

“Why Do Vertebrates Have *Decussated Corticospinal Tracts*? ”

— A Comparative Study of Morphological Models

From Ancient Marine Worms to the First Fish

Inside an Aquarium

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Acknowledgements

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Many thanks also to Quanta Magazine for publishing a nicely illustrated, timely article introducing me to the “topological constraints on 3D wiring” paper¹—one that at first glance appears to be “an interesting math problem” for my upcoming STEM fair project—that started me down the decussation rabbit hole. Suffice to say, the twists and turns along the way—how this quickly morphed into an empirical study of evolutionary biology—were most unexpected!

¹ The Shinbrot and Young (2018) paper contains a number of flaws in its reasoning. In addition, the fact that our nerve fibers are *twisted*—and not *shifted laterally*—escapes mention in its superfluous “alternative crossing strategies” section. So I decided to investigate further.

Abstract

What if we could recreate evolutionary history inside an aquarium? What would that tell us about the greatest mystery in evolutionary biology: why do vertebrates have decussation in their corticospinal tracts?

The reason why our nerve tracts are decussated is buried deep in our evolutionary past. I investigated two leading theories: axial twist theory and somatic twist theory, that describe how the vertebrate body plan arose from the invertebrates 550 million years ago.

To test the two competing hypotheses, I built morphological models for empirical study within an aquarium environment. I chose the annelid as a reference model for ancient marine worms, who last shared a common ancestor with the lancelet, a closest living proxy of Pikaia. I constructed three ancient marine worm models with distinct topological configuration of the oropharynx and nerve cords inside a twistable body plan structure, alongside a Pikaia model.

I conducted buoyancy tests by dropping each model into the aquarium. The effects of body density changes underwater were noted. When the stomach goes from empty to full, I observed decussation resulting from dorsoventral inversion as predicted by somatic twist theory. However, all attempts to reproduce axial twists had failed.

My study reveals how the gullet escaped the invertebrate nerve ring, through a transitory body plan adapting to bountiful food sources, followed by a somatic twist leading to decussation. My investigation uncovers an evolutionary role for deuterostomy that leads to decussated nerve tracts in vertebrates, and opens up new pathways for future research in evolutionary biology.

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“Why Do Vertebrates Have Decussated Corticospinal Tracts?”

— A Comparative Study of Morphological Models

From Ancient Marine Worms to the First Fish

Inside an Aquarium

What if we could recreate evolutionary history inside an aquarium? What would that tell us about one of the greatest mysteries in evolutionary biology: *Why do vertebrates have decussation in their corticospinal tracts?*

The reason why our nerve tracts are decussated is buried deep in our evolutionary past. In this paper, I investigated two leading theories: axial twist theory and somatic twist theory, that describe how the vertebrate body plan arose from the invertebrates 550 million years ago.

To test competing hypotheses from recent research, I conducted a comparative study of morphological models, from ancient marine worms to the first fish, in a controlled aquarium environment underwater (see Figure 1). I endeavored to morphologically *twist* marine worms of various configurations into the first fish—with properly decussated corticospinal tracts as their stomach goes from empty to full—over evolutionary time. I then analyzed model test results to connect the dots and make inferences about the likely evolutionary pathways for how the first fish evolved, as well as to draw a number of interesting conclusions from this study.

Figure 1

Buoyancy Test of Morphological Models—From Ancient Marine Worms to the First Fish.



Research Question

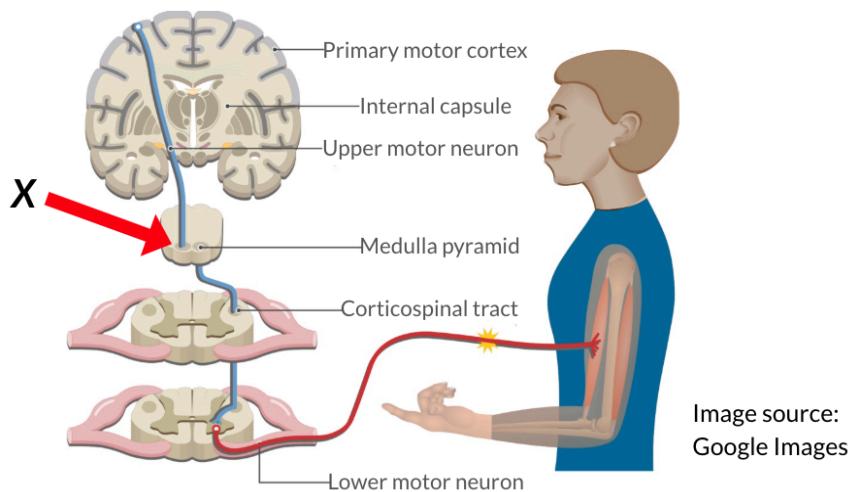
Contralateral control of the body by the brain—but why? This perennial question has puzzled many who study brain form and function. No one knows why. As it turns out, the answer is buried deep in our evolutionary past—with a hidden twist.

The corticospinal tracts connect the brain to the spinal cord. Their nerve tracts are *decussated*, or crisscrossed in the form of an X (see Figure 2). This motor pathway controls contralateral movements of the limbs and trunks: the *left* brain controls the *right* side of the body, and the *right* brain the *left* side.

All vertebrates have decussation in their corticospinal tracts. Again, no one knows why. But we can easily observe the effect of such a contralateral arrangement in a stroke patient. For example, a blockage in the left brain of the stroke patient invariably results in weakness (or immobilization) in the right side of her body. The stroke patient would thus need to use a walking stick to assist with her weakened right leg during recovery. Due to attenuated signals along the nerve tracts from the left brain to the right hand, a right-handed stroke patient's hand writings would also become noticeably smaller—but would return to normal handwriting upon recovery.

Figure 2

X Marks the Spot Where the Brain's Connections to the Body are Crisscrossed—but Why?



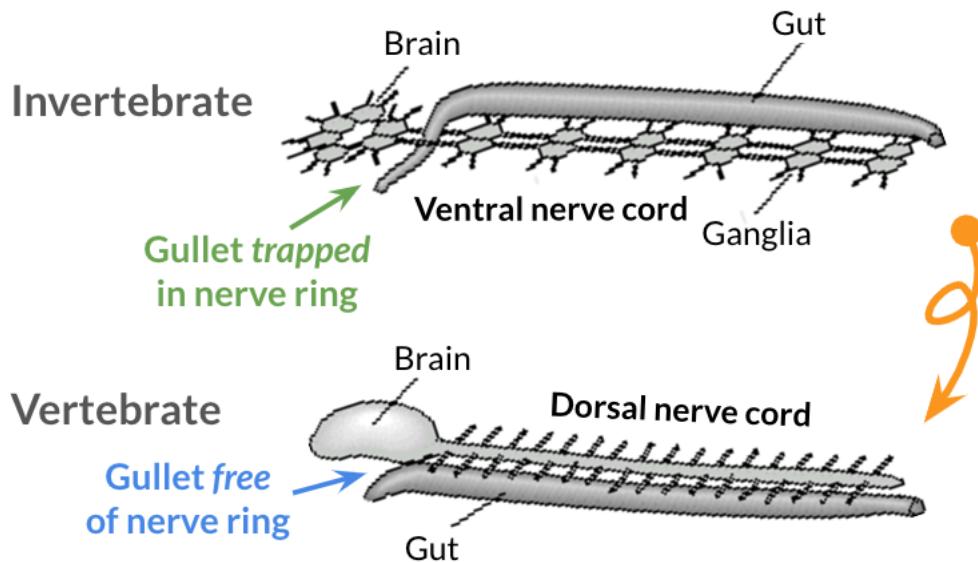
Background

Dorsoventral Inversion

A French zoologist, Geoffroy St. Hilaire, dissected a crayfish in 1822 and came up with the idea of dorsoventral inversion when comparing it with the vertebrate body plan (St. Hilaire, 1822). He noted that the ventral half of arthropods, which are invertebrates, is *homologous* with the dorsal half of vertebrates (see Figure 3). In other words, when the crayfish is turned upside down, its nerve cord is now above the digestive tract, which in turn is above the heart, as they are in chordates and vertebrates. St. Hilaire's hypothesis is "an idea considered bizarre little more than a decade ago is now both widely accepted and a fruitful source of insights into past evolutionary events." (Lacalli, 2010).

Figure 3

Dorsoventral Inversion: Evolution of the Vertebrate Body Plan—With a Twist.



Note. One can see that dorsoventral inversion does not fully explain how decussation arose because the anterior ends have not been accounted for (e.g., how did the gullet escape the nerve ring?). Image credit: Bownds (1999).

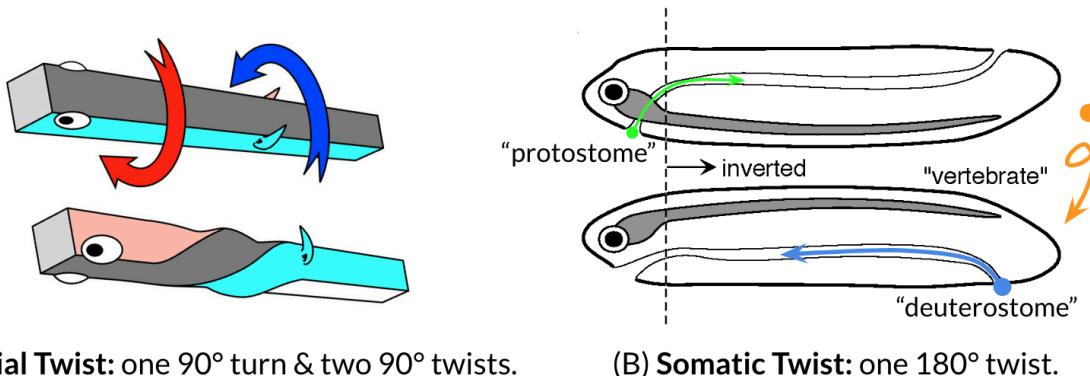
Competing Twist Theories

Two leading theories from recent research: Axial Twist Theory by de Lussanet and Osse (2012, 2015) and Somatic Twist Theory by Kinsbourne (2013) attempt to explain corticospinal tracts decussation from a dorsoventral inversion viewpoint. As illustrated in Figure 2, an axial twist requires the whole organism to turn 90 degrees to one side followed by two separate 90-degree twists of head and body in opposite directions; whereas a somatic twist entails just one 180-degree body twist. Each offers a different explanation for how decussation occurred.

Both of these twist theories have testable hypotheses for how decussation occurs—as a by-product (or “spandrel”) of dorsoventral inversion—prior to evolving into a fish. However, neither theory pinpoints a particular organism upon which their hypotheses can be empirically tested.² This ambiguity needs to be resolved in order to establish the scope of my empirical study (e.g., what animal models to build).

Figure 4

Competing Theories Try to Explain Decussation From an Evolutionary Biology Perspective.



Note. Image credit: axial twist image source from de Lussanet (2019); and somatic twist image source from de Lussanet and Osse (2015).

² de Lussanet and Osse (2012, 2015) and de Lussanet (2019) assume a fish (or fish-like organism) that is undergoing axial twist; but Kinsbourne (2013) considers somatic twist for a worm undergoing invertebrate to vertebrate transition (i.e., “The smallest worm will turn.” and “The worm did turn. It turned on itself.”).

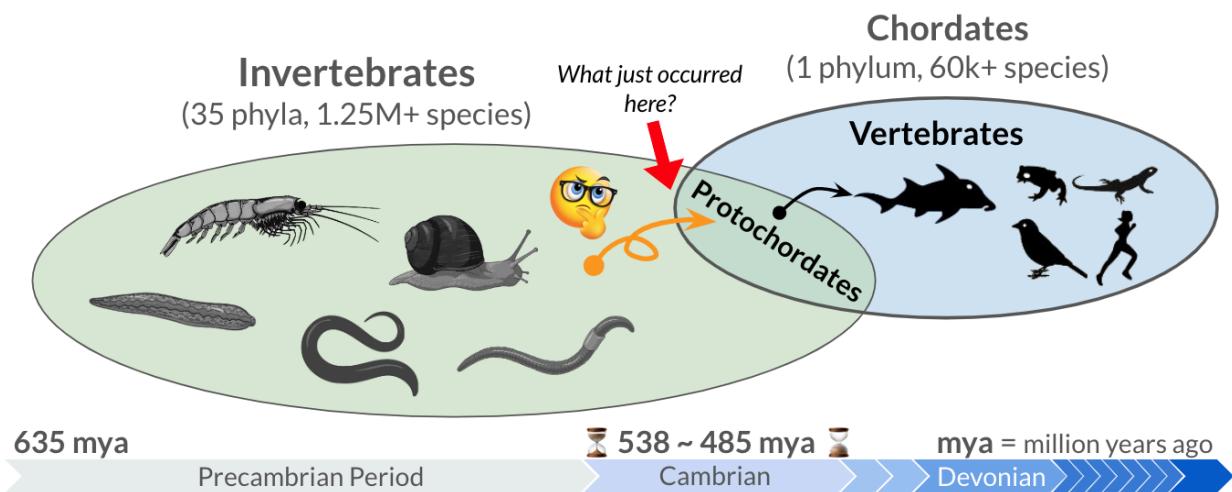
Role of Protochordates

One must, therefore, first estimate the evolutionary time frame during which a body plan twist was thought to occur so that accurate morphological models can be properly constructed.³ But where do we start?

Evolutionary biology offers a clue. We know that all vertebrates, more generally chordates, have decussation. There are over 60,000 species with decussation today. However, no such contralateral decussation arrangement can be found in any of the other 35 invertebrate phyla. They represent over 1.25 million species. From a statistical viewpoint, the intersection of chordates and invertebrates is where we should focus our attention (see Figure 5). So what just occurred here, around 550 million years ago, in the intersection of invertebrates and chordates that are the protochordates?

Figure 5

Something Interesting Happened Here When Invertebrates Evolved Into Protochordates.



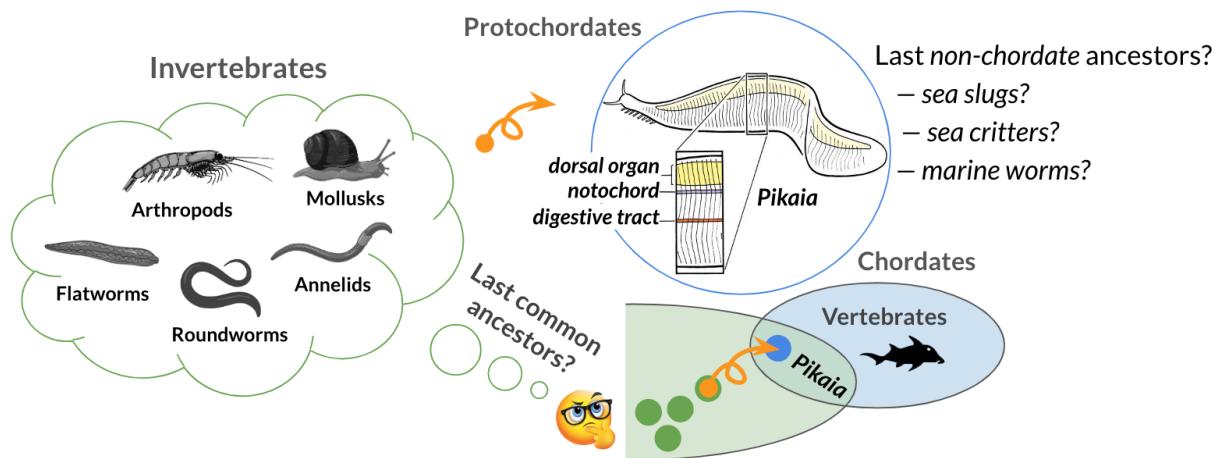
³ The invertebrate to vertebrate transition was thought to occur in the Cambrian Period, which comes before the Devonian Period ("The Age of Fish"). Contrary to suggestions by de Lussanet and Osse (2015), the axial and somatic twist theories are fundamentally incompatible and cannot be reconciled. In other words, both cannot be true at the same time.

Scope of Study

The overall body plan of vertebrates arose from the invertebrates around 550 million years ago. All vertebrates, more generally chordates, have decussation. However, no such contralateral decussation arrangement can be found in any of the other invertebrate phyla outside of the protochordates. I am curious about what occurred in the transition from invertebrates to protochordates (see Figure 6). So I decided to explore both axial twist theory and somatic twist theory in the context of ancient marine worms and the first fish—*Pikaia*.⁴

Figure 6

Exploring Twist Theories for Ancient Marine Worms as They Evolve Into a Protochordate.



Note. *Pikaia* image credit: Lacalli (2012).

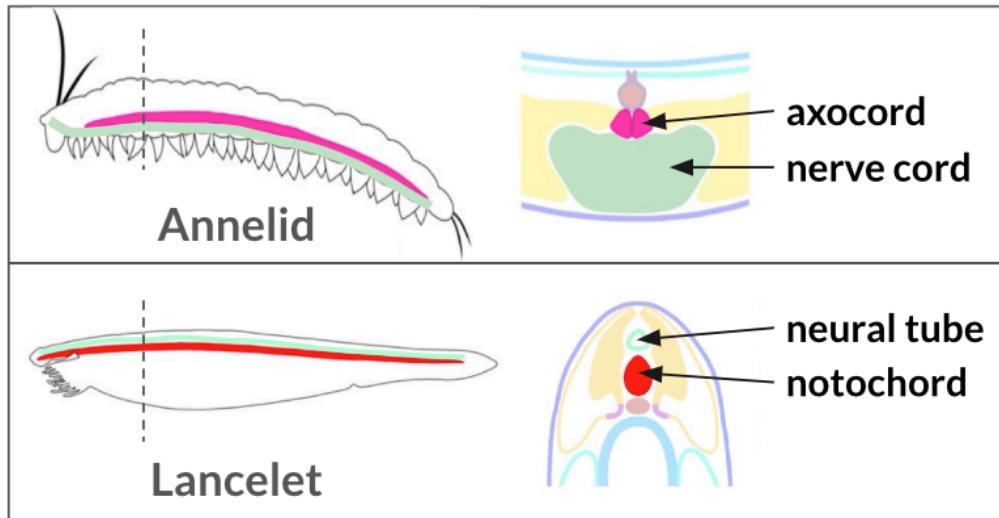
⁴ Trying to pin down the last non-chordate ancestors, e.g., sea slugs, sea critters, or marine worms, of *Pikaia* is beyond the scope of this paper. My study does not require it because they all share the same invertebrate body plan. The established facts are sufficient for the purpose of model building.

Models, Materials and Methods

Morphological Models: A Comparative Study

Figure 7

Annelid and Lancelet: Reference Models and Their Body Plan Specifications.



Note. See how the two body plans are dorsoventrally inverted? Image credit: Sui et al. (2021).

I chose the annelid as my reference model for ancient marine worms, who last shared a common ancestor with the lancelet, a protostome and the closest living proxy of Pikaia. Figure 7 illustrates the body plans of my chosen reference models: the annelid and the lancelet; which specify the morphological design of twistable body plan structures I shall construct next.

Model Construction: Submersible, Twistable Body Plan Structures

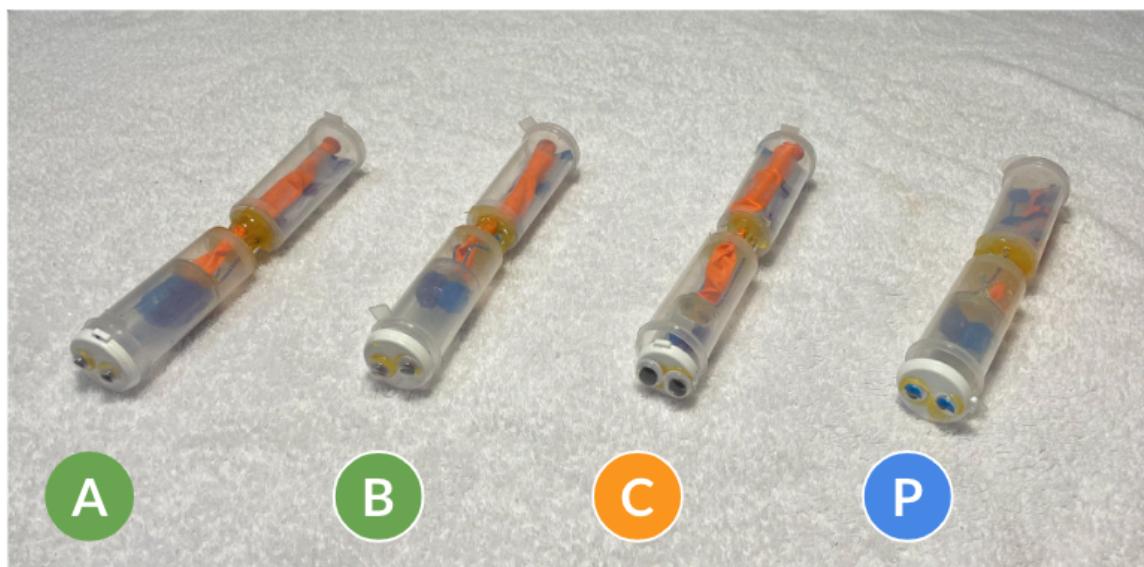
Using the materials and tools gathered as shown in Figure 8, I glued together plastic tubes and vials to make submersible, twistable body plan structures. I made 3 models of marine worms: **A**, **B**, and **C**, one for each topological configuration of oropharynx and nerve cords. Models **A** and **B** follow an invertebrate body plan, but model **C** follows an intermediate *transitory* body plan. I also made model **P** for Pikaia, following a vertebrate body plan (see Figure 9).

Figure 8

Materials and Tools for Building Twistable Body Plan Structures for Use Inside an Aquarium.

**Figure 9**

Twistable Body Plan Structures: 3 Ancient Marine Worm Models and 1 Model of Pikaia.

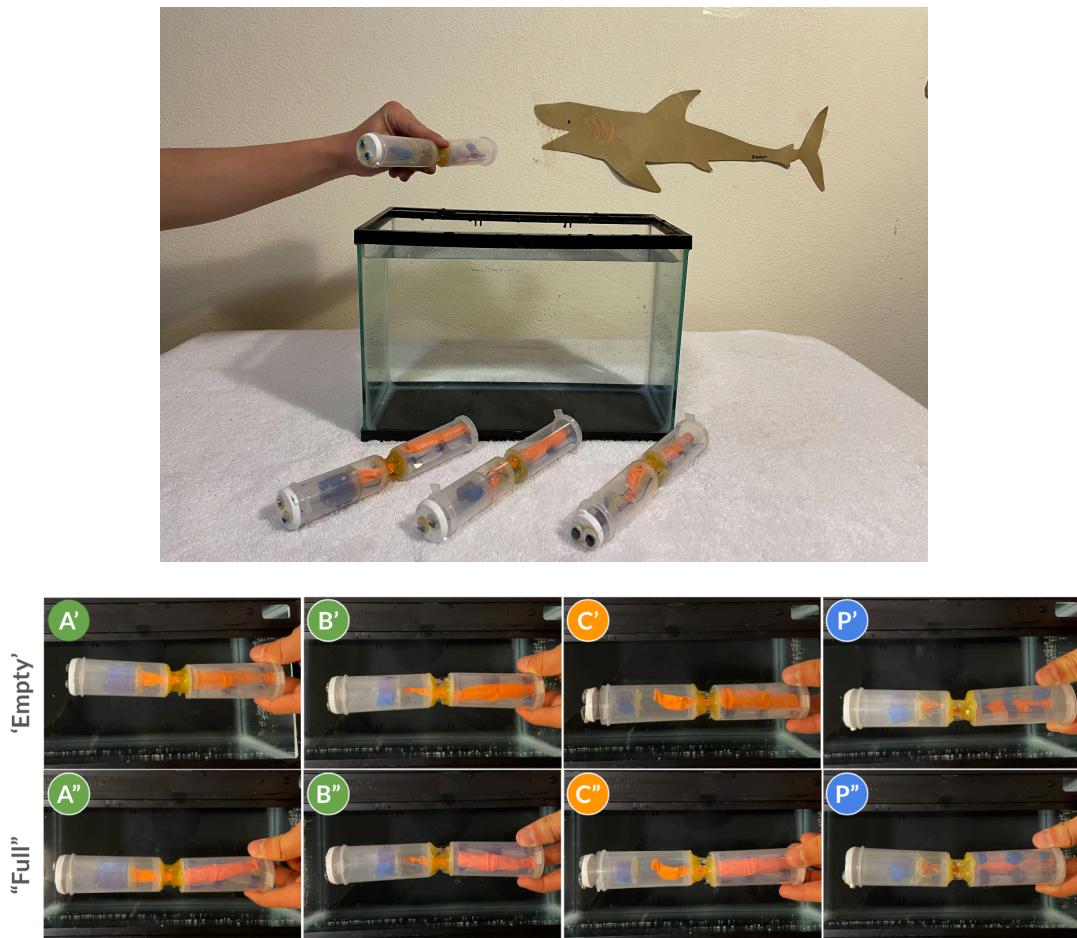


Model Testing: Conducting Buoyancy Tests Inside an Aquarium

Next, I conducted a series of buoyancy tests by dropping each model into a water-filled aquarium, alternately with their stomachs empty or full (see Figure 10). I noted the effects of body density changes underwater as the stomach goes from empty to full. That's how I plan to reproduce dorsoventral inversion empirically for ancient marine worm models. I observed decussation as predicted by somatic twist theory. However, similar attempts to reproduce axial twists had not been successful, using only simple models with a parsimonious aquarium setup.

Figure 10

Running Buoyancy Tests on 4 Models: A, B, C, and P, for When the Stomach is Empty or Full.

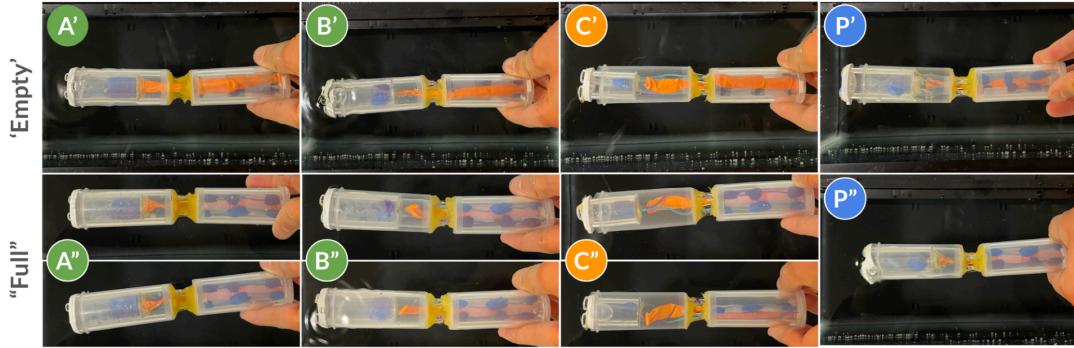


Note. These photos above were taken right above the aquarium—before dropping the models.

Results and Analysis

Figure 11

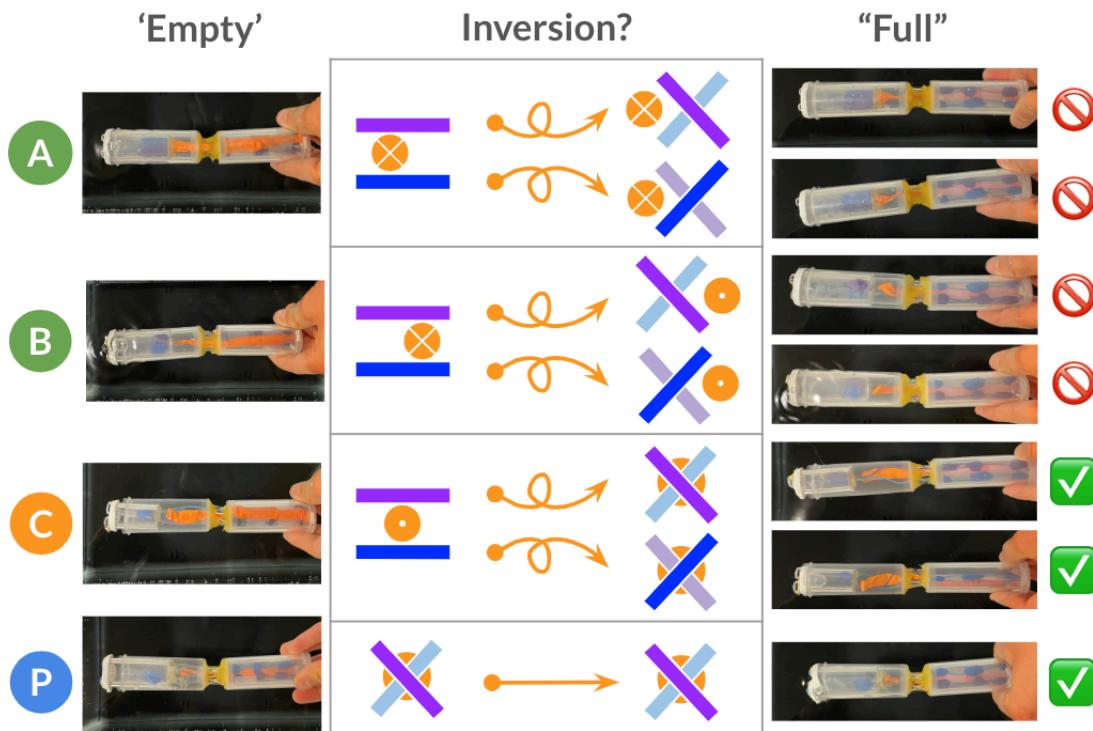
Results of Running Trials for 8 Test Cases on 4 Models to Generate 11 Outcomes for Analysis.



Note. These photos were taken with the models submerged in the aquarium while underwater.

Figure 12

Visual Summary of What Happens Underwater When the Stomach Goes from Empty to Full.



*Note. On a full stomach, only model **C** and model **P** yield a valid decussation topology.*

Discussion

What Happens When Food Sources Become Bountiful?

Here we shall study the outcomes previously described in Figure 12 to determine which of the 4 models: **A**, **B**, **C**, or **P** now look promising from an evolutionary viewpoint:

- ❖ Model **A** suffers from a decussation that tangles up the gullet when the belly is full. So this marine worm couldn't eat much—even in times of plenty—on pain of extinction!
- ❖ Model **B** results in an unusual body plan. The mouth rotates to the back—like a sea squirt—an evolutionary dead end for bottom feeders as the gullet is also choked by decussation.
- ❖ Model **C** has an initially surprising transitory body plan. The gullet develops at the dorsal side—outside of the nerve ring. This is rather unusual. So dorsoventral inversion rotates the mouth back to its ventral side while the gullet remains free from decussation. This adaptation allows for feasting during bountiful times. I believe this is how ancient marine worms evolved to become the first fish.
- ❖ Model **P** is the one with a stable body plan. Excess fat stored inside a dorsal organ keeps the body on an even keel when food becomes scarce. The gullet steers clear of decussation and avoids getting tangled up. I believe this is how the first fish managed to keep its newly evolved body plan, while continuing to evolve to become a real fish.

In summary, model **C** and model **P** are both viable from an evolutionary standpoint, but models **A** and **B** are evolutionary dead ends. I wonder if there may be a hidden path that leads from **A** and **B** to **P** so as to avoid getting trapped permanently in evolutionary dead ends?

Why are All Chordates—and Vertebrates—Deuterostomes?

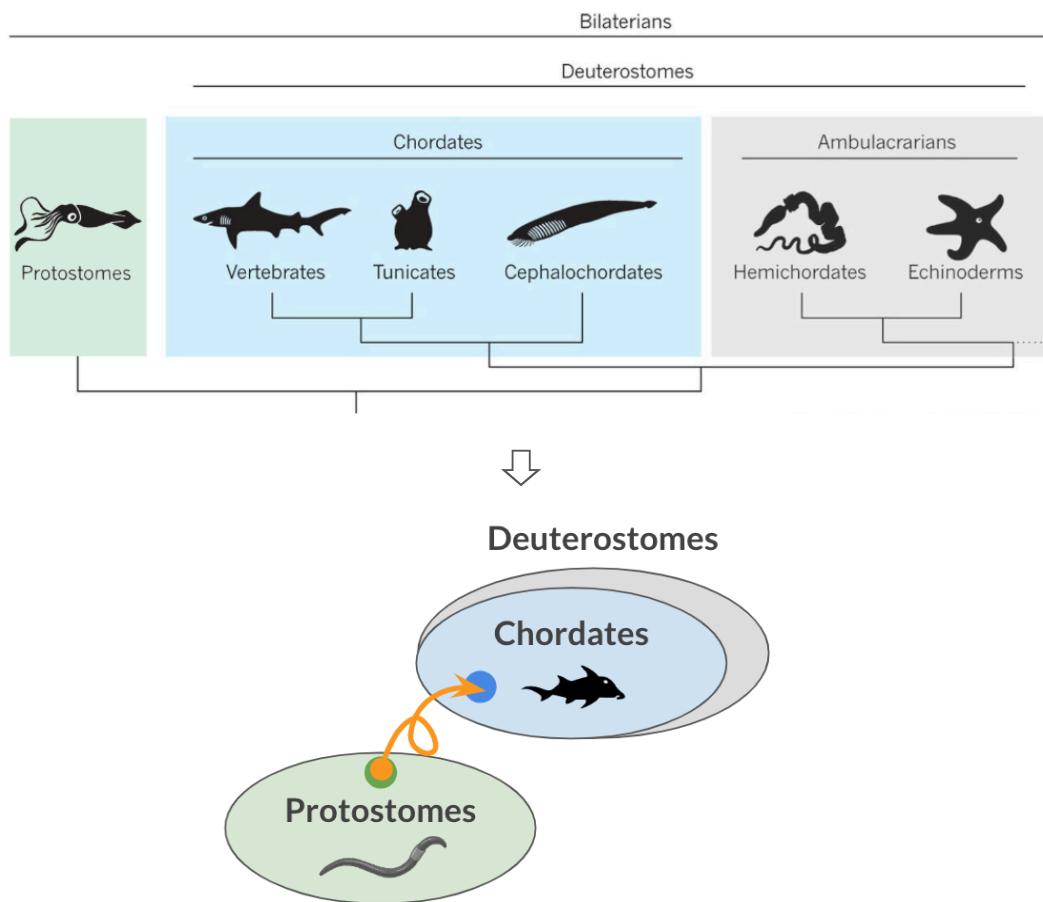
Invertebrates are protostomes (“*mouth first*”), the mouth develops first. Chordates, however, are deuterostomes (“*mouth second*”), as the mouth develops last, after the anus.

But not all deuterostomes are chordates. As one can see in Figure 13, the ambulacrarians (e.g., hemichordates like the acorn worm or echinoderms like the starfish) are deuterostomes that are not chordates. Why is that? What can developmental biology tell us about the early chordates?

I think that means deuterostomy must be a *necessary* but not *sufficient* condition for the evolution of some salient phylogenetic feature that characterizes the chordates. Looking at the Venn diagram, for example, one can safely conclude that deuterostomy is *necessary*—but ultimately not *sufficient*—for deccussation.

Figure 13

How to Construct a Deuterostomes Venn Diagram From the Phylogeny Tree.



Note. Deuterostome phylogeny image source based on Lowe et al. (2015).

How Did the Gullet Manage to Escape the Nerve Ring?

We have just now established that deuterostomy evolved as a *necessary* adaptation to prevent the gullet from developing *early*—starting near the mouth—and then running straight into the nerve ring of an embryo. So the gullet develops *later*—from the other direction—staying far away from decussated nerve tracts. The difference in embryonic development pathways between protostomes (green color) and deuterostomes (blue color) are highlighted in Figure 14.

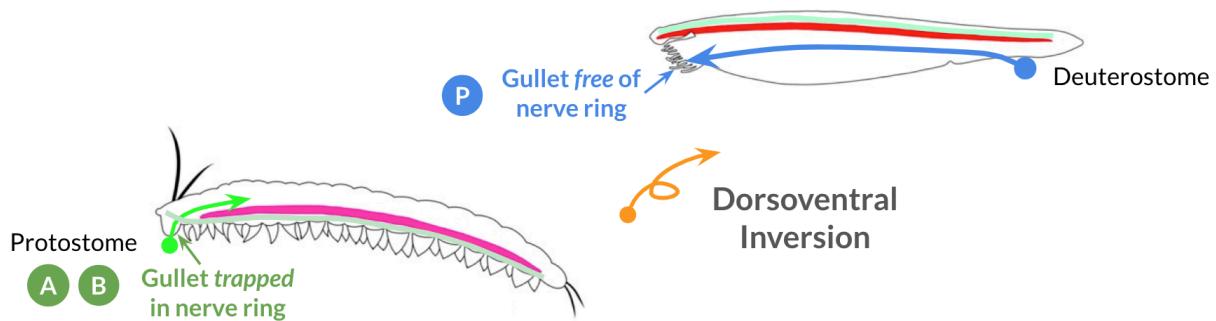
Deuterostomy is how I imagine the gullet can escape from the nerve ring of ancient marine worms, just one body twist away from evolving into the first fish. The transitory body plan of model **C** can thus be obtained by working backwards from the stable body plan of model **P**.

However, an intermediate transitory body plan, like that of model **C** on an empty stomach, is not likely to be found in fossil records due to its transitory nature. A hungry ancient marine worm is not likely to survive for very long on an evolutionary time scale. It would therefore be futile to search for a transitory body plan in the fossil records.

A disentangled gullet foreshadowed the Devonian Period (“*The Age of Fish*”), as jaws and backbones evolved to become the dominant body plan for fishes small and big.

Figure 14

Ancient Marine Worms Evolved Deuterostomy so the Gullet can Finally Escape the Nerve Ring.



Note. Image credit: Sui et al. (2021).

Conclusions

Since the pharyngeal structures of lancelets are asymmetrical to one side, the **C** to **P** inversion as shown in Figure 15 most likely reflects how the lancelet mouth develops—on the left side. I now have all the evolutionary puzzle pieces I need to adequately explain decussation.

I shall now connect the dots to infer the evolutionary pathway for how the Pikaia evolved, driven by bountiful food sources for ancient marine worms in times of plenty, over many, many generations while scraping the bottom of the seabed. Figure 16 describes this new evolutionary pathway: from body plans **A** and **B** to **P** via **C**, adding a key puzzle piece to prior twist theories.

In conclusion, my study reveals a salient aspect missing from previous research in twist theories: *how the gullet escaped the invertebrate nerve ring* (i.e., via a transitory body plan that adapts to bountiful food sources). That's what made an underwater somatic twist possible 550 million years ago and results in a decussation in the corticospinal tracts for all vertebrates today!

Figure 15

A Transitory Body Plan C — Where the Gullet Finally Becomes Free of the Nerve Ring.

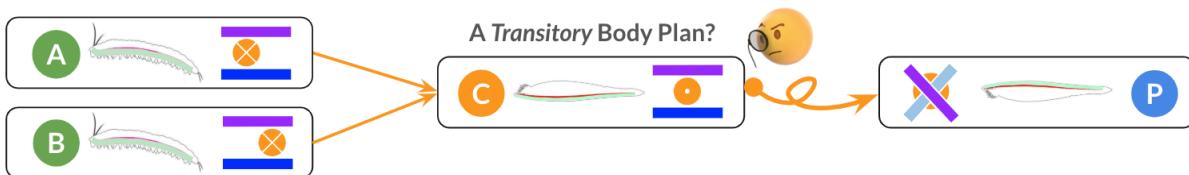
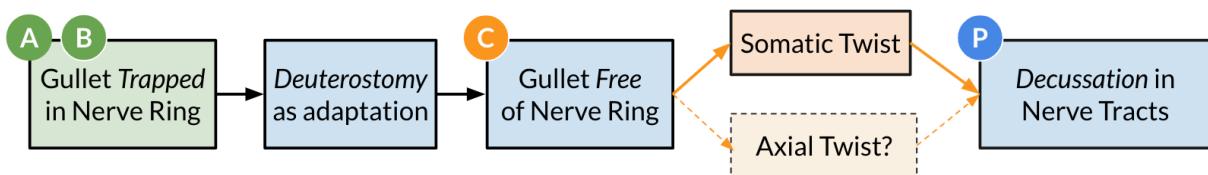


Figure 16

An Evolutionary Pathway for Pikaia: Deuterostomy to Somatic Twist via Transitory Body Plan C.



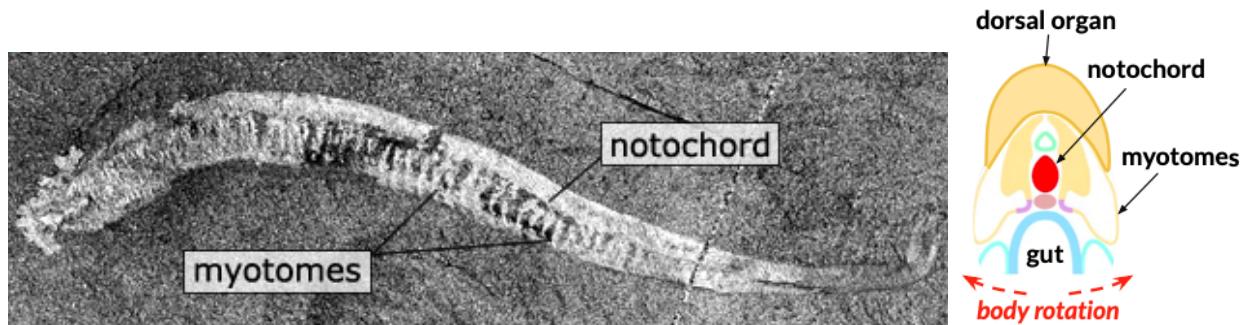
Future Directions

What does dorsoventral inversion have to do with early chordate swimming? I am curious if a ventral position for the gut—along with Pikaia's buoyant dorsal organ—gave the first fish an early advantage in swimming. That would explain why this body plan became popular among fishes, and then inherited by the vertebrates.

To do that I will first have to learn how to build Pikaia models that can swim. A Pikaia swims like an eel, using its myotomes or muscle segments for underwater propulsion, and its flexible notochord to resist body contraction. I conjecture that early chordate swimming allows the Pikaia to more easily rotate its body around the axis of the notochord, as illustrated in Figure 17, to better avoid ocean floor obstacles when trying to escape the sea scorpion!

Figure 17

The Pikaia Fossil has a Visible Notochord That May Hold the Key to Early Chordate Swimming.



Note. Pikaia photo credit: Chip Clark © Museum of Natural History, Smithsonian Institution.

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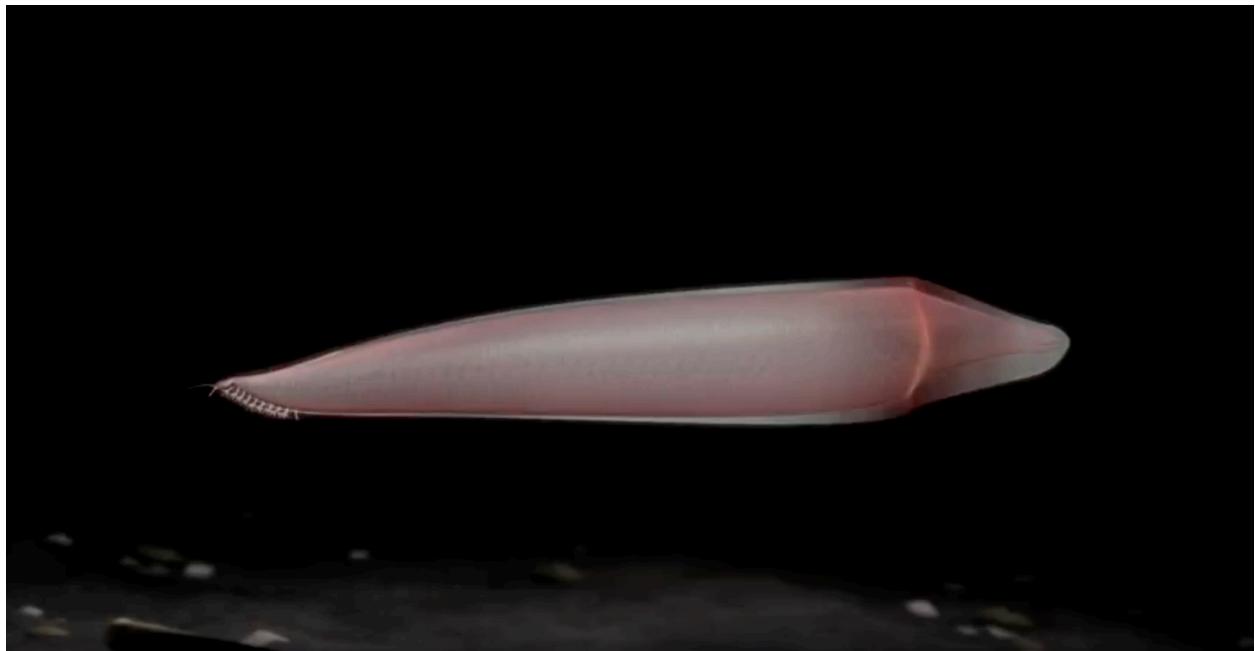
Appendix

3D Model of *Pikaia Gracilens*

Figure 18 presents a 3D reconstruction of *Pikaia* as a free-swimming deposit feeder above the seabed, as suggested by its eel-like morphology and musculature, and presence of mud in its gut in the fossil record.

Figure 18

A 3D Reconstruction of Pikaia Above the Seabed.



Note. Photo credit: animation by Phlesch Bubble © Royal Ontario Museum.