On embryos and ancestors

Fossils of tiny embryos 570 million years old may well be greatest paleontological discovery of our time

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"Every day, in every way, I'm getting better and better." I had always regarded this famous phrase as a primary example of the intellectual vacuity that often passes for profundity in our current era of laid-back, New Age bliss-a verbal counterpart to the vapidity of the "have a nice day" smiley face. But when I saw this phrase chiseled in stone on the pediment of a French hospital built in the early years of our century, I knew that I must have missed a longer and more interesting pedigree. This formula for well-being, I then discovered, had been devised in 1920 by Emile Coue (1857-1926), a French pharmacist who made quite a stir in the pop-psych circles of his day with a theory of self-improvement through autosuggestion based on frequent repetition of this mantra, a treatment that received the name of Coueism. (In a rare example of improvement in translation, this phrase gains both a rhyme and better flow, at least to my ears, when converted to English from Coue's French original: Tous les jours, a tous points de vue, je vais de mieux en mieux.)

I don't doubt the efficacy of Coues mantra, for the placebo effect (its only possible mode of action) should not be dismissed as a delusion but cherished as a useful strategy for certain forms of healing -a primary example of the influence that mental attitudes can wield upon our physical sense of well-being. However, as a general description for the usual style and pacing of human improvement, the constant and steady incrementalism of Coue's motto - a twentieth-century version of an ancient claim embodied in the victory cry of Aesop's tortoise, "slow and steady wins the race"-strikes me as only rarely applicable, and surely secondary, to the usual mode of human enlightenment, either attitudinal or intellectual: that is, not by global creep forward, inch by subsequent inch, but rather in rushes or whooshes, usually following the removal of some impediment or the discovery of some facilitating device, either ideological or technological.

The glory of science lies in such innovatory bursts. Centuries of vain speculation dissolved in months before the resolving power of Galileo's telescope, trained upon the full range of cosmic distances, from the Moon to the Milky Way. About 350 years later, centuries of conjecture and indirect data about the composition of lunar rocks melted before a few pounds of actual samples brought back by Apollo 11 after Mr. Armstrong's small step onto a new world.

An embryo of a triploblast animal in an early stage of cleavage, right, was preserved in late Proterozoic chert from southern China. It bears a remarkable resemblance to the hypothetical early life-form, above drawn by evoltionist Ernst Haeckel more titan a century ago.

In the physical sciences, such explosions of discovery usually follow the invention of a device that can, for the first time, penetrate a previously invisible realm-the "too far" by the telescope, the "too small" by the microscope, the imperceptible by X rays, or the unreachable by spaceships. In the humbler world of natural history, episodes of equal pith and moment often follow a "eureka" triggered by continually available mental, rather than expensively novel physical, equipment. In other words, great discovery often requires a map to a hidden mine filled with gems then easily gathered by conventional tools, not a shiny new space-age machine for penetrating previously (and utterly) inaccessible worlds.

The uncovering of life's early history has featured several such cascades of discovery following a key insight about proper places to look, and I introduce this year's wonderful story by citing a previous episode of remarkably similar character from the last generation of our science (literally so, for this year's discoverer wrote his Ph.D. dissertation under the guidance of one of the earlier two innovators).

When, as a boy in the early 1950s, I first became fascinated with paleontology and evolution, the standard dogma proclaimed the origin of life was inherently improbable but achieved on this planet only because the immensity of geological time must convert the nearly impossible into the virtually certain. (With no limit on the number of tries, you will eventually flip fifty heads in a row with an honest coin.) As evidence for asserting the exquisite specialness of life in the face of overwhelmingly contrary odds, these conventional sources cited the absence of any fossils representing the first half of the earth's existence -- a span of more than 2 billion years, often formally designated on geological charts as the Azoic (literally, "lifeless") era. Although scientists do recognize the limitations of such negative evidence (the first example of a previously absent phenomenon may, after all, turn up tomorrow), this failure to find any fossils for geology's first 2 billion years did seem fairly persuasive. Paleontologists had been searching assiduously for more than a century and had found nothing but ambiguous scraps and blobs. Negative results based on such sustained effort over so many years do begin to inspire belief.

But the impasse broke in the 1950s, when Elso Barghoorn and Stanley Tyler reported fossils of unicellular life in rocks more than 2 billion years old. Paleontologists, to summarize a long and complex story with many exciting turns and notable heroes, had been looking in the wrong place in conventional sediments that rarely preserve the remains of single-celled bacterial organisms without hard parts. They had not realized that life had remained so simple for so long, or that the ordinary sites for good fossil records could not preserve such organisms.

Barghoorn and colleagues dispelled a century of frustration by looking in a different place, where cellular remains of bacteria might be preserved - in chert beds. Chert has the same chemical formula (with a different molecular arrangement) as quartz: silicon dioxide. Paleontologists rarely think of looking for fossils in silicate rocks - for the perfectly valid and utterly obvious reason that silicates form by the cooling of volcanic magmas and therefore cannot contain organic remains. (Life, after all, doesn't flourish in bubbling lavas, and anything falling in gets burnt to a crisp.) But cherts can form at lower temperatures and be deposited amid layers of ordinary sediments in oceanic waters. Bacterial cells, when trapped in this equivalent of surrounding glass, can be preserved as fossils.

This cardinal insight - that we had been searching in the wrong venue of ordinary sediments rather than in fruitful cherts - created an entire field of study: collecting data from the first two-thirds or so of life's full history. Forty years later, we may look back with wonder at the flood of achievement and the complete overturn of established wisdom. We now possess a rich fossil record of early life, extending right back to the earliest potential source for cellular evidence. (The oldest rocks on earth that could preserve such data do contain abundant fossils of bacterial organisms. These 3.5- to 3.6-billionyear-old rocks from Australia and South Africa are the most ancient strata on earth that have not been sufficiently altered by subsequent heat and pressure to destroy all anatomical evidence of life.)

Such ubiquity and abundance have forced a reversal of the old view. Life of simplest bacterial grade now seems inevitable rather than improbable. As a mantra for memory, may I suggest: "Life on earth is as old as it could be." I realize, of course, that an earliest possible appearance constitutes no proof of inevitability. After all, even a highly improbable event might occur, by good fortune, early in a series of trials. (You might flip those fifty successive heads on your tenth attempt, but don't count - or bet - on it.) Nonetheless, faced with the data we now possess - that life appears as soon as it could and remains pervasive forever after - our thoughts must move to ideas about almost predictive inevitability. Given a planet of earthly size, distance from a central star, and composition, life of simplest grade may originate with virtual certainty as a consequence of principles of organic chemistry and the physics of self-organizing systems.

But whatever the predictability of life's origin, the subsequent pathways of evolution have been mighty peculiar, at least with respect to our conventional hopes and biases. The broadest pattern might seem to confirm our usual view of generally increasing complexity, leading sensibly to human consciousness; after all, the early earth sported only bacteria but now features people, ant colonies, and oak trees. Fair enough, but any scrutiny of general timings or particular details leaves little faith in any steady pattern. If greater size and complexity bestow such Darwinian blessings, why did life take so long to proceed "onward," and why do most of the supposed steps occur so quirkily and so quickly? Consider the following epitome of major events.

Fossils, as stated above, appear as soon as they possibly could in the geological record. But life then remains exclusively at this simplest so-called prokaryotic grade (unicells without any internal organelles - that is, no nuclei, chromosomes, mitochondria, and so on) for about half its subsequent history; the first unicells of the more complex eukaryotic grade (with the conventional organelles of our high-school text figures of an amoeba or paramecium) do not appear in the fossil record until about 2 billion years ago. The three great multicellular kingdoms of plants, fungi, and animals arise subsequently (and, at least for algae within the plant kingdom, more than once and independently) to eukaryotic unicells. Fossils of simple multicellular algae extend back fairly reliably about 1 billion years, and far more conjecturally to as many as 1.8 billion years.

But the real enigma - at least with respect to our parochial concerns about the progressive inevitability of our own lineage - surrounds the origin and early history of animals. If life had always been hankering to reach a pinnacle of expression as the animal kingdom, then organic history seemed in no hurry to initiate this ultimate phase. About five-sixths of life's history had passed before animals made their first appearance in the fossil record, some 600 million years ago. Moreover, as previous essays in this series have explained in far greater detail, Earth's first community of animals - which held nearly exclusive sway from the time of its appearance right up to the dawn of the Cambrian period, 543 million years ago - consisted of enigmatic species with no clear relation to modern forms.

These so-called Ediacaran animals (named for the locality of first discovery in Australia, but now known from all continents) could grow quite large - up to a few feet in length - but apparently contained neither complex internal organs nor even any recognizable body openings of mouth, anus, and so on. Many Ediacaran creatures were flattened forms, in a variety of shapes and sizes, built of numerous tubelike sections complexly quilted together into a single structure. Theories about the affinities of Ediacaran organisms span the full gamut-from viewing them (most conventionally) as simple ancestors for several modern phyla to interpreting them (most radically) as an entirely separate, and ultimately failed, experiment in multicellular animal life. An intermediate position now gaining favor (a situation that should lead to no predictions about the ultimate outcome of this complex debate) treats Ediacaran animals as a bountiful expression of the range of possibilities for diploblastic animals (built of two body layers), a group now so reduced in diversity (subsisting only as corals, jellyfishes, and their allies) that living representatives provide little understanding of full potentials.

Modern animals - except for sponges, corals, and a few other minor groups - are all triploblastic, or composed of three body layers: an ectoderm, forming netvous tissue and other organs; mesoderm, forming reproductive structures and other parts; and endoderm, building the gut and other internal organs. (If you learned a conventional list of phyla back in highschool biology, all groups from the flatworms on "up"-including the five "big" phyla of annelids, arthropods, mollusks, echinoderms, and vertebrates-are triploblasts.) This three-layered organization seems to act as a prerequisite for the formation of conventional, complex, mobile, bilaterally symmetrical organisms with body cavities, appendages, sensory organs, and all other accoutrements setting our standard picture of a "proper" animal. Thus, in our parochial manner (and ignoring such truly important groups as corals and sponges), we tend to equate the problem of the beginning of modern animals with the origin of triploblasts. If the Ediacaran animals are all (or mostly) diploblasts, or something even more genealogically divergent from triploblastic animals, then this first fauna does not resolve the problem of the origin of animals (in our conventionally limited sense of modern triploblasts).

A 570-million-year-old fossil embryo, right, shows hexagonal cells still constrained by membranes. Ernst Heackel's speculative illustration of early life, above, was published long before any fossil corroboration.

The story of modern animals then becomes even more curious. The inception of the Cambrian period marks the extinction, perhaps quite rapid, of the Ediacaran fauna and the beginning of a rich record for animals with calcareous skeletons easily preserved as fossils. But the first phase of the Cambrian, called Manakayan, lasting from 543 to 530 million years ago, features primarily a confusing set of spines, plates, and other bits and pieces called (even in our technical literature) the SSF, or "small shelly fossils" (presumably the disarticulated fragments of skeletons that had not yet evolved to large, discrete units covering the entire organism).

The next two phases of the Cambrian (called Tommotian and Atdabanian and ranging from 530 to about 520 million years ago) mark the strangest, most important, and most intriguing of all episodes in the fossil record of animalsthe short interval known as the Cambrian explosion and featuring the first appearance of all animal phyla with skeletons subject to easy preservation in the fossil record. (A single exception, a group of colonial marine organisms called the Bryozoa, makes its appearance at the beginning of the next, or Ordovician, period. Many intriguing "inventions," including human consciousness and the dance language of bees, have arisen since then, but no new phyla or animals of starkly divergent anatomical design.)

Recent finds of fossil embryos indicate that the history of complex animals extends as far back as 570 million years - well before the Cambrian explosion, which gave rise to most modern phyla.

The Cambrian explosion ranks as such a definitive episode in the history of animals that we cannot possibly grasp the basic tale of our own kingdom until we achieve better resolution for both the antecedents and the unfolding of this cardinal geological moment. The second discovery treated in this essay, announced in February 1998 and also based on learning to look in a previously unsuspected place, has thrilled the entire paleontological community for its promise in unraveling the previously unknown history of triploblast animals before the Cambrian explosion.

If the Cambrian explosion inspires frustration for its plethora of data - too much, too confusing, and too fast - the Precambrian history of triploblast animals engenders even more chagrin for its dearth. The complex animals of the explosion, so clearly assignable to modern phyla, didn't arise ex nihilo at their first moment of fossilization, so what (and where) are their antecedents in Precambrian times? What were the forebears of modern animals doing for 50 million prior years, when Ediacaran diploblasts (or stranger creatures) ruled the animal world?

Up to now, we have engaged in much speculation while possessing only a whiff or two of data. Ediacaran strata also contain trails and feeding traces presumably made by triploblast organisms of modern design (for the flattened and mostly immobile Ediacaran animals could not crawl, burrow, or feed in a manner suggestive of activities now confined to triploblast organisms). Thus, we do have evidence for the existence, and even the activities, of precursors of modern animals before the Cambrian explosion, but no data about their anatomy and appearance-a situation akin to the frustration we might feel if we could hear birdsong but had never seen birds.

A potential solution - or, at the very least, a firm and first source of anatomical data - has just been discovered by applying the venerable motto (so beloved by people, including yours truly, of shorterthan-average stature): Good Things Often Come in Small Packages, or, to choose a more literary and inspirational expression, Micah's statement (5:2), taken by the later evangelists as a prophecy of things to come: "But thou, Bethlehem . . . though thou be little among the thousands of Judah, yet out of thee shall he come forth unto me that is to be ruler in Israel...."

In short, paleontologists had been looking for conventional fossils in the usual (and visible) size ranges of adult organisms: fractions to a few inches. But a solution had been lurking in the realm of smallersized creatures just barely visible (in principle) but undetectable in conventional practice - in the domain of embryos. But who would ever have thought that delicate embryos might be preserved as fossils when presumably hardier adults left no fragments of their existence? The story, a fascinating lesson in the ways of science, has been developing for more than a decade, but has only just found application to the problem of Precambrian animals.

Fossils form in many modes and stylesas original hard parts preserved within entombing sediments or as secondary structures formed by impressions of bones or shells (molds) that may then become filled with later sediments (casts). But original organic materials may also be replaced by percolating minerals-a process called petrifaction, or, literally, "making into stone," a phenomenon perhaps best represented in popular knowledge by gorgeous specimens from the Petrified Forest in Arizona, where multicolored agate (another form of silicon dioxide) has replaced original carbon so precisely that the wood's cellular structure can still be discerned. (Petrifaction enjoys sufficient public renown for many people to mistakenly regard such replacement as the primary definition of a fossil. Not at all; any bit of an ancient organism qualifies as a fossil, whatever its style of preservation. In almost any circumstance, a professional would much prefer to work with unaltered hard parts than with petrified replacements.)

In any case, one poorly understood style of petrifaction leads to replacement of soft tissues by calcium phosphate process called phosphatization. This style of replacement can occur within days of death, thus leading to the rare and precious phenomenon of petrifaction before decay of soft anatomy. Phosphatization might provide a paleontologist's Holy Grail if all soft tissues could thus be preserved at any size in any kind of sediment. Alas, the process seems to work in detail only for tiny objects up to about 2 millimeters in length. (Since 25.4 millimeters make an inch, we are talking about barely visible dots, not even about bugs large enough to be deemed "yucky" when found on our dinner plates or in our beds.)

Still, on the good old principle of not looking gift horses (or unexpected bounties) in the mouth (by complaining about an unavailable better deal), let us rejoice in the utterly unanticipated prospect that tiny creatures - which are, after all, ever so abundant in nature, however much they may generally pass beneath our exalted notice might become petrified in sufficient detail to preserve their bristles, hairs, or even their cellular structure. The recognition that phosphatization may open up an entire world of tiny creatures, previously never considered as candidates for fossilization at all, may spark the greatest burst of paleontological exploration since the discovery that 2 billion years of Precambrian life lay hidden in chert.

The first hints that phosphatization of tiny creatures might resolve key issues in the early evolution of animals dates to a discovery made in the mid-1970s and then researched and reported in one of the most elegant (but rather sadly underappreciated) series of papers ever published in the history of paleontology: the work of German scientists Klaus J. Muller and Dieter Walossek on the fauna of distinctive Upper Cambrian rocks in Sweden known as Orsten beds. In these layers of limestone concretions, tiny arthropods (mostly larvae of crustaceans) have been preserved by phosphatization in exquisite, three-dimensional detail. The photography and drawings of Walossek and Miller have rarely been equaled in clarity and aesthetic brilliance, and their papers are a delight both to read and see. (For a good early summary, consult Muller and Walossek: "A remarkable arthropod fauna from the Upper Cambrian 'Orsten' of Sweden," 1985, Transactions of the Royal Society of Edinburgh, vol. 76, pp. 161-172; for a recent review, see Walossek and Miller: "Cambrian 'Orsten'-type arthropods and the phylogeny of Crustacea," in R. A. Fortey and R. H. Thomas {eds.}, Arthropod Relationships, London: Chapman and Hall, 1997.)

By dissolving the limestone in acetic acid, Walossek and Muller can recover the tiny, phosphatized arthropods intact. They have collected more than 100,000 specimens following this procedure and have summarized their findings in their paper of 1997 cited above:

The cuticular surface of these arthropods is still present in full detail, revealing eyes and limbs, hairs and minute bristles . .. gland openings, and even cellular patterns and grooves of muscle attachment underneath. . . The maximum size of specimens recovered in this type of preservation does not exceed 2 mm.

From this beginning, other paleontologists have proceeded backward in time, and downward in growth from larvae to early embryonic stages containing just a few cells. In 1994, Xi-guang Zhang and Brian R. Pratt found balls of presumably embryonic cells measuring 0.30 to 0.35 millimeters in diameter and representing, perhaps, the earliest stages of adult trilobites, which are also found in the same Middle Cambrian strata (see Zhang and Pratt: "Middle Cambrian arthropod embryos with blastomeres," 1994, Science, vol. 266, pp. 637-38). Just last year, Stefan Bengston and Yue Zhao reported even earlier phosphatized embryos from basal Cambrian strata in China and Siberia. In an exciting addition to this growing literature, these authors traced a probable growth seriesfrom embryos to tiny near adults-for two entirely different animals: a species from an enigmatic extinct group, the conulards; and a probable segmented worm (see Bengston and Zhao, "Fossilized metazoan embryos from the earliest Cambrian," 1997, Science, vol. 277, pp. 1645-48).

When such novel techniques first encounter materials from a truly unknown or unsuspected world, genuinely revolutionary conclusions often emerge. In what may well go down in history as the greatest paleontological discovery of the late twentieth century, Shuhai Xiao, a postdoctoral student in our paleontological program; Yun Zhang, of Beijing University; and my colleague (and Shuhai Xiao's mentor) Andrew H. Knoll, have just reported their discovery of the oldest triploblastic animals, preserved as phosphatized embryos in rocks from southern China estimated at 570 million years of age (and thus even older than the richest Ediacaran faunas found in strata about 10 million years younger {see Xiao, Zhang, and Knoll, "Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite," 1998, Nature, vol. 391, pp. 553-58}). These phosphatized fossils include a rich variety of multicellular algae, showing, according to the authors, that "by the time large animals enter the fossil record, the three principal groups of multicellular algae had not only diverged from other protistan {unicellular} stocks but had evolved a surprising degree of the morphological complexity exhibited by living algae."

Given our understandably greater interest in our own animal kingdom, however, most of the attention will be riveted upon some smaller and rarer globular fossils, averaging half a millimeter in diameter and found phosphatized in the same strata: an exquisite series of earliest embryonic stages, beginning with a single fertilized egg and proceeding through two-cell, four-cell, eight-cell, and sixteen-cell stages to small balls of cells representing slightly later phases of early development. These embryos cannot be assigned to any particular group (more distinctive, later stages have not yet been found) but their identification as earliest stages of triploblastic animals seems secure, both from characteristic features (especially the overall size of the embryo during these earliest stages, which remains unchanged as average cell size decreases to pack more cells into a constant space) and from their uncanny resemblance to particular traits of living groups (several embryologists have told Knoll and colleagues that they would have identified these specimens as embryos of living crustaceans had they not been informed of their truly ancient age).

Elso Barghoorn, Knoll's thesis advisor, opened up the world of earliest life by discovering that bacteria could be preserved in chert. Now, a full generation later, Knoll and colleagues have penetrated the world of the earliest known ancestors of triploblast animals by accessing a new domain where phosphatization preserves minute embryonic stages but no known process of fossilization can reliably render potentially larger phases of growth. When I consider the cascade of knowledge that proceeded from Barghoorn's first report of Precambrian bacteria to our current record spanning three billion Precambrian years and hundreds of recorded forms, I can only conclude that the discovery by Xiao, Zhang, and Knoll places us at a gateway of equal promise for reconstructing the earliest history of modern animals, before their overt evolutionary burst to large size and greatly increased anatomical variety in the subsequent Cambrian explosion. If we can, thereby, gain any insight into the greatest of all mysteries surrounding the early evolution of animals - the causes of both the anatomical explosion itself and the "turning off" of evolutionary fecundity to generate new phyla thereafterthen paleontology will shake hands with evolutionary theory in the finest merger of talents ever applied to the resolution of a historical enigma.

Two final comments might help to establish a context of both humility and excitement at the threshold of this new quest. First, we might be able to coordinate the growing direct evidence of fossils with a potentially powerful indirect method for judging the times of origin and branching for major animal groups: the measurement of relative degrees of detailed genetic similarity among living representatives of diverse animal phyla. Such measurements can be made with great precision upon large masses of data, but firm conclusions are hard to obtain because various genes evolve at different rates that also maintain no constancy over time, and most methods applied so far have made simplifying (and probably unjustified) assumptions about relatively even ticking of supposed molecular clocks.

For example, in a paper that received much attention upon publication in 1996, G. A. Wray, J. S. Levinton, and L. H. Shapiro used differences in the molecular sequences of seven genes in living representatives of major phyla to derive an estimate of roughly 1.2 billion years for the divergence time between chordates (our phylum) and the three great groups on the other major branch of animals (arthropods, annelids, and mollusks) and 1 billion years for the later divergence of chordates from the more closely related phylum of echinoderms (see Wray, Levinton, and Shapiro, "Molecular evidence for deep Precambrian divergences among metazoan phyla," 1996, Science, vol. 274, pp. 568-73).

This paper sowed a great deal of unnecessary confusion when several uncomprehending journalistic reports, and a few careless statements by the authors, raised the old canard that such an early branching time for animal phyla disproves the reality of the Cambrian explosion by rendering this apparent burst of diversity as the artifact of an imperfect fossil record (signifying, perhaps, only the invention of hard parts, rather than any acceleration of anatomical innovation). For example, Wray et al. write: "Our results cast doubt on the prevailing notion that the animal phyla diverged explosively during the Cambrian or late Vendian {Ediacaran times}, and instead suggest that there was an extended period of divergence . . . commencing about a billion years ago."

But such statements confuse the vital distinction, in both evolutionary theory and actual results, between times of initial branching and subsequent rates of anatomical innovation or evolutionary change in general. Even the most vociferous advocates of a genuine Cambrian explosion have never argued that this period of rapid anatomical diversification represents the moment of origin for animal phyla - if only because we all acknowledged the evidence for Precambrian tracks and trails of triploblasts even before the recent discovery of embryos. Nor do these same vociferous advocates imagine that only one wormlike species crawled across the great Cambrian divide to serve as an immediate common ancestor for all modern phyla. In fact, I don't see that it matters one whit (for the reality of the explosion - although it matters a great deal for other evolutionary issues) whether one wormlike species carrying the ancestry of all later animals, or ten similar wormlike species already representing the lineages of ten subsequent phyla, crossed this great divide from an earlier Precambrian history. The Cambrian explosion embodies a claim for a rapid spurt of anatomical innovation within the animal kingdom, not a statement about times of genealogical divergence.

The following example should clarify the fundamental distinction between times of genealogical splitting and rates of change. Both rhinoceroses and horses may have evolved from the genus Hyracotherium (formerly called Eohippus). A visitor to the Eocene earth, about 50 million years ago, might determine that the basic split had already occurred. He might be able to identify one species of Hyracotherium as the ancestor of all later horses, and another species of the same genus as the progenitor of all subsequent rhinos. But such a visitor would be ridiculed with justified scorn if he then argued that later divergences between horses and rhinos must be illusory because the two lineages had already split. After all, the two Eocene species looked like kissing cousins (as evidenced by their placement in the same genus) and only gained their later status as progenitors of highly distinct lineages by virtue of a subsequent history, utterly unknowable at the time of splitting. Similarly, if ten nearly identical wormlike forms (the analogs of the two Hyracotherium species) crossed the Cambrian boundary but evolved the anatomical distinctions that would make them great phyla only during the subsequent explosion, then the explosion itself remains as real-and as vitally important for life's history as any advocate has ever averred.

This crucial distinction has been recognized by most commentators on the work of Wray et al. Geerat J. Vermeij, in his direct evaluation (Science, 1996, page 526), wrote that "this new work in no way diminishes the significance of the VendianCambrian revolution." Fortey, Briggs, and Wills added that "there is, of course, no necessary correspondence between morphology and genomic change." (See BioEssays, 1997, vol. 19, p. 433.) In any case, a recent publication by Ayala, Rzhetsky, and Ayala (Proceedings of the National Academy of Sciences, vol. 95, 1998, pp. 606-11) presents a powerful rebuttal to Wray et al.'s conclusions. By correcting statistical errors and unwarranted assumptions, and by adding data for twelve additional genes, these authors provide a very different estimate for initial diversification in late Precambrian times: about 670 million years ago for the split of chordates from the line of arthropods, annelids, and mollusks; and 600 million years ago for the later divergence of chordates from echinoderms.

We are left, of course, with a key mystery (among many others): where are Precambrian adult triploblasts "hiding" now that we have discovered their embryos? An old suggestion, dating from the 1870s and devised by the bombastic German theorist Ernst Haeckel (who was, nonetheless, outstandingly right far more often than random guesswork would allow) held that Precambrian animals had evolved as tiny forms not much larger than, or very different from, modern embryos-and would therefore be very hard to find as fossils. (The similarity between Haeckel's speculative ancestors and Xiao, Zhang, and Knoll's actual embryos is almost eerie.) Recently, in a brilliant paper, E. H. Davidson, K. J. Peterson, and R. A. Cameron (Science, 1995, vol. 270, pp. 1319-25) have made a powerful case, based on genetic and developmental arguments, that Precambrian animals did originate at tiny sizes, and that the subsequent Cambrian explosion depended upon the evolution of novel embryological mechanisms for greatly increasing cell number and body size, accompanied by consequent potential for greatly enhanced anatomical innovation. If Haeckel's old argument, buttressed by Davidson's new concepts and data, has validity, we then gain genuine hope, even realistic expectation, that Precambrian adult triploblasts may soon be discovered, for such animals will be small enough to be preserved by phosphatization.

As a final point, this developing scenario for the early history of animals might foster humility and generate respect for the complexity of evolutionary pathways. To make the obvious analogy we used to regard the triumph of "superior" mammals over "antediluvian" dinosaurs as an inevitable consequence of progressive evolution. We now realize that mammals originated at the same time as dinosaurs and then lived for more than 100 million years as marginal, small-bodied creatures in the nooks and crannies of a dinosaur's world. Moreover, mammals would never have expanded to dominate terrestrial ecosystems (and humans would surely never have evolved) without the supreme good fortune (for us) of a catastrophic extraterrestrial impact that, for some set of unknown reasons, eliminated dinosaurs and gave mammals an unanticipated opportunity.

Does the earlier story of Ediacaran "primitives" versus contemporary Precambrian ancestors of modern animals differ in any substantial way? We now know (from the evidence of Xiao, Zhang, and Knoll's embryos) that animals of modern design had already originated before the Ediacaran fauna evolved into full bloom. Yet "primitive" Ediacara dominated the world of animal life for at least 50 million years, while modern triploblasts waited in the proverbial wings, perhaps as tiny animals of embryonic size, living in nooks and crannies permitted by much larger Ediacaran dominants. Only a mass extinction of unknown cause, which wiped out Ediacara and initiated the Cambrian transition 543 million years ago, gave modern triploblasts an opportunity to shine-and so we have.

In evolution, as well as in politics, incumbency offers such powerful advantages that even a putatively more competent group may be forced into a long period of watchful waiting, hoping for an external stroke of good luck to pick up the reins of power. If fortune continues to smile, the new regime may even gain enough confidence to invent a comforting and commanding mythology about the inevitability of its necessary rise to power by gradually growing better and better - every day and in every way.

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