The shape of life: how much is written in stone?

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Summary

Considering the enormous diversity of living organisms, representing mostly untapped resources for studying ecological, ontogenetic and phylogenetic patterns and processes, why should evolutionary biologists concern themselves with the remains of animals and plants that died out tens or even hundreds of millions of years ago? The reason is that important new insights into some of the most vexing evolutionary questions are being revealed at the interfaces of palaeontology, developmental biology and molecular biology. Attempts to synthesise information from these disciplines, however, often encounter their greatest hurdles in considerations of the radiation of the Metazoa. Ongoing challenges relate to the origins of body plans, the relationships of the metazoan phyla and the timing of major evolutionary radiations. Palaeontology not only has its own unique contributions to the study of evolutionary processes, but provides a lynchpin for many of the emerging techniques. ***BioEssays*** **22:1142–1152, 2000.**

Introduction

There is a huge battery of methods to study extant organisms including: (1) detailed morphological studies, (2) physiological and biochemical experiments, (3) behavioural observations, and (4) studies of heritable changes within populations. All these can, in principle, be related back to the interaction of the organism with the environment, and understood in the context of behavioural and evolutionary ecology. Information is available at tremendously high temporal resolution (the "ecological" time scale), and armed with it, we can tease apart the mechanisms by which the genome, phenotype and environment interact in the processes underlying natural selection. But Life has a history spanning something in the region of 3.5 billion years, with Metazoa originating at least 530 million years ago.[1] The extant biota is just one time slice of this history. However great our understanding of the phylogeny, genetics and biomechanics of living animals, we could never have predicted the earlier existence of dinosaurs from looking at birds and reptiles, or that of giant 5m long sea "scorpions" (eurypterids) from studying living scorpions, spiders and mites. Although fossils provide us with less-detailed morphological and palaeobiogeographical information, and at much lower temporal resolution (occasionally, fossils can be dated to within a few tens of thousands of years), they record evolutionary change over tens or hundreds of millions of years, rather than human lifetimes. Palaeontology serves to remind us of the enormous difficulties in attempting to extrapolate from the ecological scale to the overarching geological timescale.[2,3] It reinforces how seldom Life follows the most obvious or parsimonious route, and demonstrates that evolution shows little respect for the original function that a structure or organ system fulfilled.

In his book *Wonderful Life*,[4] Stephen Jay Gould raised a challenging prospect. What if our traditional picture of the evolution of complexity, a cone placed on its tip, is not merely an oversimplification but is closer to the inverse of the reality? (Fig. 1). The hub of his argument was that fossils from the Cambrian represent a range of anatomical design or "disparity" far exceeding that observed at any time thereafter. Can our picture of the overall "shape of Life"[5] really be dictated by fossil discoveries at a handful of localities from a single period? In fact, many of the discrepancies concerning the relationship of palaeontology with the rest of biology are at their most extreme in our understanding of the events of the Cambrian.[6] No subsequent radiation remotely approaches its apparent magnitude,[7,8] or matches its potential impact on our broadest understanding of macroevolution through (and even before) the Phanerozoic. The way in which we interpret the various strands of evidence can result in radically different "icons" for the history of Life (Fig. 1). In this article, we will discuss this evidence to illustrate palaeontology's unique ability to reveal major events in evolutionary history and its role in helping to provide answers to some of the questions that these events raise.

Fossils and phylogeny

Any attempt to appreciate the diversity of living things requires a solid understanding of their phylogeny. Studies of morphology, embryology and molecules have at various times claimed superiority of their methods in the effort to resolve the relationships of major groups. However, the last ten years have seen wider recognition of the need for a synthesis of all the data.

The difficulties of recognising and coding morphological homologies have long bedevilled phylogenetics. Fifteen years

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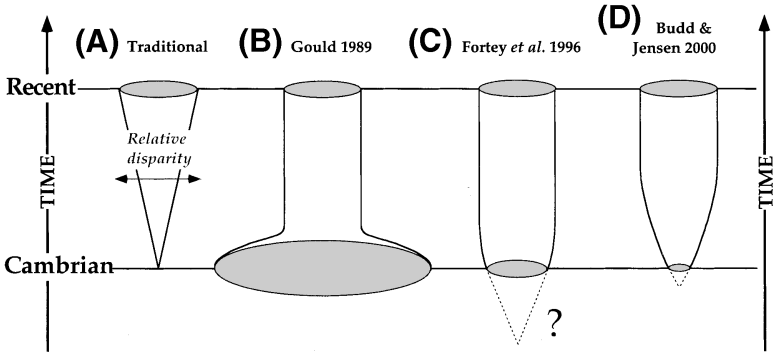

Figure 1. Cartoons depicting four models of the evolution of morphological diversity among the Metazoa through time. **A:** Traditional model. Metazoa originate very simply, and become more complex through the course of the Phanerozoic. **B:** Gould 1989. Many Cambrian fossils have characters or combinations of characters not seen in extant phyla. These problematic fossils are considered to be as morphologically distinct from each other, and the modern phyla, as the modern phyla differ from each other. Disparity in the Cambrian was far greater than at any time since. A period of bodyplan decimation at the end of the Cambrian reduced disparity to levels near those of the Recent. **C:** Fortey et al. 1996. Multivariate morphometric approaches estimate Cambrian and Recent disparity to be similar. Evidence from phylogeny, palaeobiogeography, trace fossils and molecular clocks imply an extensive period of Precambrian cladogenesis prior to the appearance of the first body fossils. **D:** Budd and Jensen 2000. Few Cambrian fossils can be accommodated within phyla defined strictly with reference to the Recent fauna (crown groups). Most Cambrian stem lineage forms lacked some of the defining features of modern phyla, which suggests the former were considerably less disparate than the latter. Cladogenesis producing the stem lineages of modern phyla probably occurred in the latest Proterozoic, but no earlier.

ago, the rapid advances in techniques for DNA sequencing across a wide range of species appeared to offer an assumption-free solution to the problem, and a virtually limitless reservoir of characters. Early molecular phylogenies, however, often had irreconcilable differences with the results from decades or even centuries of morphological and palaeontological study. It is now appreciated that there are problems identifying genes and gene products that evolve fast enough to capture the rapid branching that appears to occur during periods of major radiations, but slow enough to preserve this phylogenetic signal over tens or hundreds of millions of years. A number of methodological variations also concern the alignment of data and the most suitable model for their analysis. Most importantly, perhaps, there is a growing understanding that appropriate sampling of taxa from different groups is vital for accurate phylogenetic reconstruction by cladistic methods.[9] Several recent studies have highlighted the benefits of analysing molecular data in conjunction with data from morphology and fossils.[10]

The relative roles played in determining phenotype of changes in the coding sequences of genes (i.e., the protein that they code for) versus changes in the regulatory mechanisms that influence the location, timing or extent of gene expression are still not well understood.[11] The apparent extent of average molecular divergence does not equate directly to the magnitude of morphological change, nor can it indicate the adaptive significance of particular anatomical changes to the organism. Furthermore major radiations of groups in the fossil record often occur over relatively short geological intervals. They are recognised by the diversity of new morphologies produced, while the molecular bases for these can only be inferred. If morphological change is great and average molecular change is slight, it may be easier to reconstruct phylogeny from morphology than molecules alone. Once sister lineages have split, the same random independent molecular changes that make molecular clock calibrations of divergence dates possible in the first place begin to overwrite and obscure the molecular phylogenetic signal.[12] Morphology, in contrast, can remain remarkably constant over similar periods. Modern horseshoe crabs and coelacanths illustrate this to the extreme. Moreover, "slow" morphologies can have "fast" clock times, and vice versa. The addition of data from fossils may, however, allow the immediate morphological consequences of a radiation to be more fully explained. Fossils often represent lineages that have subsequently become extinct, but provide unfamiliar combinations of characters vital for teasing apart rapid, basal branching sequences.[13] Despite their value, fossil evidence is still often judged inferior to molecular evidence. For instance, while the myriad snapshots of past morphology (fossils) are often dismissed as unimportant,[14] the much rarer preservation of phylogenetic information in fossil biomolecules generates enormous interest.[15] The latter presently, however, have much more restricted application for increasing phylogenetic resolution, or generating new topologies, but may revitalise morphological hypotheses of relationships that had fallen out of fashion, or been otherwise discounted.

In order to reconstruct accurately any signal (in this case the correct sequence of cladistic branching), it is necessary to sample at an appropriate rate (to code a large enough and wide enough range of taxa). Recent groups can be widely separated from their nearest living relatives by large, otherwise extinct branches of the phylogenetic tree. Without the information from fossils, these orphaned groups can be difficult to place phylogenetically. For example, most cladograms incorporating fossil data concur that the nearest

relatives of the modern chelicerates are numerous fossil arachnomorph taxa, including the trilobites.[16] In contrast, in analyses that omit fossils, the chelicerates are variously resolved throughout the arthropod tree. This "mobility" may well reflect the phylogenetic isolation of chelicerates in the modern fauna. Moreover, cladistic analyses that include arthropod fossils often resolve the Arachnomorpha (Chelicerata, Trilobita and numerous Cambrian fossils) as the sister group of the Crustacea.[17,18] Those that omit them (whether derived from morphological data, molecular data, or both) typically resolve the Arachnomorpha (Chelicerata) in opposition to the mandibulates (Crustacea and Atelocerata).[19,20] In general, the deeper and more ancient a cladogenetic sequence, the less chance there is of resolving it robustly using only data from extant forms.

Molecular phylogenies often sample even the extant fauna very sparsely and irregularly. Many early analyses included only a limited number of classical study organisms, with little consideration of their suitability (as representative of their group) for resolving phylogeny. Undersampling of taxa is likely to yield anomalous results, as the "noise" associated with variable rates and long-branch attraction swamps the phylogenetic signal. For example, some nematodes (including the model *Caenorhabditis elegans*) are known to have substitution rates that are up to three times greater than those of other animal groups.[21] This will tend to increase their apparent estimated ages and may alone account for their basal positioning in sparser trees for the Metazoa.[22,23] Even if taxa are pruned from the presumed correct phylogeny, serious problems occur when re-optimisations of morphological characters over the pruned tree are used to deduce ancestral morphologies or bodyplans. Reconstructions of the common ancestor of protostomes and deuterostomes as segmented[24,25] may reflect this practice.[1] More generally, homoplasies (convergent traits), synapomorphies (shared traits) and autapomorphies (unique traits) cannot be correctly assigned.[26] For these reasons, and others, many workers have pressed for the analysis of "complete" phylogeny, coding all the species within a clade of interest. Clearly this is not possible for all but the smallest groups, but it emphasises the need to ensure adequate sampling at all levels.

Fossils, clocks and fuses

Reconciling molecular clock estimates of divergence times with those from fossil evidence remains a major challenge. Molecular clock estimates for the divergence times of many major sister clades are often much older than their more visible radiations in the fossil record (the "phylogenetic fuse").[27] There is room for confusion between the first fossil representative of a clade (possibly lacking some or even many characters shared by later members of the group) and the visible radiation of a group as fossils (this may happen long after the first fossils are recorded). Moreover, the estimated timing of the divergence of a clade from its sister clade (typically deduced from molecular and palaeontological data), the timing of the cladogenesis that effected the radiation (this may predate both the first fossil and the radiation of fossils) and the order of cladogenesis (on which subject molecular clocks are silent) are all logically distinct.

Molecular divergence time estimates require some knowledge of phylogeny and reliable fossil dates for the first occurrences of some component groups. The quartet method[28] uses well-supported pairs of sister-group terminals (four taxa in total) for which the dates of first fossil occurrences are well established. Fossils therefore provide dates for two of the three internal nodes of the cladogram. These are likely to be minimum estimates because the oldest fossils for a particular pair of terminals may not have been discovered or recognised as belonging to the groups in question. The incorrect assignment of older fossils is possible, but the dates of origin of most taxa have historically been refined downwards rather than up. Rates of random substitution (the speed of the clock) for any number of molecules can be calculated for each pair of terminals, and these rates can then be used to extrapolate a range of dates for the basal node. Several quartets of taxa can usually provide a suite of estimates for any given basal divergence time. Estimates markedly older than the first fossils can encourage a redoubling of palaeontological effort with a specific goal in mind. For example, certain molecular data suggest Early Cretaceous radiations of modern bird and mammal orders (twice the age of the earliest fossils); however hundreds of years of intensive collection have failed to identify such fossils.[29,30]

The first body fossils of almost all multicellular animal phyla with mineralized skeletons appear in a geologically short period in the Cambrian from 530 to 520 million years ago.[8] Rocks dated between 565 and 530 Ma and perhaps later record fairly large, soft-bodied animals (the so-called Ediacaran fauna), many of which have an organisation superficially similar to cnidarians. The relationships between Ediacaran organisms and the rest of the Metazoa remain contentious, however.[6] Some workers regard them as an early offshoot from the metazoan tree: an experiment in multicellularity with no successors. Others regard them as Cnidaria and relatives of that group, while controversial proposals for close affinity between particular Ediacaran genera and other metazoan phyla have also been made.[31] Darwin was convinced that there must be a stratigraphic hiatus between the Precambrian and Cambrian (increasingly accurate dating of volcanic ash beds either side of the boundary has laid this idea to rest, Ref. 32) or that Precambrian metazoans were present but somehow not fossilised.

Even the most conservative molecular clock estimates for the timing of the basal split of metazoans predate the classical Cambrian radiation. Recent work on 18 protein-coding genes removed all data that failed to preserve regular clock-like

behaviour.[33] This analysis dated the protostome–deuterostome split to 670 Ma, and the echinoderm–chordate split to 600 Ma. Work on the clock-like genes for adolase and triose phosphate isomerase[34] placed the split between sponges and the rest of the Metazoa at 900 Ma, with the cephalochordate–vertebrate split near 700 Ma. Earlier estimates from six protein-coding genes and 18S rRNA[35] yielded a considerably older protostome–deuterostome split of 1.2 Ba, while the echinoderm–chordate divergence was dated to 1.0 Ba. The oldest dates of all place the protostome–deuterostome split at 1.5 Ba.[36] Disagreement over methodology and the most appropriate sources of data therefore leaves a huge margin of error (c. 800 My), but all agree on Precambrian origins for these major meatozoan divergences.

Several workers have highlighted the possibility of elevated rates of molecular change during times of rapid radiation.[28,36,37] If rate estimates are derived from divergences between lineages evolving at ''normal'' rates, this will tend to push the apparent dates of explosive divergences engendering accelerated rates too far back in time. Unfortunately, tests for rate variation[38] can only detect differences between sites, and differences between parallel lineages. Since there is no absolute benchmark, such tests are insensitive to overall changes in rates that affect all parallel lineages in concert. In acknowledging these limitations, recent work has investigated what rates would be necessary in early Metazoa to account for the discrepancy between fossil and molecular dates, rather than attempting to pinpoint the divergence.[37] Molecular data can only be made compatible with, at very latest, a Vendian (late Precambrian) divergence of the Metazoa by assuming rates universally higher than those observed throughout the Phanerozoic, and applying these to all of the fifty or more mitochondrial and nuclear genes so far considered. It is difficult to see why all nucleotide positions should a priori be affected by rate elevation, nor has any possible mechanism for this, with empirical support, thus far been identified.

A link between small organismal size (implying shorter generation times and faster metabolism) and the possibility of elevated rates of molecular change has also been proposed.[39] While this might have some bearing on the radiations of mammals or birds,[27,29,40] empirical evidence for this relationship among invertebrates is lacking, and the branches supporting minute or infaunal invertebrate groups are not consistently longer than their nearest macroscopic relatives.[37] A role for elevated levels of atmospheric oxygen in accelerating rates of substitution during the Cambrian has also been suggested.[39]

Ultimately, clock estimates all rely on dates from fossils for calibration. The divergence between mammals (synapsids) and birds (diapsids) at 350 Ma is often the only direct calibration date available. Other dates are often inferred partially or wholly from this one.[44] More rigorous clock estimates will inevitably require additional and more accurate fossil calibration dates. Stem groups (see below) often have long durations, making rigorous phylogenetic analyses of fossils and living taxa vitally important. Calibration groups with good records should be selected; particular caution must be exercised in accepting fossil dates based on fragmentary material, particularly where these ages are substantially older than the more-reliably assigned fossils.

Fossil stems and crowns

Palaeobiologists often distinguish ''crown groups'' from ''stem lineages''.[41] Crown groups equate to the last common ancestor of all the living forms in a group, plus all its descendents. Stem lineages, in contrast, include the fossils that preserve transitional morphologies on the way to the crown. Examples in the literature include crustaceans[42], cheliceriformes, arthropods,[43] birds, mammals[44] and tetrapods.[45] Taxa along the stem often present unfamiliar combinations of characters, but may sometimes be vital for reconstructing phylogeny. Stem group taxa enhance an understanding of the events preceding the radiation of the crown group.

The distinction between crowns and stems may help to clarify the phylogenetic basis of the taxonomy of modern organisms, but the imposition of modern taxonomic constructs on the past is entirely arbitrary. It has been argued that, because many Cambrian fossils fail to fit strict crown-group definitions of Phyla based on the extant fauna (Fig. 2), many phyla sensu stricto must have originated long after the Cambrian (rather than before it).[41] This suggests that metazoan origins extended far into the Phanerozoic, and there is no need to explain either exceptional speed (the classical, initial ''explosion'' is much smaller than previously supposed and its consequences much more protracted) or the non-preservation of fossils long into the Proterozoic. Not surprisingly, the crown groups of phyla on this definition have stems that record the acquisition of some important characters. Even the most basal Cambrian stem-group fossils, however, have a suite of characters sufficient to mark them out as close relatives of modern annelids, onychophorans, arthropods, priapulids, molluscs, brachiopods and the majority of the other living phyla.[46] This is not an inevitable consequence of early cladistic branching topology. The whole history of the Cambrian might only have recorded variously derived flatworms or some other group, with all the characters of other phyla appearing staggered through the Phanerozoic. Other workers have proposed the gradual emergence of many of these characters through tens or hundreds of millions of years of the Proterozoic, but leaving no appreciable fossil record.[47] Certainly there are few fossils that are claimed to link existing phyla,[48] and still fewer that suggest divergence of animal phyla far into the Phanerozoic. In the context of the Cambrian explosion, it is necessary to explain the sudden appearance of forms exemplifying so many of the defining

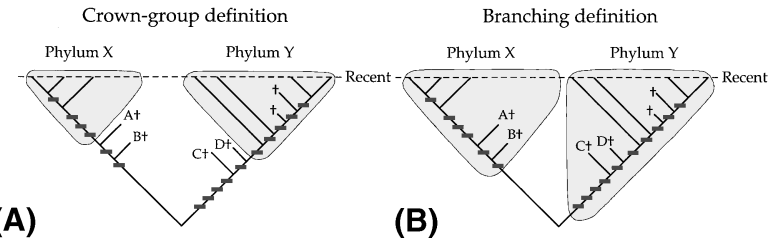

Figure 2. Two possible definitions of Phyla. † = extinct, fossil taxon, ▬ = synapomorphy. **A:** The crown-group definition of Budd and Jensen 2000 includes the last common ancestor of all extant forms, plus all its descendents. Some of these descendents may themselves be fossils. Crown-group definitions are entirely arbitrary, but are easy to implement and utilise "text-book" descriptions of phyla. Fossil taxa A and B lack several of the synapomorphies defining the crown group, and their relationship with the extant members of Phylum X may be difficult to determine. Fossil taxa C and D share many characters with the crown group of Phylum Y, and lack few of its synapomorphies, hence their affinities should be more obvious. **B:** The branching definition of phyla includes stem group representatives. It has the advantage of reflecting basal evolutionary branching, but often requires a more critical appraisal of the affinities of fossils. Neither definition is entirely satisfactory. The distinction between them is merely taxonomic, and should not be allowed to detract from the much more important biological issues of morphological differentiation and the significance of character complexes.

features of modern phyla (and in several cases, classes[27]), and so often which can be readily assigned to the stem lineage of one modern phylum rather than another. If the stem lineages of modern phyla are represented by body fossils extending to the base of the Cambrian but not beyond it, there is still an explosion in the record to explain. At the other extreme, problematic fossils may appear more morphologically eccentric than they actually are, merely because definitions of higher taxa based on the familiar crown groups exclude them. This highlights the need for rigorous cladistic analysis in palaeobiology, avoiding the "false security" offered by "text book" taxonomy that overlooks fossil data.[18]

Additional evidence for the Precambrian cladogenesis of metazoans comes from palaeobiogeography, the distribution of ghost ranges (stratigraphic gaps between sister taxa, Ref. 49) through the Phanerozoic, and phylogeny[47]. If stem-group representatives of the major Phyla were present some way back into the Precambrian, why are no body fossils preserved? Explanations have been offered in terms of extremely low preservation potential, small numbers of individuals,[50] or the small size of individuals.[47] This last, "sub-millimetric" hypothesis of animal origins argues that lineages could evolve many or most of the defining features of modern phyla without skeletons and without exceeding meiofaunal or planktonic proportions.[47,51] Some workers[41] strongly object to this, maintaining that there is no coherent explanation for the evolution of complex excretory, circulatory, muscular or support systems at such sizes, while their retention in secondarily miniaturised forms is thought more probable. However, the extent to which such systems may have evolved preadaptively in minute animals is difficult to assess. Some objections to the submillimetric hypothesis appear to centre on implausibility of deriving the complete and integrated complex of all the features of the living phyla without achieving a "moderate" size. This may be true, but assumes that crown-group definitions of phyla are the only statements with any significance, and overlooks the enormous morphological differentiation possible in small forms. Several phyla and larger clades (e.g., Arthropoda, Mollusca, deuterostomes and lophophorates) have living, minute, basal representatives or sister groups, and a number of other phyla (e.g., Gastrotricha, Gnathostomulida, Rotifera) are exclusively minute with no evidence that their diminutive stature is secondary. Perhaps a more significant objection to the submillimetric model is the requirement for parallel and simultaneous evolution of large size and/or hard parts in numerous independent lineages, which also implies the existence of some environmental trigger. Sedimentary environments in the later Precambrian capable of preserving non-skeletonised infaunal organisms with sufficient resolution (e.g., black shales, cherts and phosphorites) have so far yielded only algae, with the evidence for simple animals being equivocal. [52] This is not surprising, given that several modern small-sized phyla — including meiofaunal ones — have little or no fossil record.

Models of extensive Precambrian cladogenesis have not received universal acceptance, and some workers prefer to read the record more literally. An explosion within the window allowed by the body-fossil evidence also requires a plausible trigger. Proposals include the evolution of hard parts (enabling the production of skeletons), the evolution of collagen, the development of eyes[53] (spawning an arms race between predators and prey, and tightening the ecological web), some critical level of atmospheric O_2 or CO_2,[54] a sustained period of phosphogenesis, the upwelling of nutrients from the deep ocean, or a rise in temperature (the "snowball Earth" model). None of these possibilities, however, provides an entirely satisfactory explanation.[52] Rather than seeking recourse to a single environmental trigger, the correlated progression model suggests that a succession of changes in the environment were necessary (but not in themselves sufficient) to permit the acquisition and exploitation of a series of bodyplan innovations.[55]

Fossils, morphological plasticity and canalisation

A major set of issues concern the concept of the "body plan" and the factors that affected evolution of the major metazoan groups. Several arguments concerning the fixation of elements of bodyplan design have focused on the arthropods.[4] Their systematics, in particular, illustrates some potential pitfalls of viewing history solely in terms of what is known of the extant biota. The three Recent arthropod classes and the trilobites are conveniently defined on the basis of the number of post-acronal somites and limbs incorporated into the cephalon. For example, crustaceans primitively possess five pairs (antennules, antennae, mandibles and two pairs of maxillae for handling food), while chelicerates primitively have six pairs (chelicerae, pedipalps and four pairs of walking legs). Because head patterning defines recent groups so straightforwardly, some workers have argued that the structure of the cephalon is pivotal for body-plan design in arthropods. Certain aspects of the body plan are thought to have become canalised or entrenched (see Rutherford, this issue). These are features upon which many others essential to the functioning of the organism are subsequently built. This "developmental burden"[56] would make changes in patterning features very difficult, as any change would entail numerous cascading consequences for the rest of development.

Why have no fundamentally new head segmentation patterns arisen since the Cambrian? The fossil record offers some interesting insights. As many as thirty Cambrian arthropod genera have totally unfamiliar numbers, combinations and types of head appendage, which exclude them from the four great classes. On the one hand, if primacy is ascribed to head segmentation then these groups are as anatomically distinct from each other and the modern classes as the modern classes are distinct from each other.[4] This implies vastly greater "disparity" of anatomical design in the Cambrian than at any time since, and has implications for the magnitude of the Cambrian explosion (Fig. 1). On the other hand, cladograms based on morphological characters coding both fossil and recent arthropods demonstrate that head segmentation is among the most labile of all characters.[17,18,57] In general, the major clades that emerge are defined by characters other than those of the cephalon.

Another vital difference between Cambrian and recent arthropods is evident in the specialisation of their appendages.[58] Recent genera have far more appendage morphologies, on average, than their Cambrian counterparts (7.5 and 4.1 respectively).[59] Moreover, appendages in Cambrian arthropods are far less likely to be differentiated from those anterior or posterior to them, than appendages in recent forms. The mean diversity of appendage morphologies is therefore significantly lower in Cambrian forms compared with extant arthropods (h=0.92 and 1.55, respectively). Head and trunk limbs in Cambrian genera often show only the smallest morphological differences: the only evidence of tagmosis (regional differentiation) is often the division of the dorsal cuticle and carapace. For example, *Emeraldella*[60] had antennae, followed by five pairs of gnathobasic limbs under the head shield. The anterior two pairs were probably too short to reach the ground, but the next three pairs were ambulatory and similar to the walking legs of the trunk. Virtually no differentiation between the post-antennal (or equivalent) cephalic appendages and the anterior limbs of the trunk is visible in the arachnomorph fossils *Alalcomenaeus*, *Habelia*, *Leanchoilia* and *Sarotrocercus*.[61] The arachnomorph *Sidneyia* was originally interpreted as having just a single pair of antennae within the cephalon.[62] A more recent treatment,[63] however, suggests that a point of differentiation between the fourth and fifth "thoracic" limbs might mark the head–trunk border. If this is correct, then the differentiation of a head does not even require the fusion of tergites.

Canalisation probably conserves the head segmentation of modern arthropods because they have such well-differentiated and integrated functional complexes of appendages. Many lower-level developmental systems influencing appendage morphology and other aspects of the body plan would be affected disastrously by sudden changes in the cephalic limb complement.[64] If limb specialisation is a guide,[59] there appear to have been fewer subordinate developmental systems to disrupt in Cambrian arthropods. If models of the Cambrian ecosystem that posit looser ecological interactions and weaker selection pressures are even partially correct, in any case, more variability may have been tolerated than today.[65] It is interesting to note that the groups that survived beyond the end of the Cambrian were those with the highest number of differentiated appendages, therefore, one infers, more closely integrated systems, and a greater degree of canalisation. A further implication is that mechanisms mediating morphological change may well have been different in the past.

More fossil evidence for the early lability of segmentation and tagmosis patterns is provided by trilobites. These have the most extensive fossil record of any arthropod group. Primitive members typically have many homonomous appendages, while more derived taxa (and the agnostids) begin to differentiate the limbs.[66] Some trilobite species had a variable number of segments within the thorax. These were mostly basal within the clade, and the vast majority dated from the Cambrian. For example, *Paradoxides davidis* from the Middle Cambrian had between 18 and 21 thoracic segments and *Elrathia kingi* (also Middle Cambrian) from 10 to 13.[67] By the Silurian, not only were numbers of segments within species stable, but patterns tended to be conservative within families and orders.[68] This has been construed as further evidence for progressive canalisation or entrenchment of development through time. However, rigorous cladistic analyses of trilo-

bites[67] have demonstrated that at least one species (the Middle Silurian *Aulacopleura konincki*,) reverted to a variable segment number (18 to 22) from within a supposedly "fixed" clade. Within the trilobites as a whole, there is a temporal trend for a reduction in thoracic segment number, correlating with an increase in the number of pygidial segments.[66] Species with variable segment numbers tend to be those with more segments overall, less differentiation of the appendages, and minimal distinction between the segments of the thorax and pygidium. This suggests that segments can be lost or gained with greater ease when the total number of segments is large, and their subsequent morphological specialisation slight. Modern centipedes show intraspecific variation of up to 90 segments, while most British species have a latitude between 4 and 12 segments.[69] This may be mediated by the developmental duplication of blocks of segments.[70] Greater variation in a host of other characters has also been observed for the Cambrian trilobite *Dikelocephalus minnesotensis* compared with its post-Cambrian counterparts.[71]

Macroevolutionary patterns in diversity and palaeoecology

While it may be possible to estimate phylogeny, even the deepest branching between phyla, solely with reference to the living fauna, a number of macroevolutionary questions cannot be addressed without data from fossils. These include patterns of diversity turnover (periods of elevated origination and extinction, Ref. 72), the timing and sequence of assembly of characters in major evolutionary transitions and innovations, and patterns of morphological disparity. The application of quantitative methods to these issues in the last 25 years has caused a revolution in palaeontology.

Our understanding of several macroevolutionary patterns has been greatly advanced by statistical treatments of large data sets. These methods assume that a random distribution of noise (e.g., non-monophyletic groups, variations in taxonomic practice) in huge samples will allow genuine evolutionary signals to emerge. While the precise influence of various sources of taxonomic and taphonomic bias continue to be debated, the use of fossil families and genera as proxies for species has revealed many well-known patterns in metazoan history. These include episodes of elevated origination and extinction at all magnitudes (including "mass" events),[73] the successive predominance of three faunas (Cambrian, Paleozoic and Modern) through the course of the Phanerozoic, and an overall diversity/time curve of considerable and genuine complexity.[74]

How complete is the fossil record, and to what extend can it be relied upon to document the largest-scale macroevolutionary patterns? Received wisdom holds that the quality of the record must decrease as we go back in time: older fossils are more likely to have been crushed, subducted, eroded or misinterpreted than those in younger strata. Does this invalidate studies of global change through the Phanerozoic. Palaeontological data on the order in which fossil groups appear, and morphological or molecular data used for phylogenetic inference are independent.[49] Nonetheless, the ranges of taxa through the rocks (and therefore through time) and the order of cladistic branching should both reflect the same underlying pattern of history. While fossil ranges are usually incomplete, and cladograms may be inaccurate, the overall congruence of these two sources of data through time can be informative. A study of 1000 animal and plant cladograms (predominantly at the familial level and above) throughout the Phanerozoic found no significant decrease in congruence with increasing antiquity.[75] Factors such as cladogram size, cladogram balance, temporal extent and taxonomic level were controlled throughout the data set. There is also no reason to suppose that cladograms of older fossil groups are consistently easier to reconstruct than extant groups. This strongly suggests that, at certain lower levels of resolution, the global fossil record is of approximately constant quality throughout Metazoan history. Geographical, temporal and taxonomic heterogeneity mean that caution must be exercised at other scales.

The ecological picture of community evolution depicts gradual change. Again, the fossil record illustrates the dangers of extrapolating from ecological to geological timescales. Variation in palaeoecological units have been observed at all geographical scales, and at temporal scales from several millions of years (typical species lifetimes) to geological instants (probably representing biological communities of the sort studied by ecologists).[76] Several workers offer evidence that there is macroevolutionary punctuation and stasis in communities as well as species.[77] The fossil record contains assemblages that persist for in the region of 10^5 to 10^6 My, surviving multiple transgressive cycles and tracking depositional environments. Clearly, associations of species cannot be expected to evolve in the same way as genealogical entities. Regional stasis may result from the stability of local environments, or may be a function of the emergent hierarchical properties of spatiotemporally extensive species systems that are almost imperceptible on the ecological scale.[78]

Morphological disparity

We know that there are more restrictions on the evolutionary possibilities open to organisms than strict neo-Darwinism allows.[11] Natural selection operates within the realms of what is physically possible, and with respect to phylogenetic and developmental inflexibility. Some of these limitations can be modelled by logical schemes for the combination of design elements.[79] Others can be deduced from engineering principles. While fossil groups would not be expected to have pushed all the limits of design, they often demonstrate how far within the realisable limits extant organisms lie. Modern

elephants are nowhere near the size limit for land vertebrates (or even for elephants, when extinct species are included), and the discovery of a succession of increasingly massive sauropod fossils continually push the realised bounds. Carboniferous insects reached sizes far in excess of their modern counterparts. The size of recent insects is therefore unlikely to be biomechanically constrained, and is more probably a function of the interaction between physiology and levels of atmospheric oxygen.[80] Other fossil groups elegantly illustrate convergence on strikingly similar design solutions to comparable modes of life.[11]

Some of the most challenging insights into the broadest macroevolutionary patterns come from multivariate studies of the morphological variety of fossil groups through time.[81] This range in anatomy or "disparity" is usually quantified in terms of the distribution of taxa in some form of morphospace. Morphospaces are theoretical or empirical constructs defined with reference to any number of quantifiable elements of form, which together describe aspects of morphological variation within a group of interest. Similar taxa plot close together, dissimilar taxa plot far apart. The comparison of morphospaces with phylogenies can be particularly informative in suggesting limitations on realisable morphology. We might intuitively expect clades to explore morphospaces progressively (even if not gradually, Ref. 82) through time, radiating away from a single point (the common ancestor). However, studies on numerous groups (e.g., Paleozoic blastozoans, Ref. 83, Paleozoic bryozoans, Paleozoic gastropods, Ref. 84, Paleozoic and Mesozoic Crinoids, Ref. 85, Cambrian marine arthropods, Ref. 18, crustaceans, Ref. 50, and angiosperms, Ref. 86) indicate that clades often "explore" extremes of morphospaces very early in their history, or maintain high levels of disparity at low diversity. Disparity frequently reaches high levels early in the evolution of a group (Fig. 3), rather than showing a slow increase through time. Subsequent evolution frequently serves to fill in gaps and repopulate previously occupied areas (reversals): indeed, disparity often peaks much sooner than species diversity.[81]

Arthropods and priapulids are the most abundant and diverse soft-bodied Cambrian fossils, and their early evolution probably offers a model for that of the Metazoa as a whole.[4] Disparity in both clades was about the same in the Cambrian as today.[18,87] Taken together with evidence for the relationships of other problematic Cambrian fossils (increasing numbers of which are being resolved as early, albeit stem-group representatives of recent classes and phyla) the variety of anatomical design in the Cambrian appears to be similar to today, not significantly more or less. (Fig. 1).

Explanations for early, high levels of disparity have been offered in terms of the exploration of rugged fitness landscapes and the mathematical properties of morphological hypercubes.[88] In the case of the Cambrian radiation, the question of mechanism depends greatly on the period over

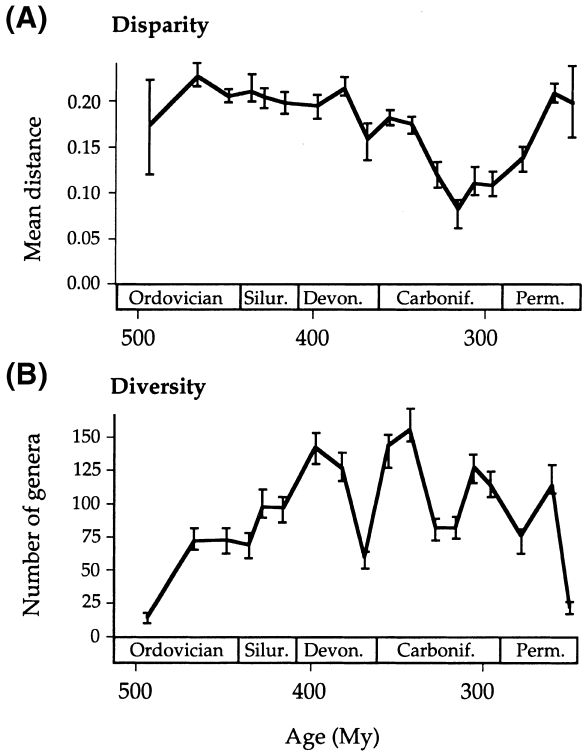

Figure 3. Patterns of crinoid disparity and diversity through the Palaeozoic. **A:** Disparity measured as the mean pairwise distance between taxa, based on discrete character data. Error bars are ± 1 s.e., based on bootstrap resampling. B: Diversity measured as the number of genera. Error bars are $\pm\sqrt{N}$, where N is the number of genera. Morphological disparity never exceeds its early levels, despite increases in diversity. Diagram redrawn from Foote, 1995.

which the radiation is believed to have taken place. A greater flexibility of early genetic systems and looser ecological interactions between individuals (the "empty barrel model") may both have increased the rate of evolution. It is unknown, however, whether this would be sufficient to generate modern levels of disparity in the interval suggested by a literal reading of the fossil record.[89]

The relationship between morphological innovation and the sedimentary environment of fossils can be particularly informative. For example, 77% of the well-skeletonised, benthic marine invertebrate orders that have originated since the beginning of the Mesozoic first appeared in high-energy, on-shore environments.[90] This is not true at the generic or species level, or for orders with a weak preservation potential, where the occurrence of fossils is more a function of preservational and sampling error. Among post-Paleozoic invertebrates and in many vertebrate and plant groups, major morphological innovations occur in disturbed habitats. Disturbed environments appear to foster the initiation or survival

of characters that subsequently define higher clades (or paraphyletic ordinal-level "grades" in some cases). The origins of groups typically assigned to higher taxonomic ranks appear to be habitat-dependent, while the origins of families and lower taxa tends to be diversity dependent. Groups may subsequently spread across the shelf, or subsequently become restricted to deeper water and more marginalized environments. This trend seems to permeate the whole of the Phanerozoic, and operate at all higher taxonomic levels.

Conclusions

Natural selection is undeniably the principal driving force behind evolution. What is less well appreciated is the importance of developmental and functional limitations, the dynamics of complex systems, and contingency. An understanding of processes operating over the observable (ecological) time scale alone is insufficient for comprehending change over geological time. Fortunately, fossils provide us with invaluable glimpses of the past. If correctly interpreted, they can offer conservative estimates of how much morphological diversity has evolved, and minimum estimates of how soon it appeared. Fossils may have an invaluable contribution to phylogeny reconstruction, and are essential for deducing past patterns of diversity, disparity and character acquisition. Attempts to reconstruct ancient biological history armed only with information from the present are destined to underestimate diversity, the richness of phylogenetic branching and the variety of form. We know that such animals as pterosaurs and tyrannosaurs are biologically possible only because we have their fossils.

An understanding of some of the remotest and most enigmatic episodes in evolution requires the synthesis of information from morphology, molecules, and the fossil record. The sudden appearance in the Cambrian of body fossils displaying many of the characters that define and differentiate modern phyla defies an entirely satisfactory explanation. The trace fossil record indicates the possibility of increasing body-plan complexity from as long ago as 1.1 billion years,[91] and certainly by 590 Ma.[8] Current molecular clock estimates for the age of the basalmost branching of the Metazoa range from latest Precambrian to 1.5 billion years ago.

Investigations of morphological variety ("disparity") and diversity through time can only be made using fossil data. Many major clades reach high or maximal levels of disparity early in their history, while diversity is still relatively low. Several multivariate studies suggest that Cambrian Metazoa were approximately as disparate as their Recent counterparts. This suggests that most principles of metazoan design had been explored by the Cambrian. Whether this disparity was generated in the time permitted by a literal reading of the body fossil record, or over a more protracted period extending far back into the Precambrian is still hotly debated. Whichever the case, the early metazoan radiation was a unique evolutionary event.

Fossils frequently demonstrate how often similar design solutions to similar modes of life are reached independently. Aspects of morphology, like the molecular systems that produce them, are constantly recycled through the course of evolution. Structures that originally served one function are conscripted to fulfil other wholly different roles. Fossils remind us that evolution is not a directed process. The evolutionary heritage of an organism is only important insofar as it facilitates and constrains variation in those parameters on which natural selection can act.

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