



Review

Cite this article: Vermeij GJ. 2015 Forbidden phenotypes and the limits of evolution.

Interface Focus 5: 20150028.

<http://dx.doi.org/10.1098/rsfs.2015.0028>

One contribution of 12 to a theme issue
'Are there limits to evolution?'

Subject Areas:

biochemistry

Keywords:

evolution, phenotypes, limits, metabolism,
natural selection

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Forbidden phenotypes and the limits of evolution

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Evolution has produced an astonishing array of organisms, but does it have limits and, if so, how are these overcome and how have they changed over the course of time? Here, I review models for describing and explaining existing diversity, and then explore parts of the evolutionary tree that remain empty. In an analysis of 32 forbidden states among eukaryotes, identified in major clades and in the three great habitat realms of water, land and air, I argue that no phenotypic constraint is absolute, that most constraints reflect a limited time–energy budget available to individual organisms, that natural selection is ultimately responsible for both imposing and overcoming constraints, including those normally ascribed to developmental patterns of construction and phylogenetic conservatism, and that increases in adaptive versatility in major clades together with accompanying new ecological opportunities have eliminated many constraints. Phenotypes that were inaccessible during the Early Palaeozoic era have evolved during later periods while very few adaptive states have disappeared. The filling of phenotypic space has proceeded cumulatively in three overlapping phases characterized by diversification at the biochemical, morphological and cultural levels.

1. Introduction

Making sense of the vast diversity of life is one of the great intellectual challenges of evolutionary biology. Over the course of its history, life has blossomed into a seemingly endless array of phenotypes (shapes, habits and physiologies), and the evolutionary tree is made up of countless branches (clades) and twigs (lineages), some prematurely pruned by extinction, others sprouting new shoots. Despite this variety, there is empty space in the tree, implying the existence of limits to evolution. It is this empty phenotypic space with which this paper is concerned.

2. Approaches to diversity

Two complementary approaches have dominated the description of and explanation for diversity. These are (i) the biodiversity approach, which documents the characteristics, origins, extinction, distribution and phylogeny of taxa, lineages and clades in space and over time and (ii) the structural approach, which uncovers the mechanics by which genes and their interactions orchestrate growth, development and evolutionary innovation.

A third perspective on diversity interprets it as an inevitable consequence of random variation that accumulates in a system of initially similar parts whose numbers multiply. This view, dubbed the spreading principle [1] of the zero-force evolutionary law (ZFEL) [2], holds that diversity arises even in the absence of constraints or forces acting on the parts. The ZFEL represents the null model against which patterns imposed by structural protocols, material constraints or natural selection must be compared. In Raup & Gould's [1] slightly different version, each variation may be adaptive, but the aggregate pattern can be described (if not explained) by random walks. In the special case of size evolution [3,4], the small-bodied ancestor in a major animal clade tends to give rise to larger descendants simply because evolution towards smaller size is

less likely. The resulting pattern, in which the mean or median size within the clade increases over time, looks like directional evolution but is instead adequately described as random variation. Causal explanations are, however, still needed for the evolution of size in particular lineages. These three approaches explore the diversity that exists. Complementing these perspectives is a fourth, motivated by the question whether and which phenotypes have failed to evolve. Here, I employ this approach to investigate empty parts of the evolutionary tree and the constraints that are responsible for these voids.

3. Selection and constraint

Any phenotypic change must be compatible with a living body that performs adequately at all stages of the life cycle. The pattern and materials of construction and modifications to them must conform to functional demands throughout life, from the zygote to the adult. Besides limits imposed by physics and chemistry, impediments to phenotypic evolution are often attributed to developmental constraints [5], but in reality they are due to natural selection, which distinguishes between what works and what does not work given the organism's circumstances.

Akin to a developmental constraint is the phylogenetic constraint, a historically preserved, invariant property possessed by all members of a clade. Any phenotypic variation that does occur within the clade is channelled in only a few directions [6]. To be sure, all lineages are marked by the stamp of history: an ancestor possesses particular, contingent traits that evolved under specific, contingent circumstances, and these traits are passed on to descendants [7]. However, this ancestral influence wanes as conditions change, new opportunities emerge and constructional innovations arise [8]. Phylogenetic constraints must therefore be universal in the short run, because no lineage lives everywhere or can do everything; but invoking such constraints in general does little more than restate the problem of limitation rather than offer an explanation for structures unrealized and adaptive pathways not taken.

The constraints imposed by ancestors and by the evolved body-plan construction of major clades are enforced by natural selection and therefore by the circumstances in which organisms develop and evolve. But natural selection also plays a role in lifting constraints, as discussed in the next section.

4. Versatility

Potential phenotypic diversity depends on the number of parts of the body (modules, domains or compartments) that are individuated [9]. These parts are semi-autonomous units that function and are constructed separately from other parts with which they share a common developmental origin and fate. The envelope of design possibilities is small when there are just a few modules, because any change will affect the function and performance of much or all of the developing body. As the number of modules increases, interactions and signals among parts become more localized, functions become more autonomous, and performance trade-offs among functions and among parts recede. The result is greater adaptive versatility [8,10], which enable a given body plan of construction to generate a greater variety and range of

adaptive phenotypes. Wagner [9] presents a comprehensive account of the mechanisms involved.

Within major animal and plant clades, younger branches are morphologically more versatile than older ones. Shell geometry in gastropods indicates a single module in the early-diverging Patellogastropoda and Vetigastropoda, and two or three modules in the later-appearing Caenogastropoda and Heterobranchia [11–13]. The segments and limbs of early arthropods show less functional differentiation than more derived clades [14–16]. When intercalary growth evolved in plant leaves, a greater variety of leaf shapes and venation patterns became possible [17,18]. Other examples come from jaw and skull evolution in fishes [19–23] and the plastron of atelestomatan ('irregular') sea urchins [24].

This widespread trend is consistent with the ZFEL but is not explained by it. The new dimensions in which variation is expressed are controlled by genes and their interactions; and the modules that are free to vary are subject to relentless selection as they interact with each other within the ecosystem of the developing body [25]. At the very least, therefore, the diversification of parts of a system in the absence of external constraint is strongly enhanced by regulation and limits enforced by selection.

A more compelling case for a large role for the ZFEL can be made for unregulated exploration of design space early in the history of major clades. This kind of variation has been documented in Early Cambrian lapworthellids [26], segment number in early trilobites [27–29], plate numbers and positions in early pelmatozoan echinoderms [30–32] and the pattern of tertiary and higher order veins in the leaves of early angiosperms [33].

Gould [34] suggested that organisms reproducing when in an ontogenetically juvenile stage are able to add major innovations and to change adaptive direction more readily than can those in which reproduction takes place at a later developmental stage. He argued that regulation of development has broken down in these progenetic lineages, not least because the time interval over which the body is tested is short. Gould [34] noted that early members of most major animal clades were small and that many of the specializations attending large size were dispensable [3]. Innovations associated with miniaturization and truncated development have been identified in the origins of angiosperms with high leaf-vein density [18] and in the origin of birds [35].

In short, the regulated plasticity and increased versatility and replaced unregulated variation are outcomes of natural selection. Versatility opens up new phenotypic territory for selection and adaptation by expanding the dimensionality of ontogeny and by making accessible new directions of diversity and specialization. In the next section, I argue that a larger time–energy budget, favoured by competition-related selection, is the crucial factor linking versatility, selection and the lifting of constraints.

5. The time–energy budget constraint

The alleviation of functional trade-offs associated with an increased versatility arises from an expansion of an individual's time–energy budget. This is expressed as an increase in metabolic rate and metabolic scope (the difference between resting and active work by an organism). Individuals with

faster metabolism gain a competitive advantage, but also require access to a high, predictable supply of resources; and those resources are largely controlled by the ecosystem—the totality of organisms and their interdependencies—in which individuals are embedded. Three pathways are available for raising the time–energy budget: (1) increasing the density and effectiveness of energy-acquiring or energy-producing structures, (2) entering into a stable, intimate partnership or trading relationship with organisms that possess complementary capacities, and (3) living in a warm environment where all processes are faster and where many functions are energetically less costly.

Besides relieving trade-offs, greater versatility and the expanded time–energy budget offer many competitive benefits. These include rapid growth, high fecundity, greater investment in offspring, the production of energy-rich defensive compounds, forceful aggression and feeding mechanisms, internal physiological homeostasis (a well-regulated internal state), sophisticated coordination between sensory and motor networks, rapid immunological responses, fast and sustained locomotion, and elaborate displays associated with mate choice. With a larger time–energy budget, passive feeding and defence and conformity of internal conditions to the external environment give way to more active responses and to greater internal control [36,37]. Versatility may arise under permissive conditions, but its potential is realized as competition propels lineages to occupy many roles in ecosystems.

Of course, constraints remain; but selection under an increasing range of circumstances—most of them created or modified by life itself—has globally pushed back the limitations under which multicellular living things evolve and operate. The extent to which selection does so depends on the supply and accessibility of resources. Animals in much of the deep sea are severely constrained by cold and a meagre nutrient supply. Freshwater habitats can be productive, but most are island-like. We have shown that the intensity of competition and predation on remote terrestrial islands (and by extension in freshwater) is less than in similar mainland or oceanic habitats [38]. Large productive ecosystems in which the community as a whole regulates and stabilizes consumption, production and resources permit the highest diversity of phenotypes and ways of life without completely eliminating evolutionary constraints.

6. A catalogue of forbidden phenotypes

How do these ideas about constraint apply to phenotypes that do not exist? To answer this question, we must call on our imaginations and knowledge of existing diversity to conjure up organisms that make functional sense but that have never evolved or have done so only under very limited circumstances. This is not a frivolous exercise; on the contrary, it forces us to test the limits of our understanding of development, selection and history. The 32 phenotypes I discuss in the following sections (summarized in table 1) often point to energetic limitations, but they also lay bare empty space in our evolutionary understanding.

The cases discussed below are not exhaustive. For example, I do not discuss size limits, which are imposed by a combination of material constraints, the physical environment and the size-dependent acquisition, retention and internal transport of nutrients, gases and metabolic products. Despite

general scaling laws, size limits are rarely absolute and have been frequently transcended over time in major clades. I also mostly exclude limits imposed by structural materials (but see the section on biomineralization below). Animals often rely on materials they do not themselves synthesize, implying that material constraint can be overcome by exploiting already existing sources.

6.1. Wheels

No animal uses wheels to move about, presumably because suitable expanses of pathways of flat, even ground are for the most part unavailable in nature [39] and perhaps also because structures like wheels that rotate without limit and in a consistent direction on an axle are difficult to build in the context of a developing animal body. Some whole organisms form almost perfect spheres or wheels by rolling up so that the front and hind ends touch, enabling the animal to roll away from enemies [40]. Examples include some terrestrial caterpillars, cockroaches, isopods, millipedes and spiders, and marine stomatopod larvae and fossil trilobites [36,41]. Active rolling is achieved in some spiders [40] and in scarabaeid dung beetles. The latter roll dung balls and may even climb onto and ride these balls to prevent overheating [42,43]. Rotation is known in flagella and, in modified form, in the screw-like leg joints of curculionid weevils [44], but none of these cases amounts to wheeled transport.

6.2. Pollination and dispersal

Plants with aerially emergent flowers are often assisted in sexual reproduction by mobile pollinating animals, which often fly fast and over long distances between flowers. With the possible exception of short-distance pollination of seagrasses by fishes [45], there is no evidence that water-dwelling organisms are aided in cross-fertilization by aquatic animal vectors. The effectiveness of gamete dispersal in the buoyant medium of water may erase any benefit that animal assistance can offer. Moreover, small animals are more constrained in the speed and distance of movement in water than in air [46]. The same explanation may account for the rarity of animal-mediated dispersal of propagules in aquatic (especially marine) habitats. Animal-assisted dispersal of spores, seeds, fruits and small organisms is extremely widespread on land. Some intertidal marine gastropods and many small freshwater animals are dispersed by birds, but evidence of dispersal of water-dwelling algae and animals by mobile aquatic animal vectors is limited. Algal fragments and small animals can be locally dispersed after surviving passage through the digestive systems of animals [47]; and freshwater unionoid bivalve larvae parasitize and are dispersed by fishes. Parasitic species without a free-living stage also depend on their hosts for dispersal, but the primary host is often a bird or other land-derived animal. Marine animal-assisted dispersal before the evolution of marine tetrapods may therefore have been even less common than it is today.

6.3. Biomineralization

Biomineralization, the formation of calcium- and silicon-based minerals inside or outside the body, is extremely widespread in multicellular organisms and has evolved dozens of times [48–53]. Nevertheless, there are major clades in the tree of life in which biomineralization has apparently never evolved (table 1). In some cases such as insects and several other

Table 1. List of forbidden phenotypes among living multicellular organisms.

animal-assisted gamete fertilization in aquatic environments
animal-assisted propagule dispersal of species with free-living life stages in marine environments
biomineralization in fungi, Ctenophora, Platyhelminthes, Nematoda, Chelicerata, Myriapoda, Hexapoda, Hemichordata and Bryophyta
rigid reef-like structures in freshwater
bioerosion in freshwater
conchicolity (living in and moving about in shells after the death of the original builder) in freshwater
endothermy in Ctenophora, Cnidaria, Porifera, Platyhelminthes, Nematoda, Crustacea, Chelicerata, Myriapoda, Lophotrochozoa, Hemichordata, Tunicata, Echinodermata, small marine mammals, fungi, non-angiosperm plants, Rhodophyta, Phaeophyta and Chlorophyta
non-methanogenic Archaea in parasitic or mutualistic partnerships with eukaryotes
photosymbiosis in Ctenophora, Bryozoa, Cirripedia, Echinodermata, fishes and flying animals
chemosymbiosis in Cnidaria, colonial animals, Porifera, Cephalopoda, Echinodermata, Tunicata, Chordata, terrestrial animals and planktonic animals
aerial phytoplankton
capture of living animals by plants and algae other than angiosperms
specialized scavenging in mammals
annual herbaceous growth in land plants outside angiosperms
woody stems in bryophytes
basal leaf (or blade) growth in plants and algae outside angiosperms and laminarialean algae
roots for sedimentary uptake of nutrients in algae outside siphonalean and charophyte green algae
herbivory in Ctenophora, Porifera, Cnidaria, Platyhelminthes, Araneae, Myriapoda, Scaphopoda, Cephalopoda, Chondrichthyes, adult Amphibia and Serpentes
algal diet in marine turtles and marine birds
piercing-and-sucking herbivory on freshwater vascular plants by insects
gelatinous freshwater plankton
envenomation in Porifera, Ctenophora, Crustacea, Hemichordata, Tunicata, Bryozoa, Brachiopoda, water-dwelling plants, algae and fungi
gastropod opercula that bite
communication by sound in basal Metazoa, Lophotrochozoa and Echinodermata
communication by electrical signals in basal Metazoa, Ecdysozoa, Lophotrochozoa and Echinodermata
social organization in shell-bearing Mollusca, Echinodermata
eusociality in Lophotrochozoa, Echinodermata and Chordata outside Mammalia
combinatorial communication among animals other than humans
clonal reproduction in Mollusca, Brachiopoda, vertebrates and Arthropoda
live-bearing in turtles and birds

arthropod groups, the skeletal function of minerals is taken up instead by chitin. In other cases, however, skeleton formation simply does not occur.

Bacteria precipitate numerous minerals based on iron and other metals that eukaryotes have for the most part not used. Exceptions are iron-containing radular teeth in chitons (Polyplacophora) and many herbivorous gastropods.

Rigid reef-like structures built by mineralizing animals, seaweeds and microbes have existed in marine environments since the latest Ediacaran [54,55]. Their constructors are photosynthesizers or suspension-feeders. Comparable reefs are absent in freshwater. Many potential constructors are present in freshwater, but either they lack mineralized skeletons (sponges, hydrozoans and bryozoans) or they are calcified but do not form large frameworks (cemented bivalves, charophyte algae). Reef-builders in most clades (corals, vermetid gastropods, mineralized polychaetes and barnacles) are strictly marine. Unlike many marine photosymbioses, freshwater partnerships between algae and animals do not mineralize. Microbial tufa formations occur in soda lakes but

not in more typical aquatic environments [56]. Low ion concentrations could explain some of these absences, but lakes and rivers in limestone-rich areas support relatively thick shells and could be favourable to reef development. Woody vegetation originating in the Early Devonian [57] builds rigid frameworks on land, in mangrove habitats and in freshwater swamps, but the trees are always emergent.

6.4. Bioerosion

Bioerosion (the mechanical or chemical penetration of rock, skeletons or wood by non-predatory organisms) is widespread in the sea, where it first appeared in the Neoproterozoic [58]. Numerous arthropods bore into living or dead wood on land [59]; and bivalves and isopods have done so in wood washed into the sea. With the exception of the southeast Asian polychaete annelid worm *Caobangia* [60], no bioeroding organism has been identified in freshwater despite the widespread occurrence of skeletal dissolution not involving organisms. Holes in freshwater molluscan shells have been described [61], but the culprits, if any, remain unknown.

6.5. Conchicoloy: living in shells

The conchicolous habit of animals living in and moving about with shells after the original builders' death has evolved independently at least five times beginning with trilobites in the Early Cambrian [36,62]. With the exception of coastal terrestrial coenobitid hermit crabs and one hermit crab (*Clibanarius fonticola*) from a freshwater pool in Vanuatu [63], all mobile conchicoles are marine. Animals that use shells for brooding are known in all three habitat domains. The antipredatory advantage that shells offer may be reduced in most freshwater habitats, where shells tend to be thin; but this should not be true in ancient lakes and many rivers. It is also possible that the supply of shells is too low in freshwater, because predators that leave shells intact are uncommon there [36]. In many marine habitats, the supply problem has been solved by symbioses between conchicoles and sponges, hydroids, sea anemones, bryozoans or even corals that settle on and then extend and enlarge occupied shells as the conchicole grows [64]. Such symbioses are unknown in freshwater.

6.6. Endothermy

Several major clades of insects and vertebrates (birds, mammals and the opah, a marine teleost fish of the genus *Lampris*) maintain high, stable body temperatures while active under conditions of lower and more variable environmental temperatures [65–67]. Tunas, billfishes and some lamnid sharks have also evolved a form of endothermy that involves generating and conserving heat in a few organs deep within the body [68]. Insect-pollinated flowers in seven seed-plant families generate substantial heat [69]. Living leatherback turtles and Mesozoic dinosaurs and marine reptiles are warm-blooded by virtue of a low surface to volume ratio resulting from large size. Ecological benefits of endothermy include acquisition and defence of resources under a wide range of conditions and the ability to remain active for long periods. Plants benefit by dispersing attractive scents better and by providing heat for more effective pollination.

It is therefore striking that endothermy is unknown in such major animal clades as Mollusca, Echinodermata and Crustacea. It is also absent in most plant groups and in fungi. The general absence of endothermy in primarily marine clades is perhaps unsurprising in view of the high specific heat and high heat conductance of water as compared to air. The evolution of endothermy in fishes appears to be a post-Cretaceous development and may well be an evolutionary response to the successful colonization of endothermic birds and mammals from the land.

The absence of small marine mammals is strange given that some diving birds (auklets) can weigh as little as 41 g [70]. The loss of heat from an endothermic animal in water is mitigated in a large body with a high volume-to-surface ratio and by a coat of insulating fur or feathers. Perhaps birds, including small forms, spend less time in or under water than do mammals. Unlike at least some marine mammals such as cetaceans, birds must come ashore to breed; but so do seals (pinnipeds) and sea otters (*Lutridae*), which are always large.

6.7. Symbioses

Perhaps the greatest *per capita* increase in energy exploitation in the history of life before the emergence of humans resulted

from the mutualistic union of two cells representing the two great domains of prokaryotic life, the Archaea and Eubacteria. The genetic and metabolic integration of an archaeal host and a proteobacterial guest established the eukaryotic cell, whose metabolic power and genetic information exceeded those of its component cells by a factor of at least 200 000 [71]. Eubacteria of at least 11 phyla have repeatedly become mutualistic symbiotic guests of eukaryotic hosts, where they function in photosynthesis, sulfide oxidation, methane consumption, nitrogen fixation, lignocellulose digestion and bioluminescence, among other functions [71–75]. Eubacteria are also prominent as parasites in all eukaryotic organisms.

It is therefore remarkable that the Archaea have participated in very few mutualistic symbioses or pathogenic relationships [76–78]. The only exceptions—and these are physiologically and bio-geochemically important—are methanogens, which are associated with ciliates in sediments, soils and the water column, and in the digestive tracts of some arthropods and vertebrates [77,79–83].

Explanations for the apparent scarcity of Archaea in partnerships with eukaryotes are tentative and untested. One possibility is that Archaea are part of consortia with other microbes in eukaryotes, potentially compromising the intimacy between guest and host that many Eubacteria have achieved; but even if this were true, this explanation does little more than restate the problem. Abedon [78] points out that the natural history of Archaea is still largely unknown and that the Archaea as a group have been severely undersampled. Greater knowledge may therefore show that the ecologically restricted role of Archaea in symbioses is a false pattern.

Many marine and freshwater animals contain photosynthesizing organisms. Such photosymbioses have repeatedly arisen in protists, sponges, cnidarians, flatworms, molluscs, tunicates and Late Palaeozoic brachiopods [84]. A modified photosymbiosis has even evolved in a mammal, the three-toed sloth *Bradypus* [85]. Curiously, no such partnerships are known in sedentary bryozoans, barnacles or echinoderms. The hypothesis that a gigantic Permian bryozoan of the genus *Tabulipora* from Greenland contained photosymbionts was rejected [86] on the basis of inconclusive isotopic evidence, but the possibility of a partnership with algae should be re-examined. Bryozoan and barnacle skeletons need not be incompatible with photosymbiosis because they could in principle allow light to pass through to underlying tissues, as in some bivalves and foraminifers. Crinoids, fossil blastoids and other echinoderms cover the skeleton with tissue and are therefore not burdened by an exoskeletal constraint. Freshwater bryozoans lack a skeleton altogether and could, like their sponge and hydrozoan counterparts, host green algae.

There are no known aerially floating or flying photosynthesizers. The low density of air and of potential nutrients make passively floating aerial phytoplankton unfeasible [87,88]. Prolonged life in air by passively floating organisms is known in spores, pollen and tiny insects, which occur at densities high enough to feed aerial predators; but the potential benefits of photosynthesis as a supplement to the food of aerial animals are probably minimal.

Photosymbiotic animals and protists capture particles from the plankton either piecemeal with sticky or stinging tentacles or in bulk by filtration. On land and in freshwater, about 400 species of angiosperms complement photosynthesis with nutrients derived from the capture of small animals, which

they catch in leaves specialized as traps, water-filled receptacles or sticky surfaces. No such carnivory is known in algae, non-angiosperm land plants or woody species. For large epiphytes and some woody plants, an alternative solution is to be fed by ants or other insects [89,90] or to use arthropod intermediaries between them and symbiotic fungi [91]. Despite their mucilaginous surfaces, algae are typically not sticky; neither they nor non-angiosperms possess fast-closing traps. The absence of such traps is surprising, because environmentally triggered devices generating high forces are known in red algae [91] as well as in fungi, ferns and angiosperms, where these devices eject reproductive structures such as spores and seeds [92–94]. There should therefore be no strict prohibition against self-actuated traps. The high abundance and ready availability of particles and dissolved organic matter in all but the most oligotrophic waters may eliminate any benefit that algae might derive by capturing prey.

Chemosymbiosis, a partnership between aquatic animals and sulfide-oxidizing and/or methanotrophic bacteria, has evolved in foraminifers, ciliates, annelids, molluscs and crustaceans [73,80,95]; but it is entirely unknown in solitary and colonial Cnidaria [73] as well as echinoderms, living brachiopods, sponges, tunicates and bryozoans. The sea anemone *Henactis sepala* lives in carbonate-seep environments where chemosymbiosis is common, but there is no evidence yet that this cnidarian contains the requisite symbionts [96]. The combination of a low surface-to-volume ratio and the absence of active ventilation to enhance respiration may prevent cnidarians from entering into chemosymbiotic partnerships [73]. Sponges, tunicates and bryozoans are colonial animals that do ventilate actively by producing currents. It is therefore unclear why these animals did not form chemosymbioses.

Botting *et al.* [97] speculated that the Early Cambrian hexactinellid sponge *Decumbispongia yuani* was chemosymbiotic because it lacked basal structures and osculum and therefore lacked a ventilatory system. This mud-dwelling species would have nourished bacterial symbionts with sulfide obtained from the sediment. Although this scenario is plausible, I suspect that this sponge fed mainly on dissolved organic matter, as many living reef-associated sponges do [98,99].

Several brachiopods, ranging in age from the Devonian to the Late Cretaceous, and including the largest Mesozoic species, lived in seep or hydrogen-vent environments [100,101]. It is not known whether these brachiopods were chemosymbiotic. Although the large size of the Mesozoic *Peregrinella* could suggest this condition, some large seep-dwelling bivalves lack sulfide-oxidizing symbionts [102].

Planktonic animals also inexplicably lack chemosymbionts. This absence is all the more peculiar given the common occurrence of photosynthesizing and bioluminescent symbionts in planktonic animal species [72].

6.8. Specialized scavenging

Scavenging—eating dead animal matter—is common among predators and in lineages that descend from predators. Specialization to scavenging, however, is less common, being known in several groups of birds, insects and marine neogastropods. In particular, no mammals (including flying bats) are specialized to this source of nutrients. The ability to locate and then exploit large corpses for food requires keen senses and wide-ranging search. Large soaring birds are better equipped to sense and locate carcasses than ground-dwelling mammals.

Insects and neogastropods tend to rely on smaller dead animals, which are more densely distributed, and therefore can specialize on this food source without resorting to long-distance aerial searching. The scavenging gap in mammals therefore appears to represent an energy limitation.

6.9. Plant growth forms

Despite the great diversity of growth forms among land plants and marine algae, several types have failed to evolve in major clades. Herbaceous plants have evolved in clades of tracheophyte land plants except gymnosperms. Annual herbs, however, are known only among angiosperms, especially dicots [103]. The evolution of these fast-growing herbaceous plants was apparently contingent on the miniaturization of xylem strands and leaf veins, associated with increases in leaf-vein density and photosynthetic capacity [18,104], a development of angiosperms beginning 100 Ma [105]. Woody plants have evolved in every major clade of tracheophytes [106] but never in bryophytes. Finally, the grass-like habit, characterized by leaf growth at the base, occurs in several angiosperm clades but in no other clade of land plants. An equivalent growth form in which the algal thallus accretes at the base of the blade evolved in some laminarialean brown algae [107] but in no other algal clade. The phylogenetically restricted occurrence of annual herbs and basal growth reflect limits on productivity and physical defence against herbivores, respectively, in the clades without these traits, whereas the absence of woody bryophytes is the consequence of an inadequate vascular system coupled with low competitiveness.

Most terrestrial and aquatic vascular plants obtain nutrients by the roots, often in partnership with fungi. With the exception of freshwater charophytes and some marine coenocytic green algae, most algae acquire nutrients directly from the water over the whole surface [88,108]. The absence of sedimentary nutrition in most algae is puzzling because the ability to mine this rich resource enables seagrasses, which lack root fungi but do often form partnerships with chemosymbiotic lucinid bivalves that reduce the sulfide content of sediments [109,110], to become highly productive on sandy and muddy shores [36,111].

6.10. Herbivory

Herbivory—consumption of photosynthesizing tissues of attached plant-like organisms—has evolved hundreds of times in arthropods, molluscs, echinoderms and vertebrates [112–114]. Nevertheless, several animal clades with long histories lack herbivorous representatives (table 1). An apparent exception within one of these clades (Araneae) occurs in a small clade of jumping spiders in Costa Rica feeding on the ant-associated Beltian bodies of acacia trees [115]. However, it is unclear whether the plant fluids constitute an important part of the spiders' diet. The clades without herbivores overwhelmingly comprise predators. Reliance on a plant diet is usually enabled by symbiosis with bacteria that can digest cellulose or that synthesize amino acids not found in plant sap [71,116], suggesting that impediments to the establishment of a stable symbiosis may explain the phylogenetically uneven distribution of herbivory.

A specialized algal diet characterizes many marine herbivores. Turtles and birds, however, consume seagrasses (angiosperms) but no seaweeds [117]. This is surprising in view

of the large biomass of intertidal algae on temperate shores, where herbivorous geese, ducks and swans are abundant.

An energetic limitation appears to explain the scarcity of the herbivorous habit among animals capable of powerful, sustained flapping flight [118,119]. Most herbivorous birds are poor fliers or are flightless, and there are no known bats that ingest green vegetation. Even adult insects that feed on plant stems and leaves are usually not strong fliers, and larval stages that are herbivorous are flightless. Herbivory requires either a capacious digestive system or heavy equipment for fragmenting cellulose-rich plant material. These specializations require investments in heavy structures that are incompatible with high flight performance.

With origins in the Late Silurian, piercing-and-sucking is perhaps the oldest form of herbivory by terrestrial arthropods [113]. At least two post-Cretaceous marine clades (sacoglossans and the neritid genus *Smaragdia*) have also evolved fluid-feeding on algal and seagrass cells [120,121]. Although some corixids and larval haliplid beetles feed suctorially on freshwater algae, no freshwater herbivore is known to feed in this way on vascular plants [122,123]. In Hutchinson's view, slow-moving freshwater piercing-and-sucking insects would be highly vulnerable to predation, but the gastropods with this habit in the sea are also slow and would be no less vulnerable [123]. Their absence in freshwater remains a mystery.

6.11. Gelatinous plankton

Many marine planktonic organisms have a gelatinous consistency perhaps related to defence against mid-water predators. Hamner [124] noted that, with the exception of two rare hydromedusan genera, gelatinous planktonic animals are unknown in freshwater. The reasons for this extreme rarity remain unclear, but one possibility is that very few bodies of freshwater are large enough to support viable populations of such animals. Another problem may be dispersal. Whereas many freshwater species can occasionally disperse with the aid of animals moving between water bodies, this option is likely unavailable for gelatinous planktonic forms, which unlike more active swimmers may be unable to move substantial distances under their own power.

6.12. Drilling predation

Drilling (chemically or mechanically excavating a hole through the wall of an animal's exoskeleton in order to feed) evolved as a means of predation beginning in the latest Ediacaran in the sea and is practiced in modern marine communities by members of at least six molluscan clades [125,126]. On land, drilling by slugs and beetles is locally common [127,128]. Small holes in brackish water and freshwater gastropods [129] likely do not indicate drilling, but instead result from fishing crushing shells with their pharyngeal apparatus [130]. No unequivocal case of shell-drilling predation is yet known from freshwater, either by gastropods or insects. The reasons for this absence are unclear.

6.13. Venoms and toxins

The ability to inject venom into prey or enemies is widespread in animals and many trichome-bearing land plants, but there are clades in which this ability is extremely rare or absent. Envenomation has evolved several times in post-

Cretaceous mammals [131,132] and has been suggested for a Cretaceous dromaeosaurid theropod, a species close to the origin of birds [133]; but it is unknown in living birds. It is a hallmark of all marine and most freshwater cnidarians, including photosymbiotic forms, but is absent in all algae and fungi. The reasons for these absences remain obscure.

6.14. A biting gastropod operculum

Shells or tests into which vulnerable soft parts of animals can be withdrawn for protection are often sealed by a closing device. A one-piece operculum performs this function in many gastropods, many bryozoans (especially cheilostomes) and Palaeozoic hyolithid molluscs; whereas a device composed of several plates closes the test of most balanomorph barnacles. In most of these animals, the closing device acts as a passive barrier. In strombid and some other gastropods, the operculum also takes on a more active role in locomotion and in stabbing potential predators; but no gastropod has evolved an operculum that can bite intruders. Biting shell-closing devices are known in bryozoans, fossil shell-bearing cephalopods and paguroidean hermit crabs. In order for a gastropod to evolve a biting operculum, the closing structure would have to consist of at least two moving parts. This might seem difficult to achieve, but many gastropods fold the foot, on whose dorsal side the operculum is situated, as it is pulled into the shell [134]. Pedal folding could in principle be accompanied by the evolution of a two-part operculum, but no such structure is known.

6.15. Communication by sound and electricity

Sending, receiving and responding to sensory signals are important in sexual selection, the identification of food and foes and in social organization. The neural mechanisms for sensation, motor control and coordination are costly. Communication by sound is widespread in arthropods and vertebrates but almost unknown in the large clades Lophotrochozoa and Echinodermata and the basal clades Porifera, Cnidaria, Ctenophora and Platyhelminthes [135]. Animals that send acoustic signals risk detection by enemies capable of sensing such cues from a distance. Sound-sensing arthropods and vertebrates are generally fast and powerful. The low metabolic rates of most of the animals that do not communicate by sound may preclude the rapid and powerful responses needed to counter attack by these predators. Exceptions could occur in high-energy cephalopods and in some gastropods that inject instantly acting venom into fish [135]. Breure [136] reports a likely exception to the prohibition against defensive sound production in gastropods. A Brazilian land snail emits a breathy squeak together with an orange secretion when disturbed.

Plants would seem to be another obvious group in which communication by sound is precluded [135]. However, the Cuban liana *Marcgravia* guides echolocating bat pollinators to its flowers by placing an upwardly concave leaf beneath the flowers, so that the bat can use the reflected sound [137].

Communication by electric impulses is fundamental to the action of nerves in animals, but as a means of defence, searching for or attracting mates, and prey subjugation it is used by only a limited number of aquatic animals [138]. As with acoustic signalling, the use of electricity is energetically expensive, probably accounting for its absence in

aquatic lophotrochozoans, worms, echinoderms and the basal metazoan phyla.

6.16. Social organization

Shell-bearing lophotrochozoans (thus excepting coleoid cephalopods) and echnioderms have never achieved social organization, in which autonomous individuals communicate at a distance and coordinate their activity to form a choerent group. In arthropods and vertebrates—animals with generally higher metabolic rates—sociality has evolved frequently. These are also the only two animal clades in which eusociality (overlapping generations, cooperative brood care and defence, and division of labour among individuals centred on a collectively constructed or occupied home nest) has evolved, chiefly on land [139]. Sociality in general and eusociality in particular require signalling at a distance among individuals as well as long-distance foraging for scattered food sources and rapid coordinated response to danger, all energetically costly functions that become feasible only in animals with large time–energy budgets. A low-energy option explored by many clades of planktic and bottom-dwelling aquatic animals is coloniality, in which asexually generated modules remain interconnected. Both sociality and coloniality offer competitive advantages [140], but whereas colonial organization is common among sedentary as well as pelagic animals, sociality is feasible only for those terrestrial and water-dwelling species in which relatively rapid movement and joint action is possible.

Scott-Phillips & Blythe [141] have observed that combinatorial communication, in which signals comprise combinations of simpler components as in human language (and, I would add, music) is essentially unknown in nature outside the human species. In animals, each signal is associated with a given response and is therefore holistic; the effect of a sum of these signals is equivalent to the sum of its parts. Composite signals can emerge in a communication system only from within that system, and this requires that the members of that system have knowledge of, or at least intuitions about, other members' intentions [141]. The emergence of combinatorial communication is, in other words, contingent on the existence of a social organization among conscious individuals, a condition that may be satisfied by very few birds and mammals and perhaps only by humans. I note, however, that both the genetic code and the vertebrate immune system are based on combinatorial principles.

6.17. Cloning and regeneration

Most major clades of multicellular life contain lineages whose members not only regenerate lost parts, but can form new individuals by cloning, that is, by dividing the body or by budding. This ability is not confined to colonial animals such as sponges, cnidarians and bryozoans, but is also found in fungi, plants and such solitary animals as polychaete annelids, echinoderms and sea anemones [142]. Cloning and whole-individual regeneration of this kind is, however, entirely unknown in molluscs [142], brachiopods, vertebrates and arthropods. All of these animals are capable of replacing lost appendages, and arthropods and other ecdysozoans episodically shed the ectodermal organs in favour of new ones as they grow; but fully functional individuals do not arise during these replacements. Given that members of two of the three great animal clades—Lophotrochozoa and Deuterostomia—can grow individuals by fission or budding or from relatively

small parts, it is likely that these capacities have been lost in the clades that lack them.

6.18. Live-bearing turtles and birds

One of the enduring mysteries is the absence of bearing live young in birds and turtles [143]. Live-bearing has evolved many times in animals, and of course characterizes all placental and marsupial mammals, many of which, like bats and phalangers, can fly or glide like birds. Williams [143] rightly rejects all previous arguments concerning the absence of live-bearing in birds and turtles and offered no explanation of his own. To say that it is a historical artefact of ancestry is simply to restate the problem and in any case falls short of accounting for those clades in which egg-laying was ancestral and viviparity was realized in some lineages.

7. A view from the past

Despite the existence of prohibited morphological and ecological phenotypes in the living biota, most of which apply at the level of large eukaryotic clades or habitats rather than to the domain of multicellular life as a whole, there can be no doubt that evolution has become globally less constrained over time with respect to the directions and extent of functional specialization and diversity. With a few exceptions (see below), nearly the full complement of prokaryotic biochemistry and eukaryotic protein sequences had been established long before the Phanerozoic [11,144–148]. The advent of multicellular organization ushered in an age of morphological expansion [149,150]. Animal skeletons were a latest Neoproterozoic innovation, and about 80% of skeletal design space had already been occupied by the Early Cambrian [151,152].

Even during the Late Ordovician (450 Ma), long after the blizzard of innovation that led to the Ediacaran and Early Cambrian establishment of major multicellular body plans, and well after the great pulse of Early Ordovician diversification of marine life had ended, many phenotypes familiar in the modern biota had not yet appeared. Had we been there to survey the diversity of life, such phenotypes would have been deemed unattainable; yet all were eventually realized, not just in a single lineage but usually in multiple clades. A list of these phenotypes would include cutins, suberins, lignins, flavonoids, alkaloids, vascular systems, roots, leaves, rigid frameworks of stems and branches, nutrition complemented by animal matter, and basal growth in land plants; nitrogen-fixing symbiosis on land; animal-mediated dispersal/pollination; silk-producing, sound-emitting, flying, eusocial, terrestrial herbivorous, wood-boring, terrestrial shell-bearing and endothermic animals; embryos nourished within the body of an animal or plant parent; mineralized phytoplankton; and rock-excavating marine herbivores.

Within well-established Cambrian and Ordovician clades, many structures, relationships, conditions and modes of life that were to become important later had not yet evolved by the Late Ordovician. These include photosymbiotic and chemosymbiotic molluscs, the bivalved condition in gastropods, terrestrial life in gastropods and vertebrates, complex septa within the phragmocone of externally shelled cephalopods, internalization and loss of the shell in cephalopods, cementation to the substratum with a glue of calcium carbonate

and organic matrix in several animal groups (gastropods, brachiopods, bivalves and barnacles), spines on shells of several groups (brachiopods, bivalves and brachiopods), mineralized tubes in polychaete annelids, mobility in bryozoans and pelmatozoan echinoderms, jaws and teeth in vertebrates, and vascular systems in brown and red algae. A vast diversity of potent venoms also lay in the future as part of the defensive and aggressive arsenal of many gastropods, cephalopods, aculeate Hymenoptera, vertebrates and land plants.

These 35 or more categories of phenotypes that were still forbidden during the Late Ordovician indicate that a great deal of evolutionary potential inherent in previously established body plans and constructional protocols had not yet been realized. Many of the later phenotypes were responsible for, and in turn depended on, interactions that had not yet developed. Intense selection in favour of these states therefore did not exist or was counteracted by trade-offs imposed by competing factors. Evolving interdependencies among species and among ecosystems made high-energy phenotypes and modes of life possible and changed the selectional landscape [153], permitting many lineages in many clades to transcend previous limitations through innovations in construction and ecology.

Set against these gains are a few phenotypic losses. Phenotypes that were common in the Palaeozoic but now extinct include arborescent lycopods; brachiopod shells with spines, one concave and one convex valve, or hinged teeth that grew only by accretion and without resorption; external cephalopod shells that were straight, curved, or openly or asymmetrically coiled; and multiplacophoran chitons, in which each of the eight plates is transversely divided into three separate pieces. Currently, extinct phenotypes that flourished during the Mesozoic include long-necked marine tetrapods, and external cephalopod shells with spines, sexual dimorphism or irregular coiling. Still others were common in shallow-water marine ecosystems during the Palaeozoic but have since become restricted through competition and predation to deep water or unproductive habitats where interactions proceed slowly. These include adult arthropods such as trilobites that could roll up into a ball; immobile unattached skeleton-bearing animals lying on soft mud; sponges with rigid skeletons; colonial reef-building corals with low colony integration in which each polyp has just one or two neighbours; openly coiled gastropod shells, including those of larvae; shell-bearing cephalopods; and permanently attached echinoderms [36]. Importantly, however, nearly all of these formerly prominent phenotypes still persist in at least some clades even if they have disappeared in others.

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8. Concluding remarks

The evidence shows clearly that there are limits to evolution. However, almost all the 32 phenotypes that continue to be forbidden in the living biota are specific to particular major clades or environments. The tree of life as a whole, when viewed throughout its 3.5-billion-year history, reveals only one truly global prohibition: the absence of wheeled transport; but of course this prohibition was overcome culturally through human invention. All the other forbidden states now or in the past reflect functional incompatibilities, manifested by energetic limitations and trade-offs, or circumstances that did not or do not yet exist.

Selection due to competitors and predators has relaxed or eliminated many constraints over time, particularly in ecosystems with abundant, predictable and biologically well-regulated resources. It has done so by favouring those constructional and ecological innovations, including greater versatility, that expanded energy budgets of individuals and organized groups and established interdependencies that align the interests of producers and consumers [153–155]. These innovations conferred benefits in acquiring, defending, creating and controlling resources and in enhancing independence from external conditions, with the result that phenotypic diversity increased and empty space in the tree of life shrank. Although some phenotypes disappeared, the introduction of new states for the most part did not come at the expense of old ones; rather, phenotypes have accumulated over time in the biosphere as a whole.

One reviewer of this paper raised the interesting question whether the tree of life has itself grown over time and, if so, whether empty space in the tree decreased, kept pace with, or increased relative to tree size. The expansion of versatility in major clades suggests that the dimensionality, and therefore potentially the size, of the tree as a whole has increased, at least among eukaryotes. The continuing addition of novel phenotypes well after the Ediacaran–Cambrian revolution implies that, despite this enlargement, unoccupied parts of the tree have diminished in size and number. This interpretation deserves further scrutiny, but if it is correct, it would contradict Erwin's [156] contention that phenotypic space had effectively reached a plateau once the basic genetic architecture of metazoans was established by Early Cambrian time. My argument is that having the tools and building blocks available is not equivalent to the construction of workable phenotypes and forging new ecological interdependencies. Moreover, the genetic architecture of plants may not have come about until after the Cambrian.

Competing interests. I declare I have no competing interests.

Funding. I received no funding for this study.

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