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Fossil Focus: *Hallucigenia* and the evolution of animal body plans

by Martin Smith*[1]

Introduction:

Five hundred and fifty million years ago, few (if any) organisms on Earth were much more complex than seaweed. But this would not be the case for long: during a profound evolutionary event dubbed the Cambrian Explosion, natural selection generated the raw material of all the body plans we see in the oceans today. Fossil sites from midway through the Cambrian period (541 million to 485 million years ago) preserve organisms that could almost be mistaken for modern eels, jellyfish, shrimp and squid, along with members of most other major animal groupings (phyla) recognized by biologists today.

But the exceptional fossil deposits of the Cambrian period, some of which preserve fleshy bodies as well as the skeletons and bones that make up a typical fossil, also contain a catalogue of oddballs: organisms that do not, at first glance, fit into any of the modern animal groups. Some palaeontologists have suggested that this 'sonic boom' of evolution was a unique period of innovation. New body blueprints tumbled rapidly into being, some soon going extinct and others lasting until the present day — with subsequent evolution only able to tinker round the edges of the essential blueprints that were established in the Cambrian period. Such a situation is difficult to square with Charles Darwin's intuition that evolution should proceed gradually, not in fits and starts: perhaps the Cambrian Explosion requires an explanation that lies outside the processes we can observe occurring today?

New ways of thinking about fossil oddballs, however, have produced a different take on the Cambrian Explosion in which the most unusual fossils may in fact have the most to tell us about the origins of the modern animal groups.

No fossil quite exemplifies these issues like *Hallucigenia* — a prickly worm whose very name attests to its otherworldly appearance, and whose place in the tree of life has only recently been understood.

Flower-pressing the Cambrian oceans

Our clearest view of early Cambrian ecosystems comes from the exceptional fossils of the Burgess Shale — a rock formation in British Columbia, Canada — and a handful of equivalent deposits around the world. These exquisite localities harbour fossils whose soft tissue is preternaturally preserved, in the best cases including nerve cords, half-digested stomach contents or individual lenses of compound eyes. They offer a rich and fairly representative picture of a typical animal community — if not perfectly complete, then at least much fuller than the limited sample available from the mere 15% of organisms with hard parts that would fossilize in typical circumstances.

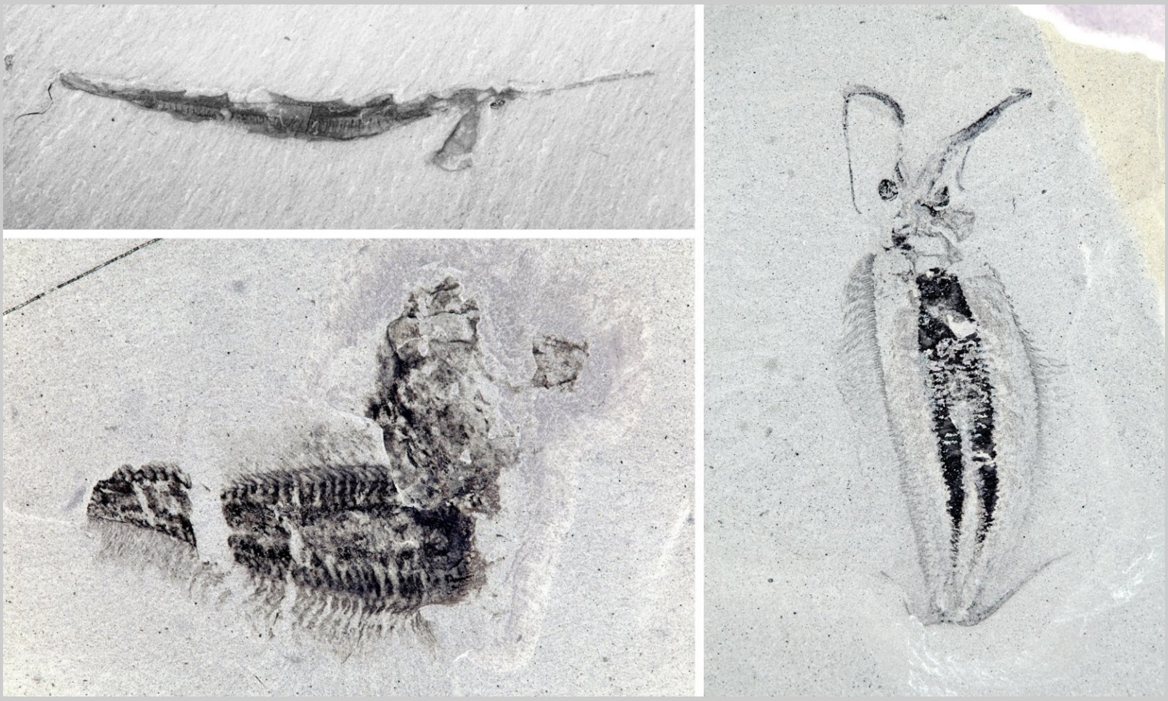

Figure 1 — *Nectocaris*, as preserved in the Burgess Shale. The same organism can look very different depending on its angle of burial, and reconstructing the original three-dimensional animal requires fossils preserved in just the right ways.

There is, however, a catch: the Burgess Shale organisms were buried quickly in undersea mudslides, and were squashed flat by sediment like a flower in a flower press. This can often make it tricky to unravel the original shape of the animal. The first specimen of squid-like *Nectocaris*, for example, was squashed side-on, folding and compacting its wide fins so they looked like a crest on the animal's back rather than the wide wing-like features that later specimens revealed them to be (Fig. 1). *Hallucigenia* has a similarly contorted history of interpretation.

A flat-pack fossil

If you've ever tried to assemble flat-pack furniture, you'll appreciate the challenges of constructing a three-dimensional object from a two-dimensional blueprint. Even if the instructions are perfectly clear, it's still possible to end up with something that doesn't quite look right.

This is certainly the case with *Hallucigenia*. The first fossils of this organism were discovered in the early twentieth century. They look like a centimetre-long hockey stick with a bulbous sac at the top of the handle, and rows of spines sticking out of its shaft (Fig. 2). At first glance, these spines look a bit like the bristles of the bristle-worms (phylum Annelida: a group that includes the ragworms and fireworms today): the animal was originally considered to be an unusual member of this group, and the fossils consigned without fanfare to a shadowy corner of a museum storeroom. But on closer inspection, the spines only occur in pairs, on a single side of the animal: the protrusions on the opposite side are not spines but curving tentacles, each ending in a hooked claw. How could such an unusual animal walk? Researchers assumed that the paired spines were stilt-like legs. A mechanical robot was even built to demonstrate that such an unlikely arrangement could produce a viable gait. And what of those flexible tentacles? Presumably their claws grabbed food and passed it down to the blob-like head at the top end of the hockey stick.

Figure 2 — The type specimen of *Hallucigenia*, and an early reconstruction showing the blob-like head, a single pair of tentacles running along the back, and the stilt-like legs. Credit: Jean-Bernard Caron/Royal Ontario Museum.

Alongside other bamboozling discoveries, this radical redescription of *Hallucigenia* brought the Burgess Shale fossils — which had until the 1970s been quietly gathering dust in museum cabinets — into the forefront of the scientific imagination. What were these uncanny organisms that crawled the Cambrian seas, and how, if at all, did they relate to the animal groups that make up the rest of the fossil record?

Putting things straight

A solution to the puzzle of *Hallucigenia* raised its head in the 1990s, when a related fossil was found in a newly discovered Chinese locality, on the flanks of Maotian Hill in Chengjiang County, Yunnan. Where *Hallucigenia* had leg-like spines, this wrinkly worm, dubbed *Microdictyon*, bore shield-like plates. These plates were thought to have served as armour, not legs: *Microdictyon* instead walked on its paired 'tentacles'. But *Hallucigenia*'s tentacles did not seem to be paired: did this mean that it had only a single row of legs? Just as an essential part of a flat-pack construction is easily lost in the packaging, a closer inspection uncovered a second row of legs buried under sediment that surrounded the fossil, which could be carefully unearthed with a dental drill. With this new data, *Hallucigenia* could at last be reconstructed the right way up. But many aspects of the organism still looked strange, not least its balloon-like head. Was this really the front of the organism — or even part of the organism at all? One daring interpretation suggested that the blobs, which looked quite different from specimen to specimen, might instead represent fluids that were expelled from the tail end of the animal after burial, as it decayed.

This controversy was not laid to rest until 2015, when the 'true' head of *Hallucigenia* was finally identified. My colleagues and I were using an [electron](#) [microscope](#) to inspect the tough carbon films that make up the spines and claws of the animal, looking for clues as to its relationships to other animal groups. In the process, the microscope beam happened to settle on the curved end of one particular specimen, where to our astonishment we found a face staring back at us (Fig. 3). Wide carbon discs corresponded to the optical pigments in the animal's eyes, and a ring of plates represented a set of the originally toughened mouthparts. Lining the throat was a gruesome array of needle-like teeth. Without question, we had found the animal's head. We soon established that the 'blob' at the other end had a distinct chemical composition from the body, supporting its identification as decay-produced fluids. The original reconstruction, then, had been both upside down and back to front.

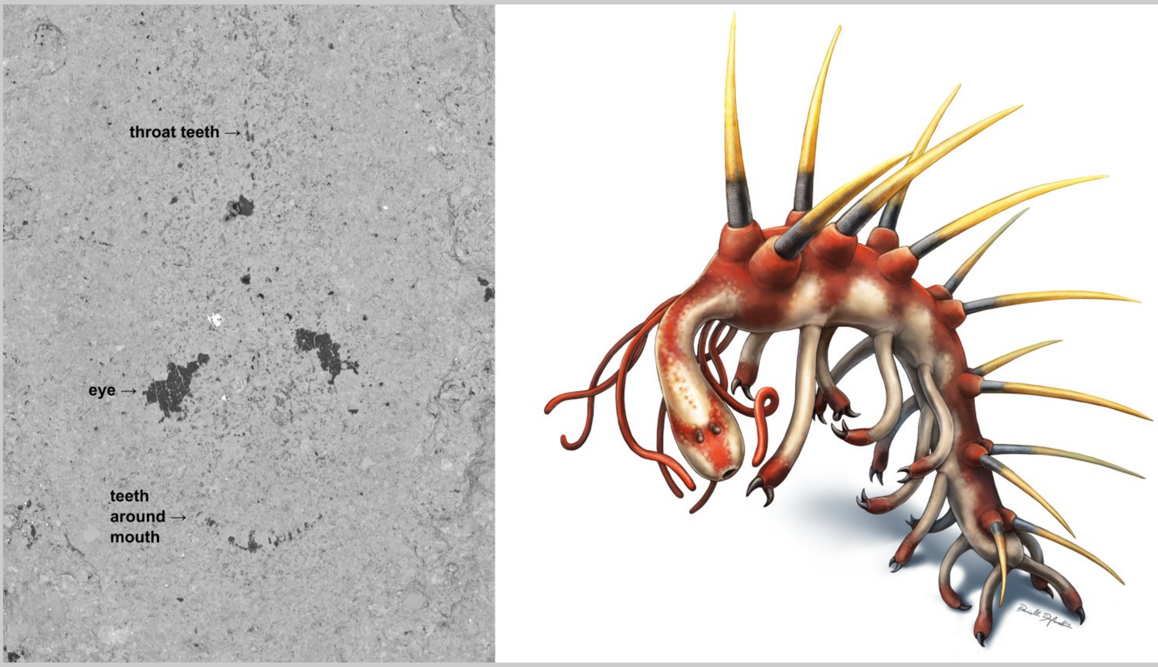

Figure 3 — Left, electron-microscope image of *Hallucigenia*'s head, showing eyes, a ring of plates around the mouth and (faintly here) teeth in the throat. Right, the most recent reconstruction of the organism. Credit: Danielle Dufault/Royal Ontario Museum

A phylum of one's own?

Even in its current (and hopefully final) state, *Hallucigenia* is an excellent example of how abnormal many Burgess Shale organisms look. Does this animal represent an 'extinct body plan' — an evolutionary experiment that ultimately failed, leading to a dead end rather than developing into a modern phylum? This viewpoint, put forward in evolutionary biologist Steven Jay Gould's best-selling 1989 book *Wonderful Life*, portrays the Cambrian Explosion as a profound event that gave rise to a vast diversity of animal forms that was gradually winnowed by chance extinctions to the select remnant of body shapes around today.

This argument focused on the features that made *Hallucigenia* so distinctive — no other organism had legs so long, a head so horrible, or such serious spines, so it must belong into a new subdivision of the animal kingdom, a new phylum. Focusing only on the differences between *Hallucigenia* and other organisms, it is easy to conclude that the animal is unique.

More recently, biologists — working with the rich data available from genetic sequences and embryonic development — have started to find deep similarities between phyla that on the surface look very different. Concentrating on these shared characteristics is the key to linking these once unrelatable groups to one another, and thus identifying the nested relationships that make up the tree of life.

The challenge lies in finding meaningful similarities. A sausage-shaped 'body' and long non-mineralized spines occur in both *Hallucigenia* and cacti, but these features are so generic as to have little biological importance. To prove a genuine relationship, we must find a specific arrangement or construction that is distinctive to a particular group. Electron-microscope analysis identifies three such characteristics in *Hallucigenia*. The ring of plates that surround the mouth closely resembles a similar configuration in a group of Cambrian predators, the radiodontans (Fig.

4, phylum Euarthropoda). A tooth-lined throat characterizes a group unfortunately termed the penis worms (phylum Priapulida). And the claws at the end of *Hallucigenia*'s legs in fact comprise two or three separate elements, stacked one inside the other — a feature only otherwise observed in modern velvet worms (Fig. 5, phylum Onychophora).

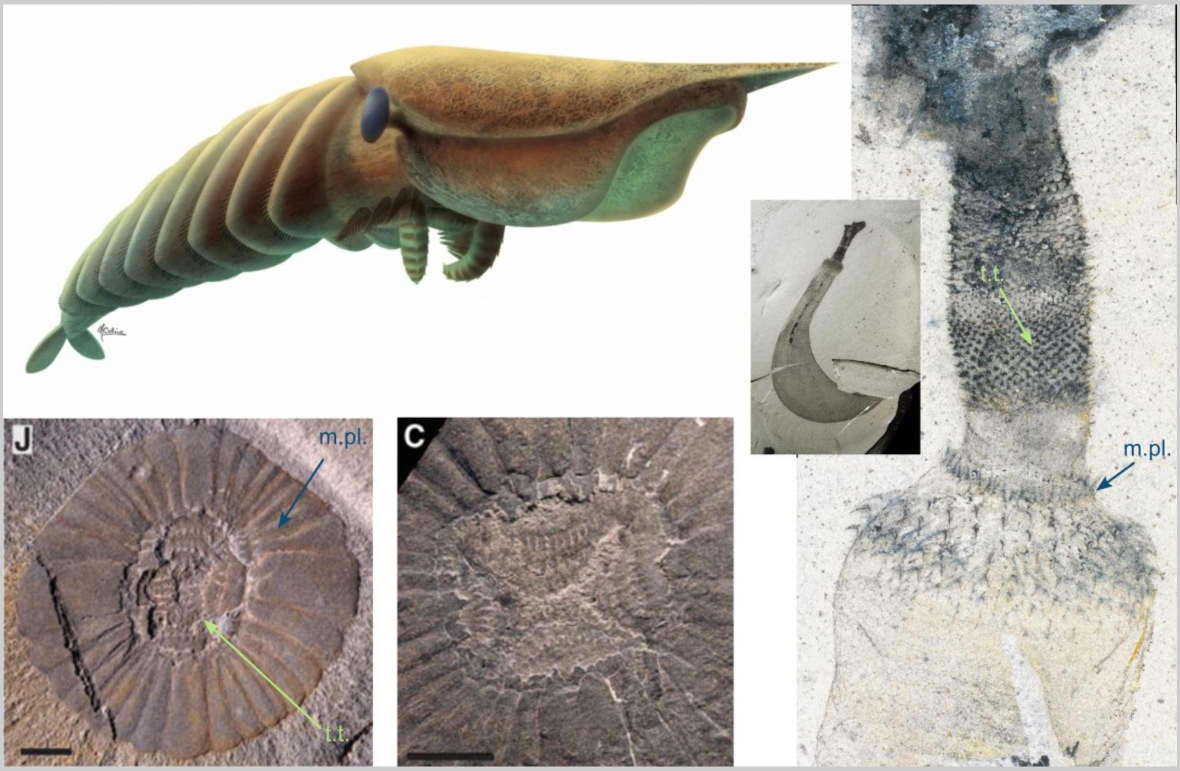

Figure 4 — Mouth apparatuses of two Cambrian fossils. Left, the anomalocaridid euarthropod *Hurdia* has a mouth surrounded with a ring of plates, and a throat lined with tooth-plates. Right, the penis worm *Ottoia* has an [eversible](#) throat lined with teeth, with a single ring of spines marking the official mouth. Abbreviations: m.pl., Mouth plates; t.t., throat teeth. Image credits: Marianne Collins; A. C. Daley, G. E. Budd and J.-B. Caron *Journal of Systematic Palaeontology* **11,** 743–787 (2013). DOI 10.1080/14772019.2012.732723 ; Martin Smith/Smithsonian Institution.

Figure 5 — Left, a velvet worm and one of its claws, consisting of a stack of three separate claw elements, here separated slightly using tweezers. Right, an electron-microscope image of a *Hallucigenia* claw, which also comprises three stacked elements.

This poses something of a riddle. It is encouraging to note that these three groups are closely related — they all moult their cuticle, or outer skin, and there is evidence that *Hallucigenia* did the same. But how can a single animal display attributes of three separate groups? In fact, this capacity to show combinations of characteristics that would never be predicted by looking at modern animals alone is what makes fossils so useful. *Hallucigenia* turns out to be something of a Rosetta Stone, with a mouthpart configuration — a ring of elements around the mouth, and tooth-like elements lining the throat — that it inherited from the common ancestor of all three groups. Penis worms can turn their tooth-lined throats inside out to ensnare unfortunate prey, but the base of this structure is always encircled by a single ring of spines — corresponding to the ring of plates around the *Hallucigenia* mouth. Some radiodontans have rings of tooth-like plates inside their mouth-ringing plates, which probably correspond to the throat-teeth of *Hallucigenia*. There are no plates around the mouths of modern euarthropods — the closest surviving relatives of radiodontans — but the fossil evidence reveals that these plates were lost at some point during euarthropod evolution.

But what of the stacked claws that velvet worms share with *Hallucigenia*? These genuinely seem to occur nowhere else in the animal kingdom. On this basis, *Hallucigenia* can be identified as an early offshoot of the lineage that led to modern velvet worms (Fig. 6). It inherited some characteristics (its mouth-ringing plates and throat teeth) from the common ancestor of all moulting animals — characteristics that were later lost in the final velvet worm lineage. It inherited its stacked claws from a more recent common ancestor that was itself a member of the velvet worm clan. Other velvet-worm characteristics — for example, their ability to shoot slime at prey — cannot have evolved until the lineage made its way onto land some 100 million years later.

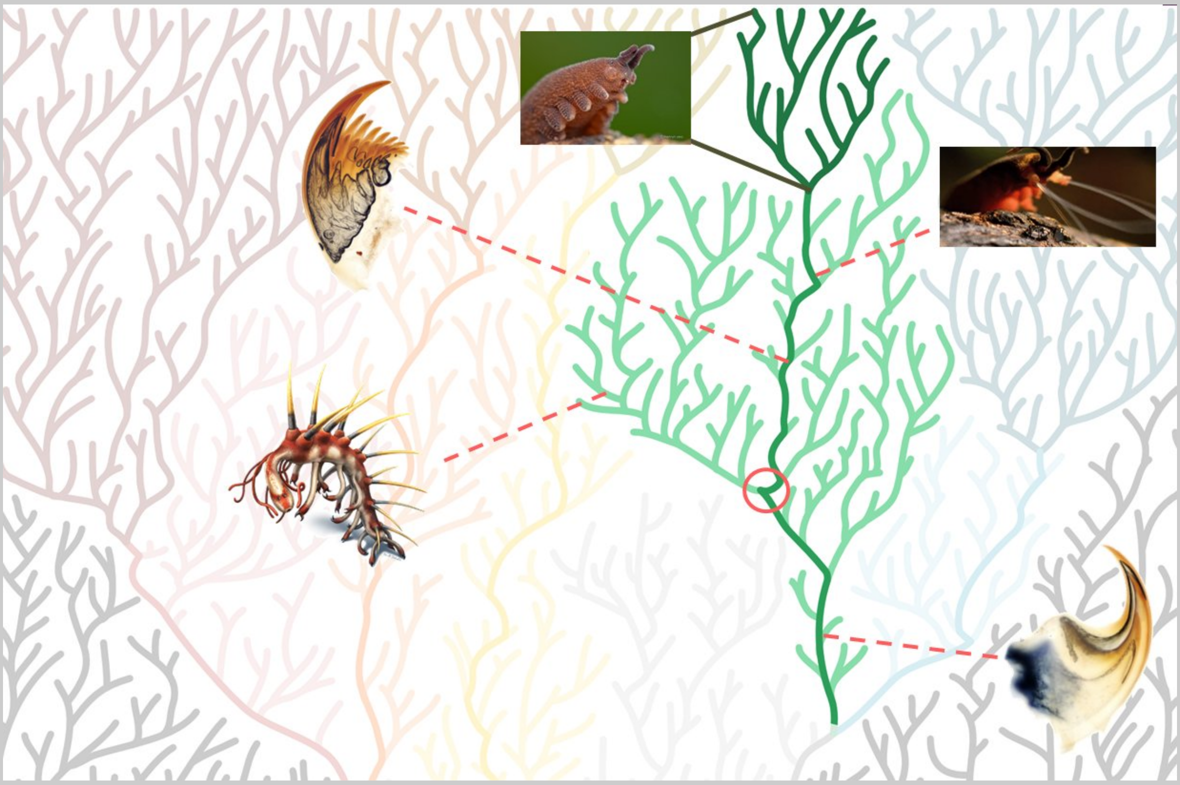

Figure 6 — Schematic tree depicting the gradual establishment of the velvet worm body plan. Stacked claws evolved before the last common ancestor of *Hallucigenia* and velvet worms (circled); toothed jaws and slime glands arose later on the lineage to modern velvet worms (dark green, top). *Hallucigenia* occupies a side-branch whose Cambrian diversity was much greater than that of the lineage leading to modern velvet worms.

Hallucigenia beautifully illustrates the gradual and piecemeal construction of the velvet-worm body plan, one component at a time. But this is not to say that it is itself a direct ancestor of velvet worms, or a 'missing link'. It is better considered as a cousin to the phylum, belonging to a tribe that has unique features of its own. One branch of this tribe must have been particularly appealing to predators, because it invested heavily in armour: the imposing arrangement of spines in *Hallucigenia*'s recently described relation *Collinsium* makes razor wire look positively cuddly. Another branch seems to have specialized in filter feeding. In this lineage, the foremost limbs — which are extremely slender in *Hallucigenia* — bear a feather-like array of bristles ideal for sweeping fine particles out of passing water currents. In fact, were a time-travelling submarine to transport you to the Cambrian sea floor, you would have little trouble spotting *Hallucigenia*'s armoured and filter-feeding relatives (Fig. 7), but may well struggle to find animals that sit close to the lineage that ultimately stood the test of time and survives today in the rotting tree trunks and leaf litter of tropical forest floors.

Figure 7 — Two relatives of *Hallucigenia*: the filter-feeding *Ovatiovermis*, and the heavily armoured *Collinsium*. Image credits: Jean-Bernard Caron/Royal Ontario Museum; Jie Yang.

Evolutionary implications

Pinning *Hallucigenia* to the tree of life makes it possible to work out the evolutionary progression that gave rise to the velvet-worm body plan. The incremental nature of this process undermines Steven Jay Gould's idea of body plans being established in the Cambrian and then remaining static. Instead, *Hallucigenia* and its kin document a gradual, step-by-step modification from the common ancestor of the moulting animals (presumed to resemble a penis worm), with the present body plan of the velvet worms not arising until substantially after the Cambrian. If body plans are evolving constructs (rather than static entities, as Gould envisaged), then it does not seem that any process beyond standard natural selection is required to account for the Cambrian explosion.

This is not to downplay the remarkable diversification that arose during the Cambrian. The diversity is emphasized by the unfamiliar appearances of *Hallucigenia* and its relatives, a variety of form that could not be predicted by looking only at the surviving velvet worms, whose species often look so similar to each other that they can only be told apart by experts with microscopes. The number of species known from the *Hallucigenia* lineage far exceeds that from the branch leading to velvet worms proper, or indeed the total number of organisms that can be linked to the vertebrates that today dominate the land and ocean. Could a Cambrian ecologist have predicted the survival of the rare and the demise of the common? Or, to borrow a phrase from Gould, if the tape of life were to be replayed, would it be *Hallucigenia* that looked normal and fish that looked like they came from another world?

Suggestions for further reading

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Nature Video: *Hallucigenia*, the worm with the missing head.

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