

From a fossil to a robot and all the steps in between
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Being almost 300 million years old, the extinct *Orobates pabsti* did not know that at some point in the future, engineers and biologists will reconstruct its fossilized bones into a robot to study how it used to walk and thus, learn more things about their own evolution. The only evidence of *Orobates*' walk, beyond its nicely preserved bone structure, was a set of also fossilized footprints left on an ancient muddy ground. These were indeed key pieces that enabled the scientists to reproduce many possible gaits with the robot, and to test their validity as *Orobates* plausible motions.

Orobates is a great candidate for understanding how land vertebrates (like us) evolved, because it represents the lineage leading to modern amniotes. That is, animals that became largely independent from water, as they were the first to develop within eggs laid on land. *Orobates* is a vertebrate that is interposed in the evolutionary tree between amphibians on one hand, and reptiles, birds and mammals on the other. Thus, the ability of these animals to effectively locomote on land (or not) seemed crucial to be studied. The scientists believed that knowing more about the locomotion of *Orobates*, will help us to also understand better at which point in time the land was colonized by animals.

Reproducing the locomotion of a fossil is a challenge, because the limited biomechanical information preserved. In order to make our study quantifiably objective, we looked at modern species that share a similar morphology with *Orobates*. We analyzed the locomotion of an iguana, a salamander, a skink and a caiman. All these animals displayed different size, mass, speed and certainly, subtle differences in the way they move. We noticed that there are three fundamental parameters that can capture the sprawling locomotion of these animals and most likely, the one of *Orobates*. We identified the posture height, this is how close the body is to the ground. The spine motion, that can vary from very stiff, almost keeping the spine straight, to a very curvy one that bends the spine sideways at every step. And finally, the amount of long axis rotation on each limb, which is a ratio of how much the shoulder or the elbow need to rotate in order to swing the leg forward. These principles create a space in which many gait solutions can be placed.

After setting up our playground, we reconstructed the *Orobates* skeleton in a kinematic animation, in which we could test if the bones collide, or otherwise, if the joints are dismembered due to exaggerated implausible postures. This kinematic simulation proved very helpful in narrowing down the possible gait solutions but also insufficient for testing their behavior under real world physics. We then created a robotic model that helped us to test our hypotheses about the animal's locomotion dynamics. Using the robot (a correctly scaled version of the skeleton, sporting the proper mass distribution, and moving at the most likely speed), we evaluated each one of the gaits under four different criteria with both biological and engineering significance. We scored the results of each potential gait according to: how much mechanical power the robot expended, how much tilting was present in the body as it walked, how similar the limb forces were to a pattern extracted from the studied extant species, and finally, how precisely the robot's foot placements matched the fossil footprints.

We then set some filters (which can be interactively manipulated in <https://go.epfl.ch/orobates>) and excluded the lowest ranked solutions after applying the metrics. By combining these exclusion results with those of the kinematic simulation for bone collisions, we end up with a very small set of the most plausible solutions for *Orobates*. Placing the data of the modern animals in the same space, we discovered that the caiman data was close to the results obtained for the fossil. We inferred that *Orobates* had terrestrial locomotion that was "advanced" in comparison to the earliest four-limbed vertebrates in terms of the metrics studied. We mean advanced in evolutionary terms, in particular

more upright, balanced and mechanically power-saving than low sprawling gaits exhibited by earlier tetrapods.

Other researchers previously assumed that the advanced locomotion that we inferred for *Orobates* only arose after the origin of the amniotes, since we now inferred it for a stem amniote, we may say that advanced locomotion evolved earlier than has been previously thought. With these results, we hope that our approach will stimulate similar research into other major transitions of vertebrate evolution.

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