

Novelty and Innovation in the History of Life

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The history of life as documented by the fossil record encompasses evolutionary diversifications at scales ranging from the Ediacaran–Cambrian explosion of animal life and the invasion of land by vascular plants, insects and vertebrates to the diversification of flowering plants over the past 100 million years and the radiation of horses. Morphological novelty and innovation has been a recurrent theme. The architects of the modern synthesis of evolutionary theory made three claims about evolutionary novelty and innovation: first, that all diversifications in the history of life represent adaptive radiations; second, that adaptive radiations are driven principally by ecological opportunity rather than by the supply of new morphological novelties, thus the primary questions about novelty and innovation focus on their ecological and evolutionary success; and third, that the rate of morphological divergence between taxa was more rapid early in the history of a clade but slowed over time as ecological opportunities declined. These claims have strongly influenced subsequent generations of evolutionary biologists, yet over the past two decades each has been challenged by data from the fossil record, by the results of comparative phylogenetic analyses and through insights from evolutionary developmental biology. Consequently a broader view of novelty and innovation is required. An outstanding issue for future work is identifying the circumstances associated with different styles of diversification and whether their frequency has changed through the history of life.

Introduction

Through the history of plant and animal life over the past 600 million years evolutionary diversifications have occurred on large and small scales in response to environmental and ecological shifts, the origin of new clades and evolutionary novelties. New habitats have been exploited, such as the invasion of land over 400 million years ago, or the rise of grasslands beginning about 35 million years ago. Mass extinctions have episodically removed extensive swaths of biodiversity, creating new evolutionary opportunities (see review by Hull in this issue). About 252 million years ago, the great mass extinction at the end of the Permian eliminated over 90% of species in the oceans and perhaps 70% on land [1]. The explosion of new groups of vertebrates in the wake of the devastation was remarkable: ichthyosaurs and turtles in the sea, and the earliest mammals and dinosaurs on land. Some evolutionary diversifications involved a single clade, as with flowering plants, yet many other events involved multiple clades, including the explosive Ediacaran–Cambrian diversification of animals (600–510 million years ago) or the radiation of birds and mammals after the end-Cretaceous mass extinction 66 million years ago. Striking morphological novelties appeared during some of these evolutionary diversifications, from appendages and eyes in the Cambrian to feathers in the Cretaceous.

Many evolutionary biologists, including the architects of the modern synthesis of evolutionary biology, have held that all evolutionary diversifications are adaptive radiations. Adaptive radiations involve the diversification of a single ancestral species into a variety of species, each specialized for distinct ecological roles. Some well-known and well-studied examples of adaptive radiations include the Galápagos finches with their wide range of beaks carefully tuned to specialized diets [2] or the diversification of an undistinguished California shrub into an extraordinary array

of silverswords on the Hawaiian Islands, including rosette plants, pincushions, shrubs, vines and even trees [3]. Larger-scale evolutionary diversifications have been seen as adaptive responses to ecological opportunities with morphological novelty arising during the radiations. One corollary of this view is the assumption that novel phenotypes arise with sufficient frequency that ecological opportunity is the controlling factor rather than the supply of novelty.

Several challenges have arisen to this comfortable view of the relationships between ecological opportunity, adaptive radiation and evolutionary novelty. Perhaps most significantly, molecular and developmental studies have shown that many phenotypic novelties may arise quite rarely and their generation may be highly contingent upon earlier, potentiating mutations. In addition, studies of evolutionary diversifications have documented a greater diversity of patterns than can be comfortably accommodated within the standard paradigm of adaptive radiations. A more robust understanding of evolutionary diversification demands a broader view of pattern rather than a rote invocation of adaptive radiations. Finally, most morphological novelties are not directly tied to adaptive radiations. Indeed in some cases the molecular and developmental origin of new phenotypic characters may often be independent of ecological opportunities, with novelty arising long before a diversification (a macroevolutionary lag). Taken together, these developments indicate the need for a more diverse and nuanced approach to novelty and innovation in the history of life.

Here, I begin with an overview of adaptive radiations and ecological opportunity, and provide examples of the variety of evolutionary diversifications identified from the fossil record. The limitations of the adaptive radiation model lead to the recognition of a broader array of patterns of evolutionary diversifications [4]. Next, I turn to the historical contingency of the

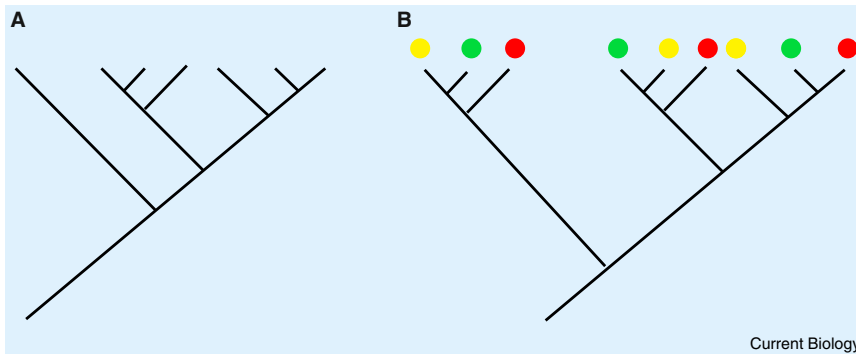


Figure 1. Schematic of the phylogenetic relationships in adaptive radiations.

(A) An adaptive radiation. (B) A replicate radiation in which a similar morphotype, depicted as boxes of the same color, occurs independently in related clades.

processes leading to some phenotypic novelties. Thus, one cannot simply assume that novel phenotypes will be available whenever ecological opportunity arises. Macroevolutionary lags and the contingent nature of novelty demand that we consider the processes generating phenotypic novelty separately from the ecological and evolutionary processes that regulate their success. Finally, I turn to the processes generating morphological novelties.

The Nature of Adaptive Radiations

The diversification of new species from a single ancestral species during an adaptive radiation is a response to ecological opportunities. Several potential types of ecological opportunity have been identified [5–7] (Figure 1A): the appearance of new resources, such as flowering plants for the diversification of many insects, or grasses providing a resource for grazing mammals; the extinction of species utilizing resources creating an opportunity for diversification, such as the diversifications of birds and placental mammals following the end-Cretaceous mass extinction that killed the dinosaurs and other archosaurs 66 million years ago; the colonization of an area with underutilized resources, as illustrated by the many adaptive radiations associated with islands and archipelagos; and ‘key innovations’ allowing use of a new or underutilized resource, such as the appearance of orb-weaving within a clade of spiders which increases the efficiency of prey capture. Key innovations have commonly been identified by diversification of the clade possessing the innovation [8–10], but despite the continuing enthusiasm for key innovations, such claims have proved difficult if not impossible to test [11,12]. Cases of each of these opportunities have been examined in both living and fossil taxa but it is difficult to recognize opportunity *a priori*, and until we understand why some clades fail to radiate given apparent ecological opportunity the power of the theory of adaptive radiations will remain limited [6].

The general model for adaptive radiation includes an initial burst of diversification and morphological change as new species specialize in different components of the ecological opportunity (known as ‘character displacement’) [13,14]. As the number of species increases, the available resources will decline, eventually limiting the number of species and causing the rate of diversification to drop. Thus, adaptive radiations are expected to be self-limiting, diversity-dependent phenomena in which competition initially spurs diversification but eventually limits the extent of the radiation. This expectation of an ‘early

burst’ of morphological change has influenced many studies of diversifications in the fossil record. The genetic underpinnings of some radiations have been dissected. For example, Darwin’s finches in the Galápagos Islands are characterized by a diversity of beak sizes and shapes representing specialized feeding habits. A transcription factor associated with craniofacial development (*ALX1*) is primarily responsible for modulating this diversity of beak morphology [15]. A more diverse set of mechanisms underlies the diversification of cichlid fish in African lakes, particularly in Lake Victoria and Lake Malawi, one of the most rapid vertebrate radiations. This diversification was driven by growth and collapse of these lakes, sexual selection and ecological specialization [16]. The rapid cichlid diversification has involved the accumulation of genetic variation through gene duplication, divergence in regulatory sequences, insertions of transposable elements, accelerated change in coding sequences and other changes [17].

In summary, adaptive radiations involve the diversification of a single clade as a result of ecological opportunities, with the new species specializing on different niches. The expectation is that morphological diversification will initially be high, but tail off as available opportunities decline.

Extensions of the Adaptive Radiation Model

Many evolutionary diversifications involve more complicated patterns than the diversification of a single clade. The *Anolis* lizards of the Caribbean are a classic example of a replicate radiation in which morphologically similar suites of species have arisen independently on different islands [18]. Although the number of species depends on the size of the island, each island has species differing in size, color and feeding strategy (ecomorphs) but convergent morphologies are found on different islands. The habitats of each island are sufficiently similar that each island has, for instance, a niche for lizards on the trunks of trees and another niche for the thin twigs of shrubs. Although it is possible that the trunk morph arose once and dispersed through the Caribbean, phylogenetic analyses have shown that most islands were colonized by a single species that then diversified into a suite of ecomorphs. A similar pattern is found with spiders on the Hawaiian Islands [19]. Such replicate radiations are of great interest to evolutionary biologists, because the deterministic patterns of evolution indicate the presence of pre-existing adaptive optima [20].

Long-lived optimal solutions to adaptive problems have been identified in the fossil record [21] (Figure 1B). For example, as canids diversified from the Eocene to today, they explored many different feeding strategies from hypercarnivores, feeding exclusively on large mammals, to omnivorous groups feeding off

a variety of animals and plants. However, it turns out that there are three optimal feeding strategies, each with an optimal body mass. The optimal strategies were repeatedly exploited by different subclades of canids, producing a pattern of iterative diversifications [22]. Post-Paleozoic echinoids (sea urchins) exhibit similar pulses of diversification over the past 250 million years as new feeding patterns were discovered [23].

Adaptive Radiations in the Fossil Record

Many adaptive radiations have been described in deep time, ranging from the fusion of the mantle to produce a siphon and allow deep burrowing among bivalves [24], the Neogene diversification of horses [25], the extensive diversification of Mesozoic mammals [26] to possibly every other clade one could examine. Early bursts of morphological and taxonomic diversity should be associated with adaptive radiations [5] and many have been identified in the fossil record, ranging from the Cambrian radiation [27] to many invertebrate [28,29] and vertebrate [30,31] clades. For example, the rapidity of the basal radiation of modern birds has been linked to the end-Cretaceous mass extinction (66 million years ago; see review in this issue by Brusatte *et al.*). A whole-genome analysis of 48 species representing all major clades of bird identified a very rapid radiation within Neoaves (all living birds except ratites, waterfowl and chickens) from the latest Cretaceous (about 69 million years ago) into the Paleogene [32]. Nearly all divergences on the level of the orders had occurred by 50 million years ago. This result strongly supports a rapid morphological and taxonomic burst of bird diversification in the Paleogene.

Whether these evolutionary diversifications actually represent adaptive radiations has been questioned, however. I have pointed out earlier that character displacement is an expectation of the adaptive radiation model, and the extension of adaptive radiations to macroevolutionary timescales is predicated on character displacement. But a growing number of cases show little evidence of character displacement [33,34]. Indeed, many radiations may not be driven by ecological divergence, but rather constitute ‘non-adaptive radiations’ resulting from geographic spread of a clade across a region [35,36]. In the case of the Ediacaran to Cambrian appearance and diversification of animals, many lineages were involved that had diverged tens of millions of years earlier. Morphological novelty was pervasive, but describing this as an adaptive radiation stretches the definition of the term beyond reason [27].

Moreover, tests of ‘early burst’ models using phylogenetic trees have raised additional questions about generality of the model. In a meta-analysis of 49 studies of body size and 39 studies of morphology in a range of invertebrate and vertebrate clades, only two studies supported the ‘early burst’ model [37]. There are alternative explanations for this result: it could reflect difficulties in testing ‘early burst’ models, or it could suggest that adaptive radiations among small clades studied by ecologists today may not scale up to those found in the fossil record [38,39]. Other studies have come to conflicting conclusions about the dynamics of diversifications. For example, a study of the diversification of dinosaurs through 170 million years of the Triassic and Jurassic identified an adaptive radiation of clades including sauropodomorphs, ornithiscians and theropods, followed by a decline in rate, which the authors interpret as a

saturation of niche space [40]. But the high rates of evolution persisted only in the lineage leading to birds, which the authors interpret as indicating continuing ecological innovation of the maniraptorian-avian lineage. Unresolved, however, is whether the evolutionary space for this trend existed at the onset or was created through a cascading radiation. In contrast, the post-Paleozoic echinoid diversification discussed above showed a more heterogeneous pattern of rates [23]: there was no early burst of diversification at the base of the clade (in fact the lowest rates were associated with the initial diversification), but pulses did occur within subclades through the history of the group as new feeding strategies were discovered. This pattern of bursts of diversification throughout a phylogeny has also been noted in other studies [22]. At least in principle, early bursts could occur in any of three variables — the number of taxa, body size, or morphological disparity (morphological diversity) — but it is not clear that early bursts should be equally likely in each metric.

So, despite the intuitive appeal of explaining many evolutionary diversifications in the history of life as adaptive radiations, careful study of some cases has not found evidence of character displacement and there is at best mixed support for ‘early bursts’ of diversification. In contrast, there is considerably more evidence that optimal solutions to particular adaptive problems may persist for tens of millions of years before diversification, as in the replicate radiations of *Anolis*, canids and post-Paleozoic echinoids.

Constructive Radiations

Most evolutionary diversifications discussed to this point are diversity-dependent. This means that the resources utilized by the diversifying clade were limited and this resource limitation eventually limited the scope of the radiation. The diversification of the Galápagos finches is limited by the number of food types available to them and the number of islands in the group. But this is not true of all radiations, and indeed the most interesting diversifications may be those that are linked, so that the radiation of one clade generates diversification in other, ecologically linked clades. For example, lucinid bivalves originated in the Silurian, but their diversity remained low until the Cretaceous where they began a remarkable radiation that persisted through much of the Cenozoic [41]. This Cenozoic diversification came about because seagrasses and mangroves had constructed a habitat of dysaerobic sediments below their root zones. Lucinid bivalves contain endosymbiotic bacteria in their gills and the bacteria thrived on the sulfide generated in the dysaerobic sediments. The seagrasses in turn benefited from the reduction in sulfides [42]. The lucinids possessed all of the adaptations required for this diversification when they arose in the Silurian, but the habitat that was to prove so beneficial for the diversification of the group simply did not exist. This is an example of evolutionary diversification linked to niche construction [43,44], where modification of a niche by one species alters the ecological, and in this case evolutionary, opportunities for another clade [45,46].

A variety of interactions between clades may occur: synergistic or co-evolutionary radiations between two clades, iterative radiations involving the sequential replacement of subclades within a single larger clade, and cascading radiations across

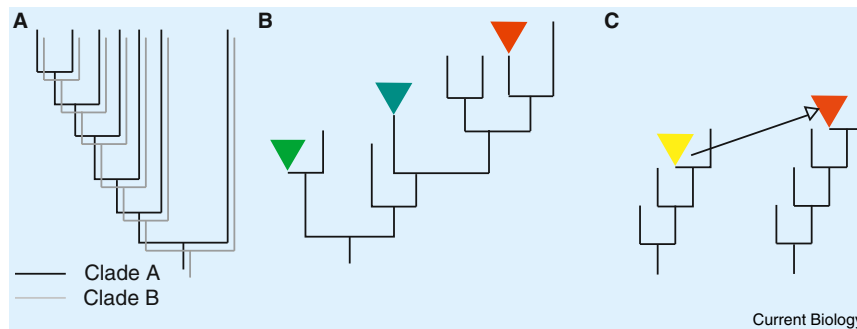


Figure 2. Schematic of phylogenetic relationships for constructional radiations. (A) Co-evolutionary diversifications between clade A and clade B, with similar patterns of diversification along the left-hand subclade. (B) A cascading diversification among subclades (shown as colored triangles) within a single clade. (C) Cascading radiation between independent clades, where diversification of one clade induces diversification of a second clade.

clades due to ecological feedbacks (Figure 2). The important point is that each of these possibilities involves the generation of new opportunities as the radiation continues. This is in contrast to the classic model of an adaptive radiation in which the suite of opportunities is available at the outset of the radiation [13]. In some cases, these opportunities may arise from environmental changes, but in most cases ecological feedbacks construct the opportunities as the radiation progresses, hence the term ‘constructive radiations’. Assumptions that opportunities are available at the outset of a radiation underlie many discussions of novelty as a ‘search’ through an opportunity space rather than the construction of the opportunities as evolution proceeds (Box 1).

One of the most widely discussed reciprocal or co-evolutionary diversifications was that between angiosperms and insect (and potentially other) pollinators [47]. Yet, this case also exhibits the complexity of establishing the extent of interaction between clades. The diversification of angiosperms since the Cretaceous [48–50] coincides with the extraordinarily rapid diversification within clades of holometabolous insects (primarily bees, flies and butterflies) [51]. But despite the attractiveness of the apparent coevolutionary diversification of plants and insects, rigorous testing of such a model can be quite difficult, particularly as phylogenetic congruence can have alternative explanations [52]. Although some ‘key innovations’ have been proposed within specific clades of plants and insects, they do not appear to have led to significant diversifications [53]. Detailed analysis shows that of the six insect pollinated plant clades only four (angiosperms, Gnetales, Bennittitales, and Cheirolepidiaceae) experienced pronounced radiations. The remarkably diverse grasses (Poaceae) are wind-pollinated. Among insects, ants, another very diverse clade, were not pollinators [54]. The late Cretaceous diversification of angiosperms also coincides with a number of other factors which complicate a simple co-evolutionary story: a diversification of multituberculate mammals as identified by dental complexity, taxonomic diversity and body size [55,56], apparent bursts of whole-genome duplication among angiosperms [57,58] and climatic changes driven by continental tectonics [59]. While there is relatively little doubt that the diversification of one clade can influence the diversification of another in a co-evolutionary fashion, disentangling the patterns of influence can be difficult. Apparent cascading radiations could represent a common response to an external environmental factor without ecological feedback between clades.

Limitations of the Concept of Adaptive Radiation

Several challenges have arisen to claims that adaptive radiations are responsible for most evolutionary diversifications. For one, many events have been identified among both living and fossil clades that cannot be explained as the outcome of diversification from a single species. Examples range from the Cambrian explosion of animals, which involved many major clades but relatively few species, to the diversification of grasses. I have already discussed cascading radiations where increased diversity was driven by ecological interactions between clades. Other diversifications, for example the spread of a genus across a continent, may be largely non-adaptive. The most striking observation, however, is the absence of evolutionary novelty associated with classic adaptive radiations. Indeed, by their nature, adaptive radiations concern the adaptive exploitation of ecological opportunities via variation on existing adaptive themes, but not the formation of the themes themselves. While the fossil record documents adaptive radiations that encompass greater morphological diversity than Darwin’s finches, mockingbirds or *Anolis* lizards, including the spread of insects and angiosperms, and the Mesozoic radiation of mammals, the origins of morphological novelties often seem to involve a different process.

Another challenge is illustrated by macroevolutionary lags between the origin of a morphological novelty and the spread of the group possessing it. For example, grasses are an obvious ecological and evolutionary success story. Grasslands are widespread in temperate environments across North and South America, Africa and central Asia. They provide critical habitat for many grazing animals. But grasslands did not spread until tens of millions of years after the origin and early diversification of grasses (Poaceae) [60]. The diversification of early animals and early insects (see Primer by Michael Engel in this issue) also features macroevolutionary lags [61], like the lucinid bivalves discussed earlier. In each case, the new clade originates and may undergo some initial diversification, but remains ecologically insignificant. Commonly, fossils from these groups are absent and only appear much later when the group expands sufficiently in abundance and ecological significance. Macroevolutionary lags arise because the environmental or ecological conditions for the success of a morphological novelty may arise long after the origin of the novelty. It is difficult to argue that the origin of these clades is a response to an ecological opportunity. Rather, these lags reveal that the origin of novelties may be decoupled from their later ecological success.

Box 1. The Topology of Evolutionary Spaces.

Since the introduction of ‘adaptive spaces’ and ‘adaptive landscapes’ during the modern synthesis [116], studies of adaptive radiation and evolutionary innovation have invoked ‘empty ecospace’, or search through a ‘space of the adjacent possible’ [117]. The metaphor of search has spread into economics and business. These approaches assume that the opportunities exploited by evolutionary innovation exist *a priori*, independent of the organisms, rather than being constructed by them during evolution. The foundational work in this area imagines a sequence of nucleotides (the genotype) that give rise to an appropriate three-dimensional structure (the phenotype). Depending on the relationship between genotype and phenotype, a single mutation in the sequence may or may not cause a change in the phenotype (many-to-one mapping). From such a scheme one can build up a network of, say, 20-nucleotide sequences each linked by a single nucleotide change. The topology of such spaces has been intensively studied using tRNA and has been applied to protein and metabolic spaces [118–122], and extended to regulatory interactions and even technology [121,122]. Discovering novelties is viewed as a search through the space of possibilities represented by the sequence space [122].

Although search may be an appropriate metaphor in some cases, there are reasons to doubt its generality. First, many operations change sequence length (insertions and deletions) and development in multicellular organisms introduces a more complex link between genotype and phenotype. Second, the time required to find innovations in sequence space grows with the length of the sequence, and thus search may not be effective for most biologically relevant sequences [123]. Third, the sequence spaces described above are regular with a definable distance (one nucleotide) between each node of the network. But even the resulting tRNA phenotype space is not Euclidean, and it may not be possible to define a distance between phenotypes [118]. The non-Euclidean nature of many phenotypic spaces is a much more general problem than recognized [124]. Despite frequent references to evolutionary ‘distance’ between phenotypes, for most phenotypes it is doubtful whether any meaningful distance can be measured. This problem likely confounds many discussions of adaptive landscapes and morphospaces. Instead, novelty and innovation require a constructional metaphor in which the possibility of new novelties and new innovations emerge through time as a consequence of prior evolutionary changes. Thus, new developmental processes and environmental changes may not represent gaining access to existing but inaccessible regions of evolutionary space [121], but the *de novo* construction of new evolutionary possibilities. Exploring the relative importance of search and construction is a critical important but largely unexplored theme within novelty and innovation.

Phenotypic Novelty and Innovation

The focus on ecological opportunity as the driving factor in adaptive radiation led to a neglect of the mechanisms underlying the generation of novel phenotypes. This has now been remedied by comparative evolutionary developmental studies (‘evo-devo’). Some authors have argued that the rate of novelty has been relatively constant, but the opportunities for successful innovation have varied with time [61,62]. A long-term evolution experiment on *E. coli* has addressed the issue of whether novelties arise regularly or are dependent upon prior, potentiating mutations. *E. coli* normally feed on glucose, but this experiment discovered a mutant form that used citrate as a food source (a *Cit+* mutant). Because the research group regularly archives samples, they were able to show that the *Cit+* mutant required potentiating mutations [63–65]. Moreover, these potentiating mutations had arisen previously in two different lines but had not been exploited because the *Cit+* mutant never occurred. Subsequent mutations also improved the efficiency of the *Cit+* metabolism. The historically contingent delivery of mutations has also been found in the evolution of cortisol specificity in the glucocorticoid receptor of vertebrates [66], in gene regulatory networks of yeast transcription factors [67], in sea urchin development [68,69], and has been examined theoretically [70]. Based on the *Cit+* mutant study, a three-phase model of novelty was proposed, involving *potentiating* mutations that are necessary preconditions for the appearance of the *novel* phenotype, followed by subsequent *refinement* as additional mutations increase or modify the novelty. While almost any prior changes could be considered potentiating this model quite properly restricted the term to

those changes that were specifically required for the success of the novelty. Elsewhere in the literature, the term ‘permissive mutations’ has also been used.

Both macroevolutionary lags between the generation of a morphological novelty and its ecological spread and potentiating mutations demonstrate that novelty does not necessarily lead to diversification. This requires distinguishing novelty as the genetic and developmental mechanisms that generate new homologous characters, and innovation as the processes involved in the ecological and evolutionary success of a clade [27]. From this perspective, phenotypic novelties may arise that never have much ecological or evolutionary success — the ‘weird wonders’ of the Cambrian Burgess Shale fauna may be classic examples. Also, novelties may persist for millions of years before a potentiating event leads to their ecological expansion, or novelties may fill an immediate ecological opportunity. Once new characters arise as novelties new character states will often arise through adaptation, as with the generation of many new types of feathers after the origin of feathers. A scenario emerges for the four aspects of novelty and innovation: potentiation, novelty, adaptation and innovation (Box 2). This model is an extension and generalization of the *Cit+* mutant example discussed previously. The distinction between novelty and innovations borrows from economics, where invention, the origin of a new technology, is distinguished from innovation, the spread or diffusion of such a technology so that it has an economic effect [71]. A critical aspect of this scenario is that some environmental and ecological potentiating events may actually occur after the novelty emerges, thus creating the conditions for the macroevolutionary lags described earlier. The final stage of innovation following

Box 2. Conceptual Framework for Novelty and Innovation.

This conceptual framework for evolutionary novelty and innovation encompasses four aspects: first, evolutionary potentiation through environmental, genetic and ecological changes; second, evolutionary novelty involving the individuation of new phenotypic parts or attributes; third, subsequent adaptive refinement encompassing initial accommodations to the evolutionary novelty in other characters of the organism; and fourth, realization via ecological establishment, which may involve the construction of new niches. It borrows from and extends an earlier model [14].

Potentiation

Classic models of adaptive radiation assume that opportunities exist, awaiting lucky clades to exploit them. But several studies of genetic and developmental changes have shown that potentiating mutations are often required before novelties can appear. As this may seem an utterly vacuous category, with almost anything qualifying as a potentiating event (to the limit of a story-teller's ability), potentiating changes must be tightly restricted to those that can be directly associated with the success of a novelty. Although such potentiating mutations can be identified in experimental evolution studies, new methods will be needed to rigorously identify them in development and morphology. Potentiation can also include environmental and ecological changes necessary for the success of a novelty.

Generation of novel phenotypes

The generation of novelty is characterized by the formation of new, individuated characters. In the cases, where the developmental basis of such characters has been studied in detail, these often involve recursively wired gene regulatory networks which are highly refractory to modification. It would not be surprising, however, to find other regulatory arrangements that lock in developmental processes.

Adaptive refinement

The integration of a novel aspect of the phenotype will often require some adaptive refinement. These changes are often not specifically part of the novelty, but may be upstream or downstream of the kernels involved, or may be functionally related to the novelty in other parts of the body.

Exploitation

The conversion of an evolutionary novelty to an innovation depends upon a suite of environmental, ecological and evolutionary conditions that may be wholly distinct from those factors associated with the formation of the novelty. When the conditions for ecological success occur much later, there may be a long lag between the novelty associated with the initial establishment of a clade and its ecological impact. Such exploitation may occur as the result of new opportunities arising, such as after an extinction event or geographic dispersal, through a change in the environment, or via the ecosystem-modifying effects of the novelty itself.

refinement distinguishes the ecological events associated with the success of novelties. Of particular interest is the involvement of niche construction and ecosystem engineering in this stage [43,46,72].

Evolutionary Novelty

Definitions of evolutionary novelty range from the highly inclusive, recognizing almost any new feature of an organism as a novelty, to the highly restrictive. These definitions have evolved as our understanding of the underlying developmental mechanisms has grown and as evolutionary theory has become more sophisticated. The increasingly restrictive definitions of evolutionary novelty over the past two decades largely reflect an effort to define the phenomenon as a prelude to more rigorous exploration of the responsible mechanisms.

Novelty was initially defined as a new structure that allows a new function [73]. Most studies emphasized ecological opportunity and assumed that novelty arises either with a key innovation at the outset of the radiation or as the cumulative effect of adaptive divergence. Thus, the expectation of morphological novelty differs depending on the specific drivers of an individual adaptive radiation [74–80]. Subsequent discussion of novelty defined it as “a qualitatively new structure with a discontinuous origin” [81], or focused on structures that are neither homologous to any ancestral structure nor serially homologous to any other structure in the same organism [82,83]. An alternative definition of novelty focuses on mechanism rather than characters, with

innovations arising from transitions between adaptive peaks and the overcoming of developmental constraints [84,85]. The critical issue in these discussions is novelty and the origin of homologous characters [86–88]. This focus on the origin of homologous characters led to the most restrictive definition: “the origin of a morphological novelty is the evolutionary process through which a novel character identity arises. In other words, an evolutionary novelty originates when part of the body acquires individuality and quasi-independence” (p. 125) [89]. Feathers are just such a novelty. Although this is a very restrictive definition of novelty, it is particularly useful because of the focus on the individuation of new characters. This is the definition that I will adopt here.

This restrictive definition of novelty links the appearance of novel characters to the structure of developmental gene regulatory networks. Specifically, it proposes that small networks of transcription factors within larger gene regulatory networks are responsible for these novel characters. Such recursively wired subnetworks of developmentally significant genes have been identified for characters ranging from feathers to heart formation. They have been described as character homology identity networks, or CHiNs [89] and kernels (Figure 3) [90,91]. CHiNs were first identified in the formation of patterns associated with new cell types, while kernels are associated with regional patterning mechanisms in developing embryos. Each concept reflects the significance of structured, hierarchical developmental gene regulatory networks in underpinning novel

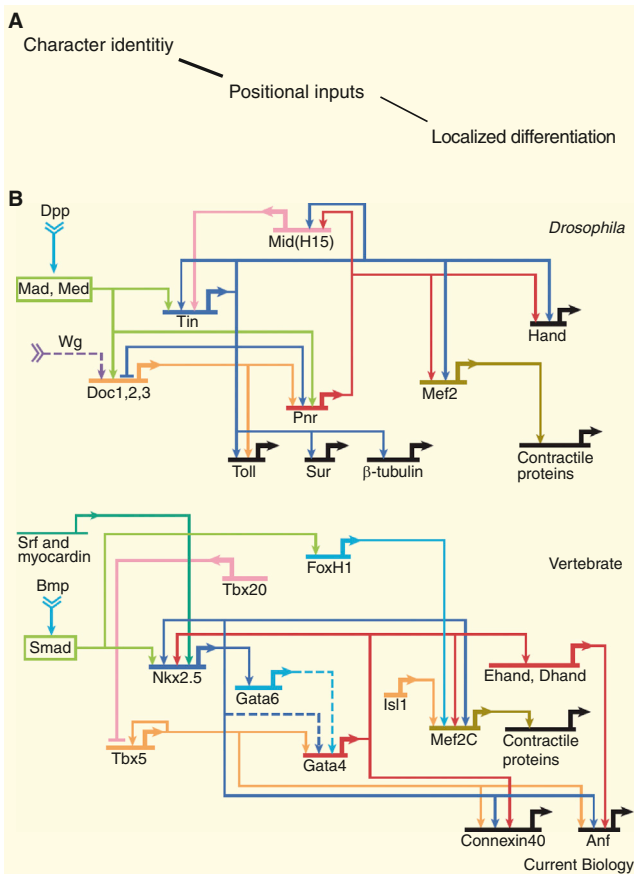


Figure 3. The hierarchical structuring of developmental gene regulatory networks.

(A) Recent comparative studies suggest that highly conserved cores of such networks define character identity, whether via regional patterning or cell type specification. Positional information then defines the embryonic locality of the character, and then at the periphery of the network localized differentiation occurs. The evolutionary lability and rates of change of these different components follow the same hierarchy, with character identity networks or kernels having the least evolutionary lability and the slowest rates of change. (B) A comparison of the gene regulatory networks involved in heart formation between *Drosophila* and vertebrates. Homologous proteins are shown in the same color. Note the preservation of the recursively wired feedback patterns. Redrawn from [82].

morphological structures. During development, character identity involves these recursively wired regulatory subnets. Positional information determines where the characters form, while the downstream components of the network are responsible for localized cell differentiation [68,92]. The focus on novel individuated structures is particularly helpful as these can, in principle, be recognized in the fossil record. Novel individuated structures also feature in major evolutionary transitions [93], critical events in the history of life including the origin of eukaryotes, multicellularity and social systems.

Although the concept of the adaptive radiation has been applied broadly through the fossil record, few adaptive radiations have generated morphological novelties. Key innovations are not necessarily morphological novelties. Mantle fusion in venerid, tellinid and mactrid bivalves was a significant and generative change in the state of a character, for example, but

was not associated with the origin of the mantle in molluscs. The sudden appearance of numerous bilaterian lineages in the fossil record at the base of the Cambrian is a paradigmatic example of a novelty event: the appearance of morphological novelties (individuation of new characters) and thus an increase in morphological disparity, but these novelties generally were unaccompanied by increases in taxonomic diversity or ecological abundance [27]. Hence the conundrum: comparative developmental data are beginning to reveal the mechanistic foundations of morphological novelties, but this tells us little about the ecological and evolutionary processes responsible for their ecological and evolutionary success. By divorcing novelty from innovation, we can explore the mechanistic basis of each process.

A developmental system that can adjust to changing environmental conditions may be one of the potentiating preconditions for some morphological novelties [94,95]. Behavioral adjustments to a new environment are often a component of such developmental plasticity and subsequent evolutionary change [96,97] and may also serve as potentiating events. There are a number of cases in the fossil record where independent evidence indicates that behavior changed before morphological adaptation, including several cases associated with morphological novelty [97]. The diet of proboscideans (elephants and their relatives) provides one example. The amount of grass consumed increased several million years before the acquisition of high-crowned teeth resistant to the abrasion of grasses [97]. Experimental studies of living species provide similar support. For example, the modern basal bony fish *Polypterus*, when raised in a terrestrial environment, exhibits induced phenotypic changes similar to those in stem tetrapods [98].

Many studies of adaptive radiation focus on changes in body size, including the origin of birds and the frequent reductions in body size found in mammals that move to islands. This poses two challenges: as novelty is defined by the acquisition of new individuated characters, changes in size alone do constitute a novelty by this definition. The importance of changes in body size for adaptive diversification is unclear as many other factors can drive size changes [38,99]. A recent analysis of body size evolution in canids since the Eocene rigorously tested the role of size in the allowing access to new evolutionary opportunities [22]. Thus, while changes in body size do not represent morphological novelty they can provide new ecological opportunities and thus drive evolutionary innovation. This example emphasizes that evolutionary innovation does not require morphological novelty, but may arise through other evolutionary processes.

Some of the complexities of applying these concepts are illustrated by considering the early evolution of birds during the Mesozoic, before the radiation of Neoaves (see review by Brusatte *et al.* in this issue). Recent studies of the developmental origin of feathers, remarkable discoveries of the appearance of wings among theropod dinosaurs and the early record of birds [100], and the dynamics of their diversification based on molecular data [32] have made birds an excellent case study of evolutionary novelty and innovation. Fossil discoveries from China have documented the morphological transition from theropod dinosaurs to early birds, preserving changes in feathers from simple filaments to complex flight feathers as well as patterns of skeletal evolution. Transitional forms have often been

preserved, documenting a 50 million year, largely stepwise trend of miniaturization along the theropod lineage leading to birds, culminating in 15 million years of particularly rapid changes in body size [101]. An important developmental novelty leading to feathers was the co-option of *sonic hedgehog* (Shh) and *Bone morphogenetic protein 2* (BMP-2), utilized in archosaur scales, to form an integrated module [102]. Critically, there are many structures in feathers that are not found in scales, including the barb and rachis [89]. These changes coincided with structural changes in the wing, formation of a lighter skeleton, a paedomorphic head with a large brain and enlarged eyes, toothlessness and complex feather types [103]. Not only did the transition to birds involve more rapid morphological changes than has been found among allied clades, there was a burst of morphological diversification among early birds [104]. Somewhat surprisingly, however, an analysis of the disparity among these taxa revealed little difference between birds and their coelurosaurian relatives [104]. Absent their fossil record birds appear to be a remarkable innovation, but with the fossil record they are the endpoint of a piecemeal and continuous record of morphological evolution among theropod dinosaurs.

Innovation and Morphological Disparity

Over the past decades, there has been considerable controversy over studies from the fossil record documenting bursts of taxonomic diversification early in the history of a new clade. Under classic models of adaptive radiation, as described earlier, however, the rate of phylogenetic diversification and the rate of morphological evolution should be most rapid early in the history of a clade, eventually slowing due to increased competition for resources or the filling of niches if the potential niches for a clade is limited, which has been described as an “early-burst” model [37,105–108]. But if, as I have argued, successful novelties may arise without accompanying diversification and there may be lags between the origin of a novelty and its successful exploitation as an innovation, one would not expect early bursts of new taxa. Moreover, ecological success may appear, at least initially, as increased abundance rather than taxonomic diversification and testing for this requires a very different type of data than used in phylogenetic comparisons.

If taxonomic diversity and disparity were linked, then diversification of taxa would be a useful proxy for disparity. Since the early 1990s, paleontologists have developed a variety of techniques for quantitatively evaluating patterns of disparity. Numerous studies of individual groups have shown that diversity and disparity are often decoupled, particularly early in the history of a clade. This pattern has been found not only for major clades [28,109–111], but also within carnivores [31], salamanders [112], trilobites [113] and anomodont therapsids [114]. A recent analysis of disparity in 98 metazoan clades through the Phanerozoic found a preponderance of clades with maximal disparity early in their history [29]. Thus, whether or not taxonomic diversification slows down most studies of disparity reveal a pattern in which the early evolution of a clade defines the morphological boundaries of a group which are then filled in by subsequent diversification. This pattern is inconsistent with that expected of a classic adaptive radiation in which diversity and disparity should be coupled, at least during the early phase of the radiation.

Conclusions and Outlook

In this review, I have argued that data from the fossil record, comparative phylogenetics and comparative developmental evolution require evolutionary biologists to broaden the traditional reliance upon models of adaptive radiation to recognize three distinct classes of diversification: first, adaptive radiations, *sensu stricto*, the diversification of a single clade in response to an ecological opportunity. Many of these events will be limited in taxonomic and morphological breadth by the extent of the evolutionary opportunity available. Second, constructive diversifications, whether involving a single or multiple clades, involving the generation of new opportunities often from ecological feedbacks that expand the evolutionary opportunity during the course of the diversification. The final class is morphological novelties as new individuated characters, a definition that encompasses a variety of phenomena including some of the major evolutionary transitions. However, I recognize that this very restrictive definition of novelty will likely need to be broadened. Macroevolutionary lags between the formation of morphological novelties and the ecological and evolutionary diversification of some clades indicates that novelties can arise through developmental evolution independent of ecological and evolutionary opportunity, which may arise long after the novelty.

Does evolutionary biology need a new research program in evolutionary novelty distinct from the existing work on adaptation and speciation [89]? Some evolutionary biologists view morphological novelty as built upon the variation existing within a species. Others, particularly many evolutionary developmental biologists, view novelty as based on evolutionary changes distinct from standing variation. Considerable experimental work will be required to test the hypothesis that evolutionary novelties are underpinned by the origin of particular gene regulatory network structures [89–91,115]. I suspect that novel individuated morphological structures will be identified that are not associated with such gene network structures, which will draw attention to the developmental mechanisms that ensure their evolutionary stability. Turning from novelty to innovation, there is great opportunity for carefully documenting the environmental and ecological circumstances under which innovations arise, how closely they are linked to morphological novelty, and whether there are particular conditions that foster increased innovation. In contrast, studies of major evolutionary transitions, and the identification of kernels and CHiNs, suggest that the nature of potential morphological novelty, and possibly innovation, has changed over time. More rigorously documenting variability in the generation of morphological novelty through time would be an important, non-uniformitarian challenge to traditional views.

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