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Andrew H. Knoll: Life on a Young Planet

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In the Beginning?

Fossils found along the Kotuikan River in northern Siberia document the Cambrian “Explosion,” the remarkable flowering of animal life that began some 543 million years ago. As Charles Darwin recognized more than a century ago, Cambrian fossils raise fundamental questions about life’s earlier evolution. What kind of organisms preceded these already complex animals? Can we find older rocks, and if we can, will they preserve a record of Earth’s earliest biological history?

Sometimes the past was shot with a hand-held camera; sometimes it reared monumentally inside a proscenium arch with moulded plaster swags and floppy curtains; sometimes it eased along, a love story from the silent era, pleasing, out of focus and wholly implausible. And sometimes there was only a succession of stills to be borrowed from the memory.

—Julian Barnes

Staring at the Sun

THE CLIFFS ALONG the Kotuikan River glow fawn and pink in the late afternoon sun (figure 1.1). Elsewhere, in North America or in Europe, a vista like this would be celebrated as a national park, its approaches flanked by campgrounds and souvenir shops. But here, in the forested wilderness of northern Siberia, its pastel beauty is both unremarkable and largely unseen. From a sheltered niche halfway up the cliff, I look up at my friend Misha Semikhatov perched high above the river, his large frame barely supported by a narrow ledge. The drop beneath his

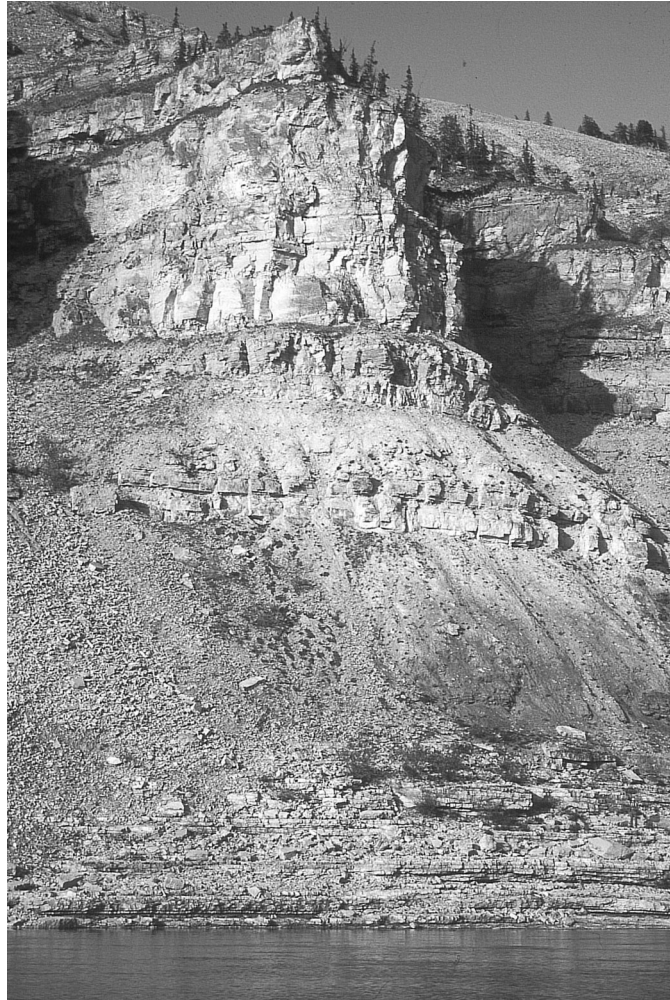


Figure 1.1. Fossiliferous cliffs along the Kotuikan River in Siberia. The distance from river level to the top of the cliff is more than 300 feet, recording some 20 million years of Early Cambrian history.

feet is precipitous, but Misha's attention is elsewhere, fixed on a layer of sedimentary rocks just above his head. To his experienced eye, the bed of crinkly laminated limestones tells of an ancient tidal flat that bordered a vanished ocean, a broad expanse of shoreline exposed at low tide, covered by thickly matted bacteria, and occasionally crossed by small animals. As I rest against the rock face, observing marginally

older beds, jotting in my notebook, and swatting mosquitoes (not necessarily in that order), I reflect on what has brought Misha and me to this remote spot high above the Arctic Circle (figure 1.2). The literal answer is a giant Soviet-era military helicopter that deposited us, a small group of colleagues, and a ton of gear some seventy miles upstream. From there, small rubber rafts floated us like Huckleberry Finn slowly down the river, through canyons of limestone, beneath circling falcons, past wolves that howl at the midnight sun, to this wild and beautiful place.

Of course, helicopters provide only one of several appropriate responses to the question of what brought us here. The deeper and more interesting answer is that these cliffs, cut over the millennia by the Kotuikan as it winds toward the Arctic Ocean, record one of Earth history's great turning points. As well as any rocks known anywhere, they document the remarkable diversification of animal life popularly known as the Cambrian Explosion. In the broadest possible sense, the Kotuikan cliffs record the beginnings of the modern world, a world in which animals swim, crawl, or walk beneath an atmosphere of breathable air. That's really what brought us here.

At river level, a series of steps rise out of the water like prehistoric ghats, hewn by nature from thin beds of limestone and dolomite. Some

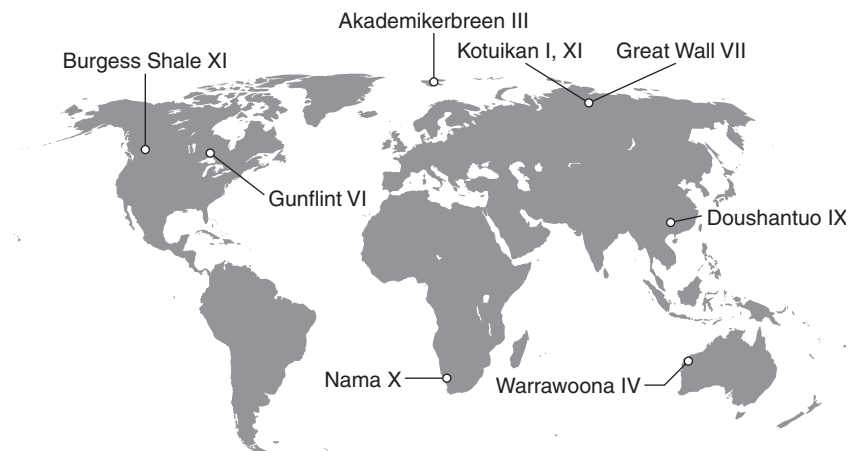


Figure 1.2. Map showing the location of the Kotuikan cliffs, along with principal localities discussed in subsequent chapters (denoted by roman numerals).

545 million years ago, these rocks were deposited as lime muds in a warm shallow seaway not unlike the modern Florida Keys. Scattered clusters of gypsum crystals record drying that episodically left coastal waters salty enough to exclude all but the hardiest bacteria. The fossils of animals are rare in these rocks, and those that can be found are simple. Only a few irregular meanders disturb bedding surfaces, the trails of small wormlike creatures that crawled along the muddy bottom in search of food.

About ten feet above the river, an abrupt shift to quartz sandstone marks the so-called Precambrian-Cambrian¹ boundary, historically the line of demarcation between the tractable paleontology of the Phanerozoic Eon (literally, the “age of visible life”) and the terra incognita of a more youthful Earth. Volcanic rocks a few hundred miles to the east date this horizon at 543 (plus or minus one) million years before the present. Above the sandstone bench purple, red, and green shales form a steep shoulder above which vertiginous cliffs of limestone rise like a wall. The shales record a flooding event, with shoreline sands pushed far to the west by the rising sea. As sediments accumulated, the sea again grew shallower, so that the overlying limestone beds record environments progressively closer to the ancient shore. Near the top of the cliff face, an irregular surface marks a point at which the sediments were exposed and eroded by some vanished forebear of the Kotuikan River, only to be drowned again as the sea reclaimed lost territory.

Beginning at the level of the sandstone bench, the rocks contain small skeletal fossils. In the lowermost beds, there are only a few forms, hollow cones of calcite little more than a millimeter long (figure 1.3a). But as we ascend the cliff, slowly and carefully to avoid a career-shortening slip, the abundance and variety of these fossils increase. So, too, do the number and behavioral complexity of preserved tracks, trails, and burrows. Near the top of the cliff, more than three hundred

¹By convention, geologic time is divided into four eons: the Phanerozoic (0–543 million years ago), the Proterozoic (543–million 2.5 billion years ago), the Archean (2.5–ca. 4 billion years ago), and the Hadean (the time interval from the accretion of the Earth to the beginning of the preserved record, ca. 4–4.55 billion years ago). The Cambrian is the initial period of the Phanerozoic Eon; thus, all earlier time is commonly, if informally, referred to as “Precambrian.” See geologic timescale on page 2.

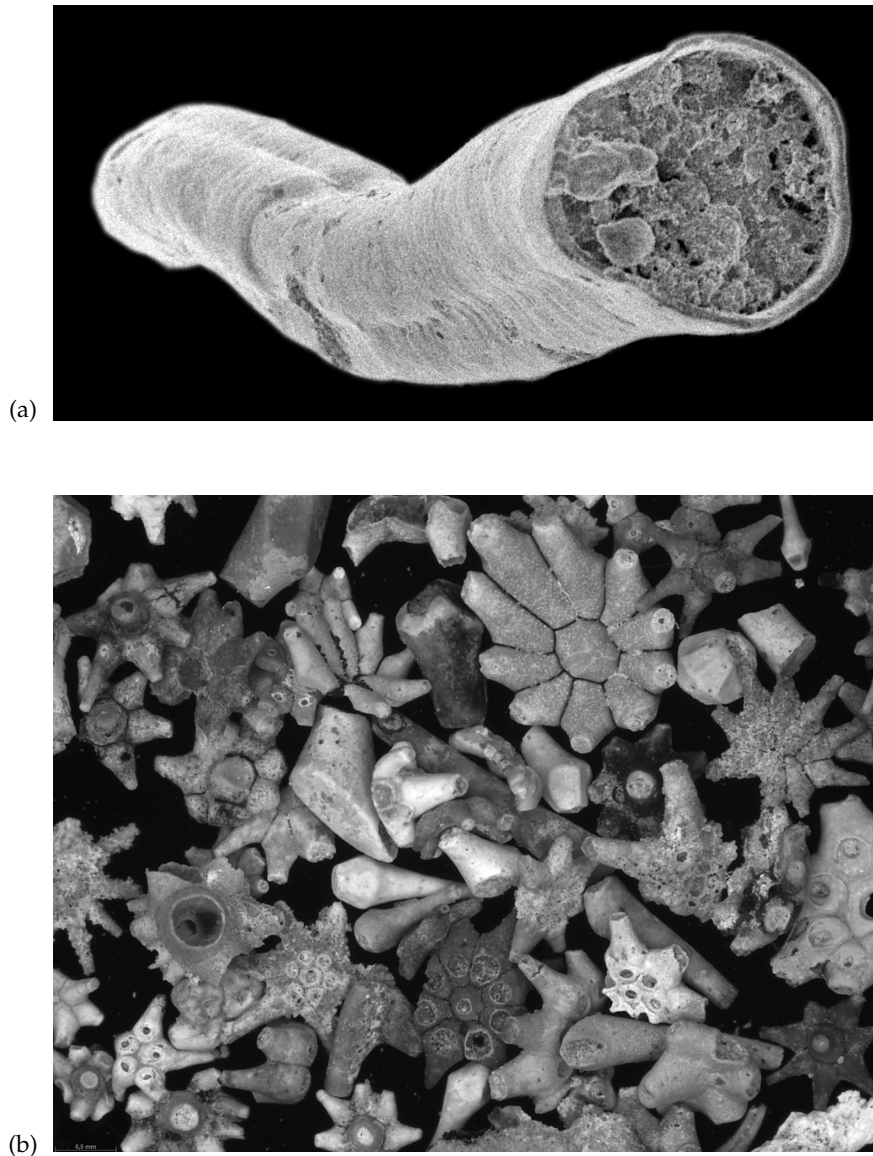


Figure 1.3. Small shelly fossils in basal Cambrian rocks. (a) *Anabarites trisulcatus*, the tiny skeletons found in lowermost Cambrian beds along the Kotuikan River. These specimens come from rocks of comparable age in China. (b) Small shelly fossils of the types found higher in the Kotuikan cliffs; most of the forms seen here are the skeletal spicules of cancellorids, enigmatic baglike animals found widely (and only) in Cambrian rocks. (Images courtesy of Stefan Bengtson)

feet above river level, rocks estimated to be about 525 million years old contain nearly one hundred different types of shells (figure 1.3b). Some, like the small cones in the cliff base, have a threefold symmetry that differentiates them from most animals alive today. Others, however, include small spiral shells that are recognizably the remains of mollusks, bivalved skeletons formed by brachiopods, and, a little higher up, the segmented bodies of trilobites. Painstakingly collected and described by Russian paleontologists, these fossils chronicle an apparently rapid unfolding of biological diversity in the Cambrian ocean. In less than 20 million years, the seafloor was transfigured from the alien to the (at least broadly) familiar. The same drama is recorded in rocks of comparable age throughout the world, providing our earliest glimpses of the animals that have populated Earth's oceans ever since that time.

Charles Darwin couldn't get this pattern out of his mind. One might suppose that Darwin, like his modern intellectual descendants, saw in the fossil record a confirmation of his theory—the literal documentation of life's evolution from the Cambrian to the present day. In fact, the two chapters devoted to geology in *The Origin of Species* are anything but celebratory. On the contrary, they constitute a carefully worded apology in which Darwin argues that evolution by natural selection is correct *despite* an evident lack of support from fossils.

Darwin envisioned natural selection as a slow but continuous process by which biological lineages diverged and gradually grew more distinct from one another. Intermediate forms that link different species are rare in the modern world because selection inexorably acts against them. But why don't we see intermediates in time? Darwin's expectation was that successive sedimentary beds should document the gradual transition from one form, perhaps seen at the base of a cliff, to its morphologically distinct descendants at the top. That such series are rare he attributed to the extreme imperfection of the fossil record.

The *Origin* is full of magisterial prose, words that are luminous as well as illuminating. Darwin's characterization of the geological record is particularly striking: "a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here

and there a short chapter has been preserved; and of each page only here and there a few lines.”

Darwin might well have embraced Julian Barnes’s description of human remembrance as a metaphor for Earth’s geological memory: sedimentary rocks provide a succession of widely spaced snapshots, not a documentary film of our planetary history. At the local level observed in a roadside or cliff face, this view is well justified, and Darwin’s arguments seem strikingly modern. We understand today that sedimentary rocks provide discontinuous records in which the boundary between two layers may represent more time than the beds themselves. But the geometry of sedimentary accumulation is more complex than the orderly layer cake commonly seen in local outcrop. Viewed three-dimensionally, the layers pinch and swell like hills in a van Gogh landscape, thickening here and changing character, thinning there to feather edge. Time represented in one place by a hiatus between beds is recorded elsewhere by sediment accumulation. Viewed still more broadly, at any point in time such locally discontinuous records are forming in many basins throughout the world. Thus, if we revisit Darwin’s metaphor for geological history, we find that while his book is missing chapters, and the chapters in hand are missing pages, we actually possess multiple copies of the text and the parts that are missing vary from copy to copy. If we have a principle for interleaving the surviving pages, it is possible to stitch together a composite record that, for the past 600 million years, at least, isn’t bad. The discipline of stratigraphy provides that principle, showing us that at least the broad biological patterns read from fossils reflect evolution and not gross inadequacies of the rock record.

Biostratigraphers have known for more than a century that species commonly appear in the fossil record fully formed, persist without much change for million of years, and then disappear. The sense conveyed by this pattern, that form changes episodically rather than continuously, doesn’t arise because species appear only once, in a single bed. It is justified because species commonly occur in many successive beds with little change, or at least little *directional* change, from bottom to top—a pattern we can’t explain away as the product of sedimentary incompleteness (at least not without making assumptions that, in many cases, we know to be implausible). Recognizing this, Niles Eldredge and Stephen Jay Gould argued in 1972 that it is this stratigraphic pattern of

“punctuated equilibrium”—and not Darwin’s picture of gradual change—that is most consistent with modern evolutionary theory. Most new species arise not from the insensibly gradual transformation of large populations but rather by the rapid differentiation of small, isolated populations at the periphery of the main group. The transformations envisioned by Darwin occur, but they take place rapidly and locally, after which populations of the descendant species are constrained by natural selection to stay more or less the same until competitors or shifting environments spell their doom.

The everyday comings and goings of fossil species can be reconciled with both evolutionary expectation and geological reality, but what about the spectacular pattern seen in the Kotuikan cliffs? How do we explain this biological transformation of the oceans? If Darwin was concerned about the general lack of transitional forms in the fossil record, he was truly disquieted by the apparently abrupt appearance of abundant, diverse, and anatomically complex animals in the oldest Cambrian beds:

There is another and allied difficulty which is much graver. I allude to the manner in which numbers of species of the same group, suddenly appear in the lowest known fossiliferous rocks. . . . The case must at present remain inexplicable; and may be truly urged as a valid argument against the views herein entertained.

Of course, the *Origin* does offer an explanation, and it is the one we might expect—massive record failure at the base of the Cambrian System. It isn’t, wrote Darwin, that no life preceded the fabulously complicated snails and trilobites of the Cambrian, but rather that their ancestors’ record lay in older beds that are deeply buried, destroyed, or undiscovered. In another memorable passage, Darwin insisted that

if my theory be true, it is indisputable that before the lowest Silurian² stratum was deposited, long periods elapsed, as long as, or probably far longer

²In the mid-nineteenth century, debate about how to define and differentiate the Cambrian and Silurian Systems remained unresolved. Darwin employed Londoner Roderick Murchison’s term Silurian for the oldest fossiliferous beds, despite the fact that his Cambridge mentor Adam Sedgwick had coined the name “Cambrian.” Not until 1879 did Charles Lapworth cut the Gordian knot, retaining Cambrian for the lower part of the disputed system, Silurian for its upper portion, and Ordovician (after the Ordovici, an ancient and putatively obstreperous Welsh tribe) for the contested interval of overlap.



Figure 1.4. Upstream along the Kotuikan River, showing the angular unconformity between the latest Precambrian-Cambrian succession seen in figure 1.1 and an older package of sedimentary rocks that lies beneath it.

than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown periods of time, the world swarmed with living creatures.

Back along the Kotuikan River, Misha and I sit on a gravel bar opposite the cliffs and consider Darwin's dilemma as we sip our evening tea. How could such complexity evolve so quickly? And if it didn't really happen so fast, where are the rocks that record life's earlier history?

The sedimentary beds in the Kotuikan cliffs aren't quite flat-lying; tectonic movements over millions of years have tilted them slightly downward to the west. Because of this, a hike toward the east, upstream along the river, reveals layers that sit ever farther below the level of the Cambrian fossils. About fifteen miles up river—some 200 feet lower in the sedimentary rock column—we encounter a sharp stratigraphic break, the base of the sedimentary package that includes the latest Precambrian carbonate rocks and basal Cambrian animals (figure 1.4). Is that the end of the sedimentary trail?

Not at all. What lies beneath these rocks is another, older succession of

sandstones, shales and carbonates. Set at an acute angle to the younger beds, this older package is itself more than 3,500 feet thick. The base of the Cambrian System is not the bottom of the stratigraphic record—not in northern Siberia, and not in many other places where tectonic circumstance has preserved sedimentary rocks deposited one, two, or even 3 billion years before Cambrian beds began to accumulate.

We can put Darwin's conjecture to the test. Is the Cambrian Explosion the beginning of biological history? Or is it the culmination of evolutionary events that extend much deeper into our planet's past?