equal force to the limb. Indeed perhaps more so, because it is interesting that Shubin et al. (2009) noted in this context that given existing developmental models "then

fins would have arisen by the co-option and ectopic deployment of outgrowth-promoting circuits at novel anatomical sites" (p. 821). Quite so; a deeply engrained reluctance to consider probabilities of evolutionary outcome also stems from the cladistic methodologies that are universally employed in this area. Here, to the first approximation, homoplasies and their consequent parallelisms are regarded as tiresome irritants, which help to explain, I suspect, the repeated surprise of the investigators as they identify mosaic evolution. Irrespective of whether mosaic evolution is universal, it raises important questions as to the integration of form, employment of developmental mechanisms, and as already emphasized the possible combinatorial restrictions on adaptive complexes. It is, therefore, refreshing to consider the trenchant review of tetrapod origins by Vorobyeva (2003). As with other workers, she remarks how "Many features of the tetrapod organization appeared mosaically and in parallel in various groups of Paleozoic crossopterygians" (p. 456), and much of her paper is an exploration of the likely importance of heterochrony (see also McNamara 1997). She concludes that "different sarcopterygians acquire tetrapod features independently," but intriguingly adds that there must exist "common latent morphogenetic potentialities" (p. 457).

While space does not permit more detailed explorations of the major evolutionary transitions, among which those associated with the Cambrian explosion are of particular interest (e.g., Conway Morris 2003a, 2006), it is likely that very much the same story will emerge. Thus, mosaic evolution will indeed be the norm. Although the cladistic methodologies will continue to face difficulties in ordering what may look like little more than a melting pot of characters, in point of fact, it is exactly these supposedly bizarre combinations of characters that will be highly instructive in at least three regards. First, they will assist in burying the myth that major transitions depend on macroevolutionary processes distinct from those involved with speciation. Second, and linked to the first point, the initial differences between groups that will ultimately be defined as phyla are trivial. Third, the evidence for parallelism in diversifications points toward the emergence

of stable combinations. This in turn indicates that at any point in history of life given solutions—such as tetrapodomorphy—are unlikely to be unique.

But what about lateral gene transfer?

Earlier in this review, it was suggested that the parallelisms in any adaptive radiation invite a regress of causal explanations that point to the heterodox implication that the configuration of the Tree of Life is pre-determined. If, moreover, appeals to "deep homologies" fail for the reasons adumbrated above, then the overall thesis presented here might still collapse for a quite different reason. Given that lateral (or horizontal) gene transfer is rampant, then the potential exists for a particular biological solution to be exported by one or other vector to a remote part of the Tree of Life. From this perspective, convergence would then be nothing more than a documentation of routes taken.

I would argue, however, that while horizontal gene transfer is frequent, this does not undermine the importance of convergence. Here is one example revolving around the oomycetes. Despite striking similarities between this group and the fungi, notably among the category of invasive plant pathogens, they are only distantly related (Latijnhouwers et al. 2003). In either case of key importance is the capacity to attack the host both by the application of turgor pressure (Money et al. 2004) and employing enzymes. It transpires, however, that a number of genes, including those involved in osmotrophy (and hence turgor control; Richards et al. 2006) and cutinases (Belbahri et al. 2008), have been transferred laterally. So in this case given the gene is not "ancestral," then perhaps we can demolish the wider concept of convergence by importing the "right sort of gene." But this is too simplistic. First, although horizontal gene transfer is rampant, and despite such conjectures as the "eye gene" ultimately stemming from a symbiotic dinoflagellate (see above), there is no simple correlation between gene transfer and convergence. One also needs to enquire as to the functions of a given protein. In other words simply identifying a specific protein, such as a cutinase, is not sufficient unless one knows what other functions it might possess and whether it has evolved more than once. Thus, in the case of cutinase, it employs a catalytic serine triad (Martinez et al. 1994), which is itself a classic example of molecular convergence (e.g., Gherardini et al. 2007). Thus in the case of oomycetes, the fact that their effectiveness depends on lateral gene transfers is only part of a wider story. The convergence between oomycetes and fungal pathogens is organismal, and the imported genes must be incorporated in a highly integrated system. In other words, such genes are necessary but not sufficient to define this convergence.

Thus in the case, for example, of osmotrophic genes, we would need to know much more about their evolutionary history and indeed possible convergences in function. Thus the specific methods of regulating turgor pressure in an ascomycete (the group from which the oomycetes evidently acquired their osmotrophic genes (Richards et al. 2006)) and an oomycete probably look to different mechanisms (Lew et al. 2004). This is notwithstanding the fact that each group shows significant similarities in the hyphal tip (where the turgor is applied) and serves as a reminder that the heart of convergence lies in the repeated evolution of an adaptive solution. To be sure that the details of any route taken will be of interest to the specialist, but in the wider context whatever route happened to be employed is surely of less importance. Evolution, therefore, describes the journey and the type of vehicle employed but is silent as to what I call the "map of life." Does not the ubiquity of convergences indicate that the "landscape" across which evolution must navigate is not one, metaphorically speaking, of rolling territory studded by occasional adaptive peaks, but rather is an extremely precipitous landscape where the bulk majority of an immense terrain is uninhabited. Accordingly evolution is constrained to follow remarkably few paths.

What is innate in evolution?

Both above and elsewhere (Conway Morris 2003b), I have outlined the concept of evolutionary inherency, that is, the notion that pre-existing configurations make subsequent evolutionary outcomes far more likely. For example, given the availability of heat-shock and stress-related proteins, then the emergence of transparent tissues employing crystallins is an inevitability. And this, of course, is reflected in the rampant polyphyly of crystallins in animal eyes. So too is transparency (Johnsen 2001), not least by employing the ingenious physics of grading refractive indices across a papillate surface. It will be very surprising if extraterrestrial organisms fail to employ exactly the same method. Nevertheless, the ideas of inherency and evolutionary inevitabilities do not feature in the majority of evolutionary dictionaries. It is intriguing, therefore, to see how the related idea of innateness is now receiving attention. From one perspective, neither inherency nor innateness should cause surprise. After all, evolution is a historical process and arises from a substrate of pre-requisites and also frequently employs co-option. Inherency and innateness, however, imply that the options are restricted, and so as concepts are important in a predictive biology. As we have already seen above, pollination syndromes seem to be "waiting to be claimed," and in a sense all convergences are arguably responding to attractors embedded in the evolutionary landscape. Yet to identify specific examples of innateness remains helpful.

Consider, for example, the crabs. As crustaceans, they are a rich source of evolutionary convergence. A striking example is the manner in which the olfactory organs of the robber (or coconut) crab have converged in terms of anatomy, behavior, and physiology on the arrangement seen in the insects (Stensmyr et al. 2005; see also Harzsch and Hansson 2008). The robber crabs belong to the anomurans, but independently, the brachyuran crustaceans, notably the grapsids, have also engaged in various sorts of terrestrialization (e.g., Anger 1995; Diesel et al. 2000). Among the more remarkable are those that occupy pools formed in the axils of plants. While the examples from Jamaica are justly well known for the complexity of their ecology, for example, in terms of parental care (Diesel 1992, 1997), their counterparts in Africa point to equally remarkable convergences, not least in terms of behavior (Bayliss 2002).

Crabs, therefore, are adept at exploring a variety of environments, but how likely is a crab per se? In fact, among the decapod crustaceans, the crab-morph (whereby the abdomen is tucked beneath a well-calcified carapace) has evolved five times, four in the anomurans and once in the brachyurans. Yet in one way this is decidedly odd. Crabs occupy an extraordinary range of habitats: from the top of mangrove trees and Tanzanian tree boles to abyssal trenches. In documenting the repeated emergence of a crab-morph Morrison et al. (2002), note that their emergence might be "an innate tendency" (p. 345). Clearly this solution reflects an all-purpose adaptability, but appeal might still be made to developmental constraints underpinning this apparent "innateness." Possibly so, but Morrison et al. (2002) remind us that while this may explain the apparent ease in evolving a crab-morph, it should not be the default assumption (and see Rüber and Adams (2001) for similar reservations with respect to convergence among cichlids). Thus, as with deep homologies, although the idea that convergences must reflect developmental restriction is certainly the case in some instances, the emerging counter-examples (e.g., Tanaka et al. 2009) suggest that no simple correlation exists. Moreover, at least in the case of crabs developmental constraints are unlikely to be the entire story because in an independent case of carciniza-tion the cycloids, an extinct and somewhat problematic group of crustaceans, have also converged on the crab-morph (Schram et al. 1997). This innateness appears to be complimentary to my arguments for an indefinite regress of predictable forms in the evolutionary tree: Give me a crustacean and I will give you a crab; give me an arthropod and again I suspect I will be able to deliver a crustacean....

Many more examples could be given, but space allows only two. The re-iterated evolution of saber-tooth morph in the cats is well-documented, with its independent evolution in the nimravids, barbourfelids, and machairodonts (e.g., Anton et al. 2004). Of equal note is despite the fact they are all extinct, the living Clouded Leopard is evidently navigating toward the same type of hypercarnivory (Christiansen 2006, 2008). Nor, of course, is this convergence confined to the placentals, because among the marsupial thylacosmilids we again find a striking saber-tooth morph (e.g., Turnbull 1978). What is also worth stressing is that among the borhyaenids the thylacosmilids represent a remarkable morphological excursion (de Muizon 1999). It seems reasonable to suggest that despite the trophic diversity of the mammals (marked, of course, by many other convergences), there was an innate tendency to terrify herbivores with hypertrophied canines. And if not death by saber-tooth then perhaps by the recurrent evolution of the leopard-morph? Consider the American cheetah. As Adams (1979) remarked when comparing this extinct cat with its African counterpart "The points of similarity are so extensive and of such a complex nature that a hypothesis attributing their origin to other than common genetic descent would require pushing the concept of parallel evolution to an unprecedented extreme" (p. 1155). Given in particular the extraordinary identity of the teeth, which effectively act as a gigantic carnassial, Adams' point is entirely reasonable, except the evidence now indicates it is convergent (Barnett et al. 2005; see also Christiansen and Mazák 2009).

As a final example of evolutionary innateness, I turn to the fascinating topic of skin coloration. Who can fail to be impressed by the blue scrotum of the vervet monkey or mouse opossum, or tactfully shifting our gaze from mammal to bird, so to an equally striking coloration in the face of the hoatzin (which in another context has independently evolved rumination (Grajal 1995))? The source of this type of coloration lies in coherent light scattering that arises from biological nanostructures that employ organized arrays of collagen. The point is that not only is this system rampantly convergent in the birds, where it has evolved something like 50 times (Prum and Torres 2003), and mammals (Prum and Torres 2004), but as these workers remark these convergences arise "because collagen has several intrinsic features that *predispose* it to evolve color-producing nanoperiodicity" (Prum and Torres 2004, p. 2167; my emphasis). These researchers also suggest that the wider prevalence of such skin coloration in the birds is because of avian color vision. The occurrences of tri- and tetrachromacy could lead us down yet other fascinating avenues of convergence, not least the independent evolution of trichromacy. Thus, among the mammals apart from the apes, this capacity has evidently evolved independently in both the New World howlers (Jacobs et al. 1996) and Australian marsupials (Arrese et al. 2006).

Molecules of choice

Where collagen underpins animal coloration (and note color vision is convergently dependant on substitutions of amino acids at key sites e.g., Yokoyama and Radlwimmer (2001)) then such observations beg the wider question of whether we can speak of "molecules of choice." In the specific case of the visual opsins, Fernald (2000) has aptly referred to their employment in eyes as "irresistible" (p. 446). While we should note in passing that the bacterial opsins are evidently completely independent (e.g., Soppa 1994; Larusso et al. 2008; see also Brown 2004), the point is that although in principle a given biological function might employ a huge number of alternatives (after all, is that not what evolution is largely all about?), in reality, nature returns to the tried and tested, molecules that actually work. A striking instance of this is found in the proteins employed for gustation and olfaction in the insects.

Opsins, of course, belong to a huge class of proteins (G-coupled protein receptors) that serve for transduction in other sensory systems. In this context, the arrangement is a classic transmembrane arrangement with seven helices. Just such a configuration is found in the olfactory system of insects, but astonishingly, it now transpires that these proteins have a completely different origin (Fig. 7). This is evident not only from the sequence dissimilarity but also the reversed configuration of the C- and N-termini (Lundin et al. 2007). That this protein must be unrelated to the classic opsin type became clear some years ago (e.g., Benton 2006). It is now evident that they belong to a class of non-selective cation channel proteins (Sato et al. 2008; Wicher et al. 2008), albeit possibly related to the so-called PAQR proteins that intriguingly have also been linked to other types of receptor (Smart et al. 2008). It surely seems puzzling that with opsins and related proteins being
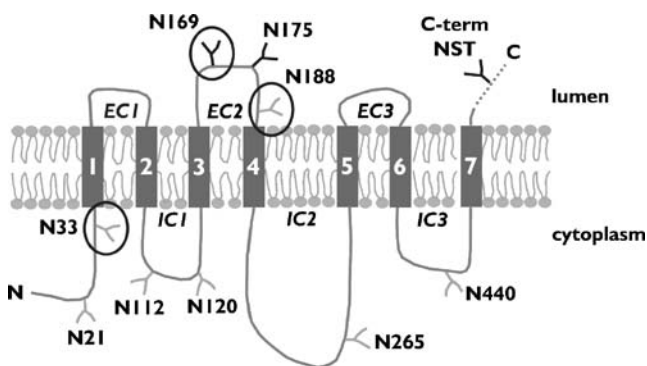
Fig. 7 The Or83b protein of *Drosophila*, an odorant receptor that is organized in the same way as a standard G-coupled-protein receptor, but is convergent. Note the seven transmembrane helices. Presumed sites for glycosylation are *circled*, those modified when inserted into *Drosophila* rough microsomes are shown in *black*, whereas unmodified sites are in *grey*. Redrawn from Fig. 1A of Lundin et al. (2007), with permission of Elsevier Press and the authors

employed elsewhere in the insect sensory apparatuses, they have opted to recruit an unrelated protein for exactly the same transduction function. What matters, of course, is that the close correspondence in structure suggests that convergence of function will ensure very much the same molecular solution.

These convergences haunt all aspects of the evolution of sensory systems. Thus, despite the radical differences in the anatomical arrangement of olfactory systems in vertebrates and insects, in reality, the differences are "skin deep" (another neglected trope in evolutionary biology, which speaks to other striking convergences such as those between tunniform fish and lamnid sharks, e.g., Bernal et al. 2003; Donley et al. 2004). And in the context of insect and vertebrate olfactory systems, Kay and Stopfer (2006) not only note how the convergences can be found at functional, physiological, and structural levels but they also remark how it represents "a beautiful case of convergent evolution." And they make the equally important point that this arrangement "may be one best way to process information about odorants" (p. 433).

In the context of the olfactory process of key importance are those proteins that serve to bind the incoming molecules. And here too we find that a protein that "ought" to be used is passed over in favor of an outsider. Thus, mammals employ lipocalins (e.g., Tegoni et al. 2000), whereas insects use proteins with a quite different molecular architecture (Graham and Davies 2002). Yet unsurprisingly they have many similarities, not only in being able to lock onto the various molecules but also with respect to their small size and very high concentrations adjacent to the olfactory surface (Pelosi et al. 2006). What is, perhaps, more noteworthy is that insects presumably could in principle also employ lipocalins. This is because these proteins are employed not only as aphrodisiacs, where they may serve to bind sex pheromones (e.g., Korchi et al. 1999), but also even in the context of convergence in the nutritive milk of a viviparous cockroach (Williford et al. 2004; see also Perry and Nalepa 2003).

These examples of "molecules of choice" need to be set against other instances where ostensibly there are two equivalents, but one evidently wins hands down. A good example involves the respiratory protein hemerythrin. As has long been appreciated, its distribution among the animals is both sporadic and apparently without phylogenetic significance (e.g., Schreiber and Storch 1992; Negri et al. 1994). It is, however, widespread among prokaryotes, and it is entirely reasonable that it was co-opted by the metazoans (Isaza et al. 2006). It is possible that this occurred early in bilaterian history and hemerythrin was then almost universally lost. This seems less plausible, but some evidence suggests that if indeed of independent origins then it was from the same bacterium, possibly a marine symbiont (French et al. 2007).

The prokaryote in question is yet to be identified. The more important point, however, is the abundance of hemerythrins among the prokaryotes (French et al. 2007) that suggests that this protein is metaphorically on the evolutionary shelf, but is practically never used. As Bailly et al. (2008) note, hemerythrins "exhibit a considerable lack of evolutionary success in metazoans" (e.p. 7), perhaps because they are mutationally more vulnerable. These authors also remark that in comparison to the remarkable globins, their counterpart has "barely maintained a foothold in living organisms" (e.p. 7).

When it comes to iron-based respiratory proteins, hemoglobin remains the molecule of choice. So too when the cation employed is copper, hemocyanin emerges as the convergent winner (e.g., Van Holde et al. 2001, Burmester 2004). But it is also important to recall Kurtz's (1999) observation that hemoglobin, hemerthryn, and hemocyanin represent "three solutions to a common problem" (p. 85). This is not to rule out other solutions where hitherto unknown metalloproteins can handle the highly reactive diatomic oxygen, but if they are ever found do not be surprised if they are convergent. This is because, as Kurtz (1999) points out, any such solution is evidently "Nature's tiptoeing along the edges of the energetic barrier separating reversible O_2 binding from O–O cleavage without crossing it" (p. 97). Here is a metaphor that although applied to respiratory proteins arguably begins to capture a new view of evolution, where the Darwinian explanation must be set in a context of biological form poised on a knife edge of possibilities, discovering the narrowest of paths that thread their way through vast landscapes of non-viability.

Does evolution possess a logic?

This view is emphatically not in conflict with the Darwinian formulations, but looks beyond them to enquire what deeper organizational principles underpin evolution. Indeed are we allowed to speak even of a logic in evolution? Unfamiliar as such terminology may be to most evolutionary biologists, in fact, it is now being increasingly used. Thus, if we re-visit the striking convergences that pervade the sensory systems when it comes to the gustatory capacities of fly and mammals, Thorne et al. (2004) identify "a remarkable convergence of anatomical as well as molecular features" (p. 1076). But intriguingly, the subsection from which this quotation is taken is entitled "Similar Logic of Taste Perception in Insects and Mammals" (p. 1076). So too while not specifically invoking a logic of organizational possibilities, in exploring the genetic circuits found in a model prokaryote (*Escherichia coli*) and eukaryote (yeast), Conant and Wagner (2003) document not only how they have evolved multiple times *within* either group but more importantly also between bacterium and fungus. Thus they

write "The finding that gene circuits have evolved repeatedly makes a strong case for their optimal design," and they continue by remarking that if the tape of life was to be re-run then "Transcriptional regulation circuits.... might come out just about the same" (p. 265). Nor are they alone in such a view. In a remarkable survey of the available mutational pathways that confer bacterial resistance to an antibiotic by the employment of β-lactamase, Weinreich et al. (2006) note that in their study that although more than a hundred pathways exist, in practice, nearly all of them are dead-ends (Fig. 8). Thus, they conclude "that intramolecular interactions render many mutational pathways selectively inaccessible, which implies the protein tape of life.... might be surprisingly repetitive" (p. 113).

It seems inevitable that many deeper organizational principles remain to be discovered in biological systems. Once again Darwinian explanations are entirely adequate to explain how to get from A to E (even if convergence shows that the order may be A→K→P→E or A→Z→B→E), but emphatically not what the organizational states must be. The evolution of innate immunity provides one such example. It is, of course, clear that this is phylogenetically very ancient, unsurprisingly so given any cell has to be able to protect itself from onslaught by microbial pathogens. However, it is evident that in part the innate immune system draws on the capacities of the remarkable peroxidases, which as Passardi et al. (2005) note "have more functions than a Swiss army knife," not least because of their fiercely oxidative capacity (Zamocky et al. 2008). In passing, we should note that the all-purpose metaphor of the Swiss army knife has been seized upon by other investigators, as in the case of an antigen membrane protein of bacteria (Smith et al. 2007). This is yet another pregnant area for evolutionary investigation, seeking to explain the astonishing versatility of many molecular systems. One such instance is the striking capacities of the β-grasp fold (Burroughs et al. 2007). So too with the peroxidases, but importantly in the context of this essay these enzymes transpire to be convergent. Thus, in addition to their classically independent evolution in animals (and actually other groups) and the prokaryotes plus fungi (e.g., Welinder 1992), in reality, there appear to be at least two more cases of independent origination (Zubieta et al. 2007; Ebihara et al. 2005).

The innate immune system, of course, involves a great deal more than the employment of peroxidases, but what is of particular importance is that although both animals and plants employ the same system of transmembrane and intracellular receptors, despite strikingly similar organization (such as the hallmark of leucine-rich repeats), this arrangement is evidently convergent (Fig. 9). As Ausubel (2005) remarks in his overview of this area "Given the compelling case for convergent evolution of innate immune pathways, an important issue is why evolution has chosen a

Fig. 8 Mutational pathways of a β-lactamase for evolution of resistance to the antibiotic cefotaxime. *Color and width of arrows* indicate the relative probability of a given pathway. Redrawn from Fig. 2 of Weinreich et al. (2006). From Weinreich et al. (2006). Reprinted with permission from the AAAS and the authors
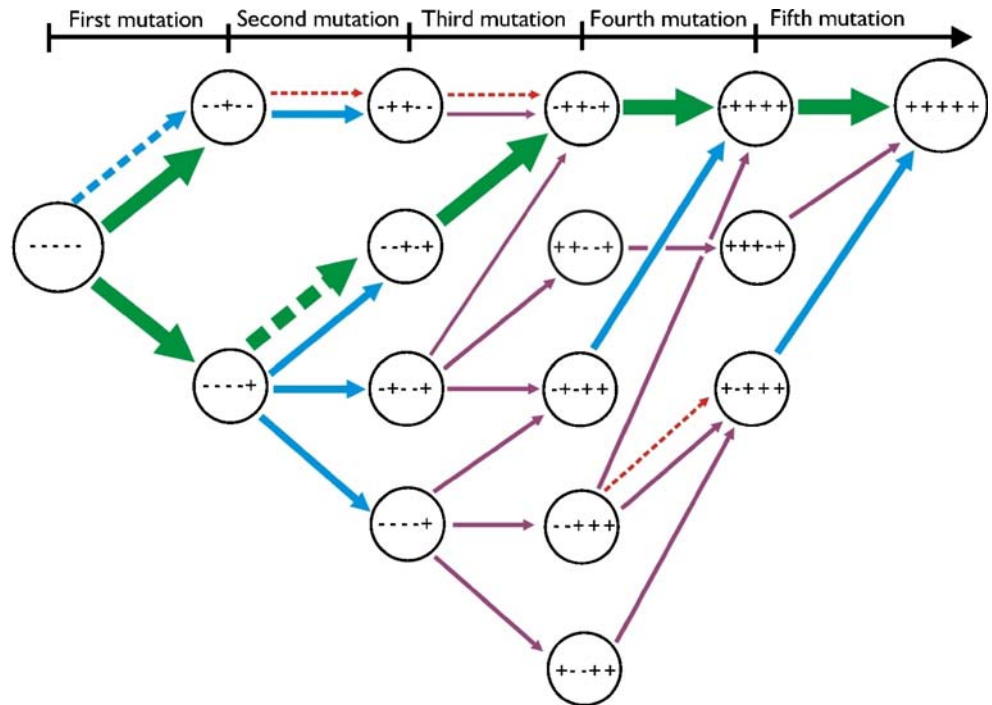
limited number of apparently analogous regulatory modules in disparate evolutionary lineages. Does this reflect inherent biochemical constraints that result from a similar overall 'logic' of how an effective immune system can be reconstructed?" (p. 977). Such an argument might apply equally to the independent evolution of the adaptive immune system, where again the jawless fish employ the leucine-rich repeats, but provide a defense against pathogens that rivals the more familiar arrangement in other vertebrates (e.g., Alder et al. 2005; Pancer et al. 2004, 2005; Guo et al. 2009).

But the logic of immune systems has wider ramifications. This is because as Blalock (1994) remarks the immune system and brain "speak a common biochemical language" (p. 504) and they communicate using a similar molecular syntax. In particular the major histocompatability complex (MHC), which classically is associated with the immune response, also plays a central role in the development

of the brain. This could, of course, be simply taken as yet another example of molecular versatility. And so in a way it is, except the employment of MHCs points to some fundamental organizational principles in evolution (Boulanger et al. 2001). In effect both the developing brain and the immune system are an engineer's nightmare: how are billions of synaptic connections or the threat from an equivalent number of antigens to be addressed? Both, of course, have a similar logic of decision-making processes, and indeed, the evidence is that it was co-option by the immune system from the nervous system rather than vice versa. Either way, it is also increasingly clear that not only is there "a common biochemical language" (Blalock 2005) but also immune and nervous systems are intimately linked in a way that re-ignites the folk-loric wisdom of mental health and emotional stability having unavoidable connections with resistance to disease.

Fig. 9 Convergence in the innate immune response system in both terms of surface and intracellular receptors. Redrawn from Fig. 1 of Ausubel (2005), with permission of the Nature Publishing Group and the author
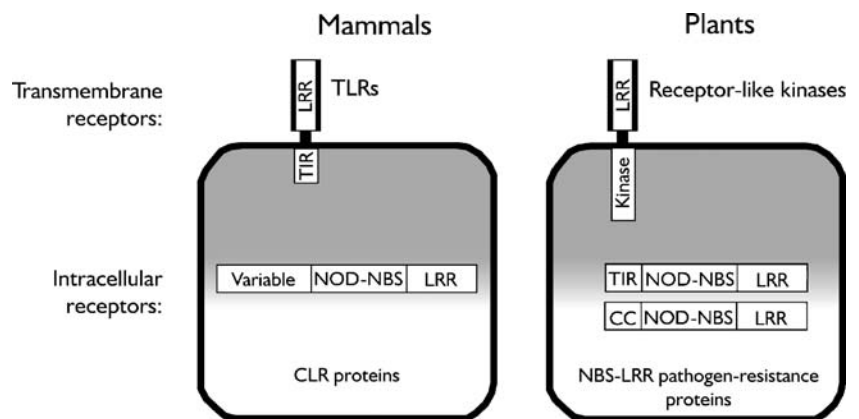
Convergent intelligence, even minds?

It would be quite wrong to suggest that Blalock is engaged in a sleight of hand, but when he writes that this work demonstrates that there is "little doubt that mind is capable of influencing the immune system" (Blalock 2005, p. 130), perhaps we are entitled to raise an eyebrow? This is because such remarks presumably presuppose a naturalistic explanation of mind, a view that Darwin espoused but also struggled with. Given that for the scientist the study of mind and consciousness is one of the great graveyards of ambition, it would be rash of me to offer any solution. Nevertheless, the recognition of inherency and convergence suggests that arguably the greatest of scientific problems can be put in some new contexts.

To begin with, there are very strong lines of evidence to suggest that not only the evolution of intelligence, but the roots of its organization, go much deeper phylogenetically than is sometimes realized. Space does not allow any extended discussion of these issues, but at this juncture it is my belief that any attempt to extend existing evolutionary thinking, especially in the context of the evolution of sensory and nervous systems, far from providing a solution to the puzzle of consciousness will be more likely lead to absurdity and paradox. Ironically, the very attempt to employ a reductionist program of ever more detailed examination of the molecular and neuronal substrates in the hope of discovering the basis of mind will lead to a self-defeating program. The invitation to work in a post-Darwinian world, however, allows us to contemplate a paradigm shift. This program is important not only because it will reinforce the argument that mentality and mind are an inevitable outcome of the evolutionary process (Conway Morris 2003b), and are far from being a contingent happenstance. The points in support of this view revolve around the phylogeny of intelligence, the pre-adaptational potential for the relevant molecular constructs, the nature of evolutionary convergence of sensory modalities, and the fact that such systems have reached the limits of their design capacities.

In terms of mentalities it is evident that complex cognitive worlds have evolved independently many times. The corvid–primate contrast is the most celebrated example (e.g., Emery and Clayton 2004; Lefebvre et al. 2004) and is perhaps most startlingly expressed in terms of the now-celebrated New Caledonian crow and its capacities as a tool-maker (Hunt and Gray 2003, 2004; Weir and Kacelnik 2006; Taylor et al. 2007; but see also Bird and Emery 2009) and a presumed correlation with brain size (Cnotka et al. 2008). Exciting as this work is, the arguments for evolutionary inevitability of intelligence will gather greater force if we expand our phylogenetic field. In this context the octopus is well known as a striking example of invertebrate intelligence (e.g., Mather 2008a), but its full capacities may still be under-appreciated (Mather 2008b). Some highlights in this respect include evidence for play (e.g., Kuba et al. 2006), as well as memory (Shomrat et al. 2008) and curiosity (Byrne et al. 2002), all features that presumably correlate with a large brain. These in turn show some striking analogies to the vertebrate brain (e.g., Young 1976). Such convergences are highly instructive. This is because not only does this elaboration of the brain arise from a molluscan arrangement also but because of what more generally is taken to be a radically different body plan.

But if crows and octopus are independent culminations of a trend to intelligence, this begs another question. How far down the evolutionary scale of animals is it sensible to descend to discover the roots of intelligence? Deeper than one might think. What about jellyfish? Here the remarkable cubozoans (or box-jellies) are instructive. To describe them as "honorary fish" is hardly an exaggeration. Not only are they effective hunters, capable of considerable agility (Satterlie 2002), but their digestive canals "bear an uncanny resemblance to the villi that line vertebrate digestive systems" (Seymour 2002, p. 72). So too they engage in courtship and uniquely for cnidarians engage in copulation (Lewis and Long 2005), and as already noted, there is also evidence for sleep (Seymour et al. 2004). Most remarkable, however, are the camera eyes (Fig. 5), convergent on the system found in cephalopods and vertebrates (e.g., Martin 2002; Garm et al. 2008). There are, however, complications. First, despite correction of spherical aberration, the point of focus is well behind the retina (Nilsson et al. 2005). Second, the camera eyes are complemented by slit and pit eyes, the former of which have a lens-like structure (Garm et al. 2008). It is, therefore, a matter of speculation as to what the eyes actually see, but it is even more problematic what the jellyfish itself sees, given it has no brain. What is likely is that visual processing occurs in the nervous tissue adjacent to the eyes, and intriguingly, the arrangement of the nervous system is bilateral (Skogh et al. 2006).

Perhaps the capacity to form an image without a "brain" is not surprising. But what about organisms without a nervous system at all? Here we encounter a palpable sense of unease. The case in point concerns the remarkable group of dinoflagellates, the warnowiids. These, of course, form a single cell but bear a bulbous ocellus. These have an arrangement and dioptric properties that are strikingly reminiscent of animal eyes, leading Taylor (1980) to emphasize how the ocelloid has "an uncanny parallelism to the structure of metazoan eyes" (p. 76). Just such a point was also made much earlier by Pouchet (1887), who insisted that if they were not found attached to a dinoflagellate they would be automatically assumed to belong to an animal. Indeed just such an assumption was made by the

German biologist Carl Vogt who insisted that a ciliate had accidentally swallowed the eye of a jellyfish (see Kofoid and Swezy 1921, pp. 482–484). And as we saw earlier, this idea has resurfaced via a proposed symbiotic transfer.

The warnowiids are hunters, employing a grappling structure that is strikingly convergent with the cnidarian nematocyst (Greuet 1971; Westfall et al. 1983). Moreover, the lens of the ocellus is capable of precise focusing (Francis 1967), but evidently the fact that a single cell can see is a step too far for some investigators. Thus Couillard (1984) remarks "if an image is really formed on the retinoid, we fail to see, in the present state of knowledge, how an integrative computer could exist to analyze it within the cell" (p. 123). It does indeed appear to be a conundrum, but I suggest that this and other lines of evidence involving sensory perception in not only protistans but prokaryotes may be relevant to ultimately understanding the molecular basis of sentience.

Whether it will explain consciousness is quite another matter, and here the evolution of sensory systems in animals may also prove instructive. In their various ways, these sensory systems provide important insights into evolutionary convergence. Among these, one of the most interesting revolves around infra-red perception. In contrast to the ability to perceive ultra-violet radiation, and despite its attendant risks this is a capacity which has evolved multiple times, it is apparent that at the opposite end of this part of the electromagnetic spectrum the incoming radiation is not sufficiently energetic to activate visual systems. Even so, in the case of the infra-red pit organ of the crotalid snakes, its structure serves to act in the same way as a pinhole camera eye (de Cock Buning 1984), and in passing, we might note that optically this arrangement has evolved at least twice (Land 2002). Infra-red perception itself is rampantly convergent, evolving independently in the pythons (de Cock Buning 1985), as well as the vampire bats (Kishida et al. 1984). As these mammals seek a blood meal, so it is unsurprising to discover a comparable infra-red capacity in the reduviid hemipterans (or bed-bugs; Schmitz et al. 2000a). Perhaps more unexpected is an infra-red capacitance in a wood-boring wasp (Richerson et al. 1972), but such surprise may be premature. In the cases outlined above the infra-red sensor depends on a thermal contrast, most typically generated by the potential target. However differential absorption of solar radiation by plants can lead to an infra-red contrast, and this is evidently exploited by foraging insects, as in the case of the western conifer seed bug (Takács et al. 2009). These authors suggest such a strategy might be more widespread than currently appreciated.

It is, however, among the beetles that we find the most remarkable examples of infra-red sensing, with at least three separate originations. These involve the so-called fire-beetles (and other groups) that fly toward conflagrations in order to lay their eggs on hot wood. Here the advantages are an absence of predators, de-toxification of the wood and access to fungi (and other organisms) that sprout soon after the fire. In one case, that of *Acanthocnemus*, the detector acts as a microbolometer and so has a similar design to that seen in the crotalid snakes (Schmitz et al. 2002). In striking contrast to the arrangement whereby a thin sheet of sensory tissue is suspended above a cavity, in the famous fire-beetle *Melanophila*, the sensory array consists of complex globular structures that ultimately derive from a mechano-receptor (Vondran et al. 1995; Schmitz et al. 2007). Intriguingly an electron dense channel at the tip of the receptor may serve as a wave-guide; if so this organ would be the infra-red equivalent of a compound eye (Evans 2005). Nevertheless, exactly how this sensor operates is uncertain, and one might reasonably assume that its undoubted sensitivity (Schütz et al. 1999) and complex construction are another one-off in the diversity of life. Not at all, because in an unrelated group of insects, specifically a heteropteran, a remarkably similar arrangement has evolved (Fig. 10; Schmitz et al. 2008). So too, while a third type of infra-red construction, that seen in a merimnid beetle (Schmitz et al. 2000b; Mainz et al. 2004) would seem to undermine any attempt to arrive at general principles, not least because it belongs to the buprestids and so is related to *Melanophila*, it transpires that its construction is similar to the aforementioned western conifer seed bug, a representative of the hemipterans (Takács et al. 2009).

Fovea and JARs

Once again the conclusion appears to be that diversity exists, but it is united by convergences. There may be, for example, several ways to achieve a biological solution, but rest assured each will be arrived at multiple times. So too in other aspects of the evolution of sensory systems we find intriguingly, but ultimately unsurprising, commonalities. I briefly review two such examples: the repeated evolution of a fovea and the so-called jamming avoidance response (JARs).

The acoustic fovea of the bats was introduced above, and is otherwise most familiar in eye. There is, however, a striking convergence in the star-nosed mole (Catania and Remple 2004), which employs its tentacular and highly tactile organ, studded with Eimer's organs (again convergent in the monotremes (Proske and Gregory 2004; Marasco and Catania 2007)) to provide not only a superb sensory structure but one that "looks like a hand and acts as an eye" (Catania 1999). This similarity is not only expressed in terms of nervous organization within the somatosensory region, pointing toward "a convergent and perhaps common

Fig. 10 Convergence in the infra-red receptors of the coleopteran *Melanophila* and heteropteran *Aradus*. Redrawn from Fig. 3 of Schmitz et al. (2008), with permission of Springer and the authors
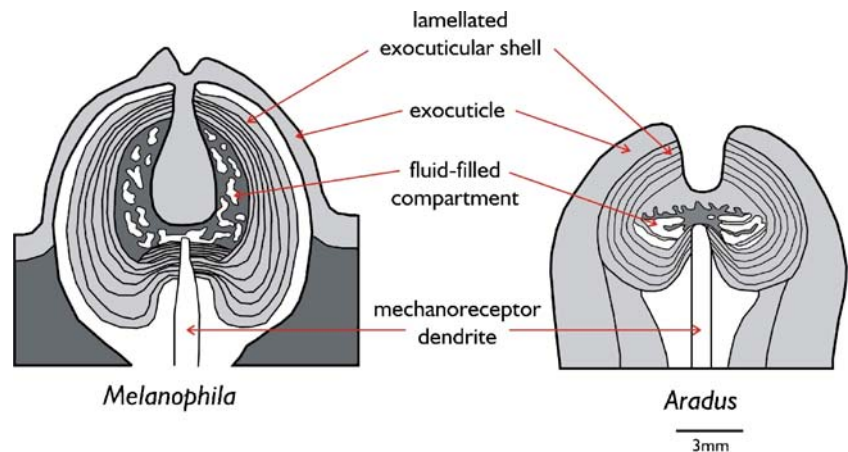
organization of highly developed sensory systems" (Catania 1999, p. 367), but even more intriguingly in terms of saccadal movements (Sachdev and Catania 2002; Catania and Remple 2004). So too among the electric fish the electrosensory lines have concentrations of nerves that have a foveal function (e.g., Hollmann et al. 2008; Pusch et al. 2008). This, of course, is just one aspect of an extremely sophisticated electrosensory system, which shows many striking convergences between the African mormyrids and Neotropical gymnotids (e.g., Hopkins 1995).

Apart from derivation of the electrogenerating organs from muscles, with capacities to live in an "electrical world" that allows navigation in crepuscular conditions and a versatile system of social communication, self-evidently, the production of simultaneous signals will be counter-productive (unless, of course, deliberate transmission is designed to foil a rival, e.g., Tallorovic and Zakon (2005)). The solution is to employ a jamming avoidance response. Such JARs are interesting not only because of their extraordinary sensitivity (a point returned to below) but also because by evolving convergently in both the gymnotid and mormyrid fish, the same algorithm is employed for signal separation (e.g., Kawasaki 1997; Green and Rose 2004). Just as these fish inhabit an "electric world," so bats live in a corresponding "acoustic world" and in principle face the same risks of signal inference. Convergently, a jamming avoidance response has evolved, but less surprisingly it is found in bats with a relatively broad frequency of sound production as against those emitting very narrow bandwidths (Gillam et al. 2007). Such JARs are very rapid, but interestingly show asymmetric and symmetric responses (Ulanovsky et al. 2004), both of which find counterparts in the electric fish (Gillam et al. 2007). In bats JARs may be important in avoiding mid-air collisions, especially in swarms (Bates et al. 2008), although this does not preclude an alternative strategy of remaining silent and listening (Chiu et al. 2008).

The edges of the physical world

These examples of convergence are introduced for several reasons. First, they may be less familiar and touch on sensory modalities that are effectively alien to humans. They beg, therefore, the question as to whether the purported differences are as important as is sometimes thought: the mind of the bat may be much more similar to ours than has been proposed (Nagel 1974). Indeed evidence from convergent evolution suggests not only that intelligence and consciousness are inevitable but also that they are universals, destined to emerge in any biosphere. Second, although often commented upon in specific instances, it is sometimes under-appreciated that the sensitivities of these various sensory modalities are not only exquisite but also at least in some cases they have evidently reached the limits of what is physically possible. Thus the retina can detect a single photon (Baylor et al. 1979), some insects can discriminate colors in starlight (Kelber et al. 2002; Somanathan et al. 2008), while the oilbirds (with their convergent echolocation employed in their cavernous habitats and nocturnal excursions) have eyes with a retinal construction whereby not only do the rod cells approach the theoretical minimum size but they have a density that is more than twice that found in the falcon (Martin et al. 2004). As these investigators remark these eyes are "pushing the limits of sensitivity" (Martin et al. 2004, p. 26).

In the context of sight the striking convergences found in the star-nosed mole have already been emphasized, but it is also worth noting that in the case of the saccadal movement, this too approaches the theoretical maximum (Catania and Remple 2004, 2005). So too in olfaction, individual molecules can be identified (Kaissling 1986), while in the realm of hearing the limits of transduction in our inner ear are almost those of thermal noise (Denk and Webb 1989). In the insects, despite the manifest differences between the Johnston's organ and cochlea, important functional similarities emerge (e.g., Göpfert and Robert

2003; Jackson and Robert 2006). Moreover, the antennal response in mosquitoes shows an extraordinary sensitivity; as Göpfert and Robert (1999) point out, if the observed deflections were to be scaled up to the size of the Eiffel Tower, then the deflection would be equivalent to the tip of the Eiffel Tower moving less than a millimeter.

In extant animals, therefore, at least some sensory systems operate close to the perceivable limits of the physical universe. And this may point to a more general, if neglected, trope of evolution. Far from being a bodge of a construction, in at least some cases, things are evidently as good as they possibly can be: The fangs of frogs (Fabrezi and Emerson 2003) and snakes (Kuch et al. 2006) provide an instructive introduction. Note also that even in cases of manifest inefficiency, of which the photosynthetic enzymes Rubisco is perhaps the most notorious example, it "may be near-optimally adapted to their different gaseous and thermal environments" (Tcherkez et al. 2006, p. 7250). Moreover, this evolutionary challenge has been met by mechanisms for the concentration of carbon dioxide, and once again, they represent convergent solutions. Foremost in this respect are the bacterial carboxysomes (which in turn have striking convergences with viruses, e.g., Yeates et al. 2007) and the rampant convergence of C_4 photosynthesis (e.g., Kutschera and Niklas 2006; Besnard et al. 2009).

Conclusions

Given the range of topics covered and the limited space to do them anything like full justice, it may be helpful to summarize briefly what the underlying strands of the argument are and why, therefore, they point to a biology that will move far beyond the Darwinian formulation (e.g., Carroll 2000; Kutschera and Niklas 2004, 2005). First evolutionary convergence is far more widespread than is generally appreciated, with the implication that the number of functional solutions is limited. This applies as much to molecular biology and cell chemistry as it does to phenotypes, behavior, and intelligence. Second, despite the immensity of the Tree of Life, the divergences that delineate its shape are unlikely to be random. Although this view is certainly heterodox, and perhaps in the eyes of some reason for a delation for heresy, I would suggest that far from being a rich bush, the Tree of Life is a much more skeletal construction, with the narrowest of branches separated by enormous areas of uninhabitable bio-space. I would further suggest that one consequence is that much of this Tree may have what is effectively a pre-determined shape. Third, all the bifurcations are the result of standard microevolutionary processes and typically the nascent character states that will enable major transitions to proceed are expressed in a number of puzzling combinations. But

this simply represents a limited number of adaptive solutions upon which the processes of optimization will be employed. Fourth, a considerable proportion of biological complexity is seeded in prior inherencies, especially at the molecular level. Fifth, the "Swiss Army syndrome," that is the unexpected versatility of molecules, suggests that building complex structures is much easier than might sometimes be thought. Sixth, although hardly touched upon, here the capacities for self-organization (see also Goodwin 1994; Kauffman 1993), although widely acknowledged, are still under-appreciated but will prove central to understanding why systems are typically very complex from an early stage. Ironically, evolutionary "simplification" is more likely to be a very derived state and probably represents adaptive stream-lining at a very sophisticated level. Finally, and perhaps most important, the reality in biology is not that very many things work "after a fashion," but to the contrary out of the unimaginably large possibilities of design hyperspace almost nothing works but when it does it usually works extremely well. The *Origin* (Darwin 1859) has had an unprecedented run of a century and a half, and perhaps uniquely in science remains a foundational text. Today our understanding of evolution is immensely widened, but naturally it remains thoroughly Darwinian. The aim of this review is not to dispute this synthesis, but simply to enquire if it is complete.

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