Frequently Asked Questions

Reverse-engineering the locomotion of a stem amniote

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Why was a robot useful for this study?

Our robotic model allowed us to test our hypotheses about the animal's locomotion dynamics, otherwise elusive to explore in an extinct animal. It factors in the real-world physics of its walk. Using a robotics approach (with the real and simulated robots) is useful to generate different gaits and quantify aspects that determine the likelihood of *Orobates* gaits, such as the mechanical power expenditure, the ability to walk without excessive tilting, the similarity of limb forces to the studied extant species, and the precision of matching the fossil trackway.

Why is *Orobates* important?

Being almost 300 million years old, the extinct *Orobates* is a key candidate for understanding how land vertebrates evolved because it represents the lineage leading to modern amniotes – that is, animals that became largely independent from water, as they developed within eggs laid on land. *Orobates* is a vertebrate that is interposed in the evolutionary tree between amphibians on one hand and reptiles and mammals on the other. What's more, *Orobates* is the oldest-known vertebrate for which scientists have associated the fossil and its fossilized footprints. Last but not least it is a beautifully preserved complete and articulated fossil specimen.

Why do you use the term reverse engineering?

We used this analogy quite loosely. Similarly to proper reverse engineering approaches and inspired by Richard Feynman's famous quote "What I cannot create, I do not understand", we started from the final 'product', that is the fossil. We then used a suite of analysis tools to better understand the structure of the fossil, simulated the functioning of the integral parts, and finally re-created the fossil as a physical model using engineering techniques.

Who Funded the project?

The project received funding from: the Volkswagen Foundation (AZ 90222), the Daimler and Benz Foundation (32-08/12), the German Research Council (DFG EXC 1027), the Swiss National Science Foundation through the NCCR Robotics (National Centre of Competence in Research, Robotics) and the UK Natural Environment Research Council (NE/K004751/1).

Where was *Orobates* found?

Orobates has been recovered from a locality in central Germany, the Bromacker quarry near Tambach-Dietharz, by an international team of paleontologists during field seasons that have been conducted yearly. It was transferred to the Carnegie Museum of Natural History in Pittsburgh, USA, and was prepared by the skilled and experienced preparator Amy Henrici. The type specimen was scientifically described in 2004 by David Berman (curator at the Carnegie Museum) and colleagues. The Bromacker quarry has produced several well preserved specimens and is famous in the community for the excellent preservation and the fact that also fossil trackways have been recovered from the same site.

Where could this method or research be taken in the future?

Our model, robot and simulations lacked actual muscles or other soft tissues, focusing more on the general motions and forces and torques of limbs and joints, but it would be fascinating to look into how muscles drive motions in *Orobates* or other extinct animals with this approach. One could apply these methods to other fossils with somewhat less confidence if they had less marvellous preservation. Or one could be creative and find ways to improve these methods: add new data on living (or even extra fossil) species to help "bracket" what the extinct animal might have done or not done, or include data on physiology or something else to help constrain the simulations and robot further. Comparable preservation (e.g. ideal matches of fossil organism and trackways) would still be a third option but maybe less likely.

What were some of the considerations that came into play as you reconstructed the way this animal walked?

We first studied the locomotion of extant species in great detail to get a better understanding of the mechanical principles of sprawling tetrapod locomotion. Those patterns that were consistent across a diverse sample of modern animals like salamanders, lizards and crocs were assumed to have also applied to the fossil. In our subsequent simulation studies we then tested a huge space of different locomotor parameter combinations and evaluated each gait for its anatomical plausibility (using an animated 3D digital Orobates), dynamic properties like energy consumption and joint torques, and also stability and precision. Each of these "filters" can be applied to the potential gaits to narrow down the plausible solutions. We also provided an interactive website alongside our paper that allows everybody to explore the solution gaits (and implausible gaits) and give different weights to the filters. Everybody is invited to check it out: https://go.epfl.ch/Orobates

What was the most surprising finding in this work?

When studying the biomechanics of a diverse sample that included salamanders, skinks, iguanas, and caimans, in other words animals that differ substantially in regard of their anatomy and ecology, we found surprisingly similar forces that are produced by the forelimbs. The identification of what appears to be a general principle of sprawling locomotion allowed us to assume this similarity also for the fossil when simulating *Orobates*. We created a visual framework (our sprawling gait space plots) that allows to plot highly diverse sprawling gaits and to detect similarities at a glance.

What made *Orobates* such a good candidate for this kind of analysis?

First of all, Orobates is one of the best preserved early Permian tetrapod fossils. It is nearly complete and articulated. Moreover, from the same site also fossil trackways have been recovered, some of which were assigned to Orobates as the trackmaker - using a correlation between the relative and absolute lengths of the digits of the body fossil and the imprints of the hands and feet. This constitutes a very rare track-trackmaker association, especially considering the age of the fossils. Last but not least, Orobates can be considered a key fossil for the understanding of vertebrate evolution since it is a very close cousin the last common ancestor of mammals, reptiles (including e.g. all extinct dinosaurs and pterosaurs) and birds.

What is new compared to other projects involving simulations or robots?

In our study, we have combined several approaches (analysis of trackways, anatomically precise simulation of joint movements, dynamic simulation and robotics) that individually all have merits, but also limitations. Due to our integrative approach we were able to minimize the limitations of the individual approaches.

What is a stem amniote?

Stem amniotes represent the transition from an amphibious lifestyle with aquatic larvae (e.g., the tadpoles of frogs) to land-living vertebrates that lay eggs on dry land and hatchlings that can live on land right away. Some authors therefore coined that amniotes completed the transition of vertebrates to land.

What does the term ‘stem’ mean?

In evolutionary terms a group of animals that evolved from one common ancestor can be divided into the ‘stem’ and the ‘crown’. The stem consists of all extinct members of the group that are part of the lineage before the first split-off of a line that leads to an extant member of the group. This split-off is defined as the crown-group node and all descendants of the crown-group node are referred to as the crown group. Please note that also the crown-group can include extinct taxa. In our case, *Orobates* is a stem amniote, but extinct dinosaurs and all extant reptiles, birds, and mammals are crown amniotes. In other words, *Orobates* is a close cousin to all amniotes.

What does the term "advanced locomotion" in the context of the study mean?

We mean more advanced in evolutionary terms, in particular more upright, balanced and mechanically power-saving than low sprawling gaits exhibited by older tetrapods (see also the previous question).

What do the terms amniote and anamniote mean?

Amniotes are land-living vertebrates that completed the transition to land by evolving amniotic (triple-layered) eggs. These eggs allowed the avoidance of aquatic larvae (such as the tadpoles of frogs) and hatchlings were prepared to live a terrestrial life right from the start. The origin of amniotes triggered a rapid evolutionary radiation and gave rise to the lineages leading to reptiles (including all extinct dinosaurs and later birds) on the one hand and mammals on the other. Anamniote tetrapods (four-limbed vertebrates) are all tetrapods that are not amniotes. These are the extant amphibians and several extinct groups. Within tetrapods (four-limbed tetrapods) thus two major lineages exist, the amphibians and the amniotes, with the amniotes being the distinctly more species-rich clade of the two (both past and present).

What did you learn that you didn't know before?

We inferred that *Orobates* had terrestrial locomotion that was advanced in comparison to the earliest four-limbed vertebrates in terms of energy efficiency, stability, and more erect gaits. Such locomotion was previously thought to have arisen only after the origin of the amniotes, so we conclude that advanced locomotion evolved earlier than has been thought.

What are the dimensions of the OroBot?

The robot is 142.23 cm long, and weights 6.2 Kg. It is 60% bigger than the fossil.
The fossil is 85.14 cm long

Were you surprised at the result that *Orobates* had a more "advanced" locomotion?

Actually, not really. This has been speculated based on the anatomy of the fossil and the trackways in previous publications. We here provided a quantitative analysis and a methodology to "open up the black-box of inference". We hope that our approach will be stimulating similar research into other major transitions of vertebrate evolution. 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 anmiote, we conclude that advanced locomotion evolved earlier than has been thought.

How was it possible to link the fossil trackways to the body fossil of *Orobates*?

The trackways have not been produced by the same individual that has been preserved as a body fossil. However, the excellent preservation of both the trackways and the body fossil allowed for correlating the lengths of each digit (fingers and toes; work done by previous researchers). It is currently accepted as the oldest known track-trackmaker association among vertebrates.

How useful is this work to other fields?

We hope that our example of 'robotic paleontology' will be picked up by other researchers to address their own research questions for any other major transition in vertebrate evolution (e.g., the origin of active flight in birds, the bipedal walk of human ancestors, etc.), or motions of unusual individual fossil organisms. We think that our approach deals with uncertainty in such reconstructions in a very innovative and transparent way and hope that it will inspire similar research. Moreover, we believe that or work demonstrates the merits of multi-disciplinary approaches and even strengthens the potential of design disciplines (here computer-generated imagery) in teaming up with scientists to create new research tools (here our interactive simulation of *Orobates*).

How long did the project take and who was involved?

This was a highly collaborative work that involved a dozen researchers ranging from biology, paleontology and computer generated imagery to robotics. Whereas the idea of reconstructing the locomotion of the fossil is from eight years ago, an integral part of the project - that is, the use of a robotic tool to make it possible, the data gathering and their analysis - started only four years ago. However, the comparative analysis of modern animals, the initial 3D reconstruction of the type specimen of *Orobates*, and the animation of the digital version of the skeleton was the focus of the early work in the project.

How expensive is the robot?

The robot materials and fabrication costs were around €20.000.

How did you validate your simulations?

To validate our simulations and our metrics, we used the same methodology to (correctly) “predict” the locomotion style of caimans and salamanders simply from their physical anatomy, trackway features and our dynamic metrics (i.e. as if they were fossilized animals). In particular our approach was capable of predicting the very sprawling gaits of salamanders, and the erect gaits of caiman.

Have there been similar robotic or simulation studies of fossils before? Can you give some examples?

Yes, similar studies into what can be coined ‘paleo-biorobotics’ have been published before our own work and we are building on these works and were inspired by them. These previous studies used either only computer models, only built physical models, or integrated both like we did. For example McInroe et al. published a fantastic study in 2016 that combined diverse analyses in inter-disciplinary fashion similar to our new paper. They combined biomechanical analyses of modern animals, mathematical modelling, measurements of drag on granular media, and bioinspired robotics to better understand the role of the tail during locomotion of the earliest tetrapods. Also, precise kinematic simulations to elucidate the functional anatomy of vertebrate fossils have been published. Highly relevant to our study is for example the study by Pierce et al. (2012) that used a 3D reconstructed skeleton of a Devonian tetrapod and assessed kinematic plausibility of movements related to locomotion on land. Finally, dynamic simulations of fossils are also available. For example, Sellers et al. (2017) used a computer model of *T. rex* to investigate its running ability using methodology borrowed from the engineering sciences. We combined all of these different approaches, which is indeed something that we do not know many examples of (but see the interdisciplinary work of McInroe et al. 2016).

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Is *Orobates* older than dinosaurs?

Yes. *Orobates* was a very ancient animal. It existed c.a. 290 million of years ago (m.y.a.) and was recovered from a site that represents the Lower Permian. It is older than the dinosaurs that existed from the late Triassic (c.a. 230 m.y.a.) to the end of the Cretaceous (66 m.y.a.). In fact, *Orobates* is a close relative to the hypothesized last common ancestor of reptiles (including all extinct dinosaurs, birds and pterosaurs) and mammals. *Orobates*'s exact age is unknown.

Can the robot swim?

The robot was designed and constructed in a similar way to the Salamander robot Pleurobot (https://biorob.epfl.ch/pleurobot), which replicated an amphibian animal that is capable of swimming. However, the purpose of OroBOT design was not swimming, just walking.

Can OroBOT be used to study other extinct animals as well?

OroBOT is a bio-mimetic robot that tries to emulate as many anatomical features of the fossil as we could (e.g., length of the limbs, exact positioning of the girdles along the spine, mass distribution and position of the center of mass). It is therefore not useful to other fossils. However, using 3D printing, the "platform" could be used for other tetrapods as well. In fact, OroBOT is based on a previous robot "Pleurobot" which successfully mimicked the gaits of a salamander.