1. Introduction

In evolution, it is customary to talk of landscapes (adaptive or otherwise), along with metaphorical corollaries such as maps, navigation and limits. In one sense, one can regard evolutionary biologists as engaging in a rather complex cartography as they map the features of the natural world. So too, many travellers use a satellite-based navigation system, guiding them across unfamiliar territory (until perhaps their way is blocked by a vast lorry wedged tightly between two quivering cottages or instead the road ends in a 30-foot drop). Old hands trust to a battered Ordnance Survey sheet, stout shoes and a shrewd idea of what, in the words of the Duke of Wellington, lies on the other side of the hill. Is our ‘map of life’ much different? In other words, are we now confident we discern at least the major roads and need only exercise caution along the narrowest of lanes? Alternatively, are the maps mostly made of blanks where motorways turn suddenly into rutted tracks or steep chasms yawn in front of us with no sign of a convenient bridge? To shift the metaphor slightly: can our Roman roads still safely carry the traffic of two millennia, or are journeys so unpredictable that intent on driving to Liverpool we are puzzled to see the sign ‘Welcome to Inverness’? Irrespective of these cartographic conceits, our choices of metaphor and model relate to our conceptions of evolution. In asking ‘what are the limits of evolution?’ we are also querying what evolution really involves. Maybe the evolution of life is, in all its grandeur, unimaginable and so like the hunt for Lewis Carroll’s Snark the best map is a perfectly blank one. Yet surely, each of the 11 papers in this volume offers us at least a sketch.

2. Preconceptions and the limits of current knowledge

It would be otiose to imagine that any scientific enterprise can avoid presuppositions of thinking nor should it fail to acknowledge the inevitability of incomplete knowledge. How we view these difficulties will, of course, bear directly on what we perceive as limits on evolution. As importantly, they invite us to look at standard problems from a fresh perspective. The paper by Hollo [1] is instructive in this regard. In his exploration of animal symmetries, Hollo deconstructs the
assumptions radial = primitive and bilateral = advanced to remind us that radial symmetries pervade advanced animals, not least in the form of tubes and tubules. Supposedly classical demarcations, therefore, dissolve on closer inspection. So too do they when we address perceived complexity. This is no easy task but again Holló is right to remind us that in its own way a jellyfish is as ‘good’ as a fish. This is less to do with the long-topped idea of a scala naturae but to recall that preconceptions of ‘primitive’ versus ‘advanced’ automatically colour our perceptions of what evolutionary limits might mean. This problem finds a related expression, returned to below, concerning the ‘skin-deep differences’ that separate supposedly disparate organisms. How we choose to view these questions matters very much indeed.

Preconceptions and the lack of knowledge are also the unwilling companion of any historical analysis, the parameters of which are crucial in deciding if the limits of evolution are ever-receding or in some fundamental sense bound (see [2]). Few would dispute, however, that the world today is a great deal more complex than it was three billion years ago, nor that at least in outline this history can be told through the blurred lens of the fossil record. What of re-running history? This is a topic which is examined in detail by Orgogozo [3] as well as Powell & Mariscal [4] in their discussions of Gould’s ‘tape of life’. The laboratory also provides fascinating lessons from experimental evolution, as exemplified by the classic work of Lenski and coworkers [5]. Despite the undoubted importance of these and parallel studies they do suffer the twin disadvantages of miniscule time scales (although the Lenski ‘world’ of parallel studies they do suffer the twin disadvantages of miniscule time scales (although the Lenski ‘world’ of Escherichia coli evolution would, on a mammalian scale of generations, be equivalent to perhaps between 100,000 and half a million years), and a focus on asexual microorganisms. Here, however, the fossil record may be informative in revealing convergent evolution such as the repeated re-invention of sabretooths [6,7] or other such examples of iterative evolution [8].

4. The importance of initial conditions and constraints

This topic is, of course, much closer to the interests (and capabilities) of most biologists and unsurprisingly is addressed in various ways by the majority of the contributors. It also overlaps with the question of evolutionary convergence in as much as both the starting conditions and routes taken might strongly limit particular endpoints. Yet to define what is meant by ‘initial conditions’ and the extent to which they might predetermine possible outcomes remains problematic. For example, a case can be made that all life is necessarily carbaquist (i.e. based on carbon and water), but supposing other substrates are possible? In this wider universe of possibilities (which is touched upon later in §9), where even silicon-based life forms might be entirely orthodox in comparison with even more outlandish arrangements, we can still enquire as to whether the actual limits to evolution are any different. In other words, could carbaquist and silico-hydrocarbon forms still be functionally equivalent?

To return to the more familiar territory of terrestrial forms, nobody doubts that the possibilities for life are hedged in with physical constraints, as even a cursory knowledge of factors such as diffusion rates or Reynolds numbers will make abundantly clear. On the other hand, as we see in the context of convergence, evolution not only has a canny knack of arriving at the same extremely effective solutions (and possibly limits) but by markedly different routes. Even so we cannot yet dismiss that evolutionary routes as well as outcomes depend not only on the nature of the map, but also on the starting point, as argued by Hoyal Cuthill [10] using models of phylogenetic constraint.

5. The completeness of adaptive explanations

Perhaps this section should come with a health warning that it offers no comfort to any shade of creationist. Nevertheless, the completeness of adaptive explanations is a legitimate question for at least two reasons. First, as Dingle and co-workers [11] explain in the context of the evolution of non-coding RNA, the forms that are accessible to the scrutiny of natural selection appear to be a minute fraction of the far larger theoretical population. Furthermore, these phenotypes are predominately those most likely to be generated by random exploration of genotype space, owing to the biased structure of the ncRNA genotype–phenotype map. In a very different context, it is easy to see why the innumerable examples of larger-scale evolutionary convergence [12,13] are almost automatically seen to be exemplars of Darwinian adaptation. This may well apply to the majority of cases, but while life forms must be ‘good enough’, it is possible adaptation could also emerge as the result of random processes and of the properties of developmental mapping functions.

6. The map of life

Our introduction opened with the metaphor of the map of life. Evolutionary convergence, the places on this map that are repeatedly revisited, weaves through many of the contributed articles, and perhaps of all the themes it is this that represents the core of this thematic volume. Central to the
claim that evolutionary convergence may be of key importance is not only its apparent ubiquity but the manner in which these convergences span all the levels of the biological hierarchy, that is, from molecular systems to behaviours such as tool-making. An obvious corollary, although one that is by no means generally accepted, is that the frequency of many biological solutions implies that other theoretically possible combinations are in reality non-viable and accordingly can never be instantiated. A further implication of much of biological hyperspace being permanently untenanted is that the evolutionary routes are exceedingly narrow and can only reach a tiny number of destinations. Yet can the apparent ubiquity of evolutionary convergence so easily be reconciled with this grand narrative? As several of our contributors, notably Stayton [14] and Powell & Mariscal [4], point out matters are not necessarily so clear cut. Stayton [14], for example, warns us as to the frequent imprecision of terminology and the danger of what we observe being conflated with what we assume the actual processes to be. So too the analyses of convergence seldom consider what might be an appropriate null model to provide the necessary yardstick. In some senses, Powell swims even further from the shore by pointing out that concepts of contingency versus attempts to formulate law-like properties that are applicable to biological systems continue to labour under a series of misapprehensions between metaphysical assumptions (i.e. this is how I believe the world to be) and epistemological protocols (these are the data I believe to be useful).

These contributions, along with those by Vermeij [15] and McGhee [16], will help to provide an important framework for future discussion. In defence of the general importance of evolutionary convergence, it may also be argued that the many dazzling examples, be they as different as the multiple inventions of carbonic anhydrase [17] or ant myrmecory [18], do more than provide an impressive catalogue raisonné and in at least two different ways contribute to the question of the limits of evolution. The first refers to the observation that certain forms are so self-evidently similar that further analysis is hardly called for. For example, that a fusiform shape is the sine qua non of fast-moving aquatic animals hardly requires comment. Such gross similarities, however, very often extend beyond so-called ‘skin-deep differences’ (see [19]). This notion stems from just such an investigation of hydrodynamic form and specifically the detailed analysis of the convergent similarities that unite teleost tuna and chondrichthyan lamnid sharks [19], not least in terms of the details in ligamentary transmission of propulsive forces and possession of endothermy. One might observe, of course, that in other respects the scalings of shark and tuna are similar. It is worth remembering, however, that some similarities operate across impressive ranges of scale, such as the gulp-feeding of pelicans and balaenopterid whales [20]. It is such analogies and the corresponding integration of functions that suggest that at least some examples of convergence are much more helpful in delineating the limits to evolution than might at first be supposed.

7. How does the barrel fill?
This question presupposes that barrels exist that can be filled. That this is not always the case is evident from Vermeij’s [15] trenchant analysis of apparently excluded possibilities, complemented by McGhee’s [16] review of the forbidden zones of morphospaces. In the latter case, the non-viability of any potential occupant is sometimes self-evident, but in many other circumstances, the reasons for exclusion—exemplified by the almost total lack of marine insects [21]—are very far from clear. Why, for example, do we find no photosymbiotic or endothermic echinoderms? Vermeij’s extensive knowledge of the natural world gives us confidence that his roster of examples is important when considering the limits to evolution. There are, however, some qualifications worth making. First, today’s biosphere is only a very thin slice of total diversity and if our knowledge of extant biotas is incomplete even more so is that of the fossil record. A favourite canard of an evolutionary omission is the absence among the marsupials of anything like a bat [22]. This is probably correct, and one can engage in thought experiments on why the route to an actively flying (as against gliding) marsupial was precluded. Yet in other respects, the development of the shoulder girdle in the bandicoots [23], a group of marsupials with a genuine placenta [24], is evidence to suggest that the transition in a marsupial to a bat-like form is less of a hurdle than might be imagined. And then, what about that Eocene Ghamidtherium? What we have available is frustratingly fragmentary but it just might be an example of the ‘impossible’ marsupial bat [25].

Nevertheless, many biological tenancies may display a ‘to let’ sign and in recognizing the potentialities of evolution this may well sharpen our thinking as to what might be the limits of evolution. How reliably we might decide what really ‘should’ have evolved or not, as against seemingly viable forms that on closer inspection suffer one or other fatal flaw, is a major challenge. Nevertheless, there are two further qualifications, one essentially historical and the other much more general. The first qualification, concerning the question of ‘excluded possibles’ of biological form, is to recall that some regions currently regarded as untenable might be accessible in terms of markedly different environments, such as intervals of elevated levels of atmospheric oxygen. The second, and more important qualification, is to remember that in any discussion of evolutionary limits we need not be ‘taxon bound’ (however interesting a topic this may be) nor excessively diverted by the continuing curiosity of some groups that arrive with great frequency at a given destination, as for example the Lamiales do in terms of the evolution of plant parasitism [26]. Rather it is that, in any such discussion of limits, we need to switch our attention to the overall likelihood of the emergence of particular biological properties. Thus, endothermic echinoderms there well might not be, and conceivably one could link this absence to their diffuse nervous system. On the other hand, if this group was to yield an endothermic species, could we be confident that it too must use a system of leaky membranes and ion transport to generate heat?

8. The march of history
As L. P. Hartley famously said, ‘The past is a different country: they do things differently there’. Indeed, they do. One difficulty in assessing the limits of evolution is that what applied in the Jurassic, let alone the Archaean, may be of limited relevance today, or 100 million years in the future. But, the contrasts between the histories of diversity and disparity outlined by Oyston and co-workers [27] show that, while there are no
absolute rules, there may be recurrences not least in the way that morphological disparity tends to saturate at a relatively early stage of the history of a clade. One might also argue for strict limitations in many other areas of biology. Among the most obvious are the energetic efficiency of nervous systems [28], the maximum size of mammalian brains [29] and the complexity of symbiotic systems [30]. If at least some envelopes of possibility are close to being reached this then has two implications. First, does this apply also to human knowledge? Second, does this apply ‘out there’? Regarding the former implication, it would be too much to expect this brief overview to address the limits of human knowledge, other than to observe that there is little obvious correlation between the advancement of knowledge sensu lato and evolutionary constraints. However, de Vlader & Szathmáry [31] present an important step forward in applying an evolutionary view to cognition, by providing a formal link between standard evolutionary theory and the selection of neuronal networks in the brain (Darwinian neurodynamics). The second implication, the question of extraterrestrial life, is also riddled with imponderables, but it is to this last theme we briefly turn.

9. The limits of extraterrestrial life

In one sense, and one sense only, the contributions to this thematic set are parochial because they remain Earth-bound although at least in the case of non-coding RNA the results of Dingle et al. [11] might well be of universal significance. What, however, of alien biospheres (if there are any)? Do they fill in another remote corner of biological hyperspace or do at least the Earth-like planets form a sort of super-Venn diagram with much in common? McGhee [16] throws down the gauntlet with his ringing proclamation that if there are any life forms on the hydrocarbon worlds such as the moons Titan or Triton then they ‘would look nothing like life on Earth’ and by implication have no eyes to view the splendour of Saturn’s rings or the blue vastness of Neptune. Maybe even on our planetary doorstep the limits of life lie far beyond what we might expect? Alternatively, could it be that the silicon-based life forms that might disport themselves in the icy oceans of these moons employ camera-like eyes suspiciously close to those of cephalopods and ourselves? Time will tell.

Competing Interests. We declare we have no competing interests.

Funding. Our work is supported by the Templeton World Charity Foundation, the Department of Earth Sciences, Cambridge, and St John’s College, Cambridge.

Acknowledgements. We thank Vivien Brown for the expeditious typing of numerous drafts. We also thank the contributors to this thematic volume for their stimulating contributions and timely delivery of manuscripts, as well as Tim Holt and colleagues at the Royal Society for their editorial assistance.

References


