Reverse Engineering of an Early Tetrapod Fossil: Reconstructing Locomotor Characteristics

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1 Introduction

Early four-limbed vertebrates (i.e. early tetrapods) evolved the salient capability to move on land. The identification and reconstruction of locomotor characteristics in key tetrapod fossils that display a transitionary morphology thus holds huge potential for the understanding of early tetrapod evolution [1–3]. Additionally, an understanding of the evolutionary constraints and adaptive significance of the earliest mechanisms of legged locomotion on land may aid the conceptualization of bio-informed legged walking machines. However, functional inference from usually incomplete, fragmented and distorted fossil material remains problematic [2].

Orobates pabsti (Diadectomorpha) is an early tetrapod from the lower Permian (ca. 300 mya) of Thuringia, Germany [4]. The fossil species can be regarded as a key fossil due to its specific position in the tree of life very close to the origin of the evolutionary successful amniotes, i.e. all non-amphibious modern tetrapods. *Orobates* might furthermore present an ideal test case for an attempted locomotor reconstruction, because not only a nearly complete, articulated body fossil has been preserved, but also fossil trackways from the same site were assigned to this species [5]. The combination represents the oldest secure track-trackmaker association known.

In a highly integrative and interdisciplinary approach, *Orobates* was here studied with the goal of narrowing down the range of plausible locomotor characteristics in a transparent and reproducible way.

2 Methods

Our methodology comprises four main aspects (detailed below). Based on quantified evidence from these diverse approaches, we step-wise excluded unlikely postures and gaits of *Orobates* to narrow down the range of plausible solutions (i.e., the solution space) [6].

2.1 Production of a digital model of *Orobates*

The holotype specimen was digitally modeled from micro CT scans (Fig. 1A,C). Segmentation of bone fragments from surrounding matrix was done in AMIRA®. Bone fragments were fused in MAYA® and reduced bone surface meshes were generated in Z-BRUSH®. Subsequently, distortion was corrected in MAYA® using symmetry criteria and indirect evidence from additional fossil material [7].

2.2 Comparative motion analysis of modern animals

A sample of four modern sprawling species was used in a comparative motion analysis in order to identify general principles of sprawling locomotion. The species were chosen to cover a wide spectrum of different morphologies, ecological adaptations, and phylogenetic positions. X-ray motion analysis was conducted to visualize and quantify skeletal kinematics of walking trials (Fig. 1D-F). Simultaneously, we measured the ground reaction forces of individual limbs [8].

2.3 Interactive simulation of fossil kinematics

Using the digital model, a manipulable simulation of the fossils locomotion within the fossil trackways was created in MAYA® (Fig. 1G). The animation of *Orobates* was informed by the kinematics of the analyzed modern species. The simulation allowed us to systematically vary several parameters that contribute to the generation of propulsion. This simulation, while not accounting for dynamics and other biomechanical important constraints, specifically allowed us to identify anatomically plausible parameter combinations. We labeled all trials with bone collisions and/or joints de-articulations as not plausible. By this, domains of plausible solutions were identified in the search space.

2.4 OroBOT

A robotic replica of *Orobates* dubbed OroBOT, was created using 3D printed skeletal parts and off-the-shelf actuators. The design and fabrication of OroBOT uses a methodology similar to that of Pleurobot [9], a tetrapod walking machine to study salamander locomotion. An additional OroBOT model was created in the robot simulation environment WEBOTS™ in order to conduct dynamic simulations. We identified solution gaits according to energy consumption, stability, and precision of matching the fossil trackways (Fig. 1H). OroBOT is a physical platform to demonstrate reconstructed locomotion on the granular soil substrate the fossil trackways were created on (Fig. 1B).

3 Results

The digital model revealed the exact size of the skeleton and its constituent parts. Mass was estimated to have been approx. 4 kg. The center of mass position was determined while taking into consideration the sensitivity to uncertainties in mass estimation of individual body segments. Bony structures of the shoulder and hip joints constrained the amount of possible protraction. Long-axis rotation in shoulder and hip was hardly constraint, especially in the hip [7]. The analysis of the modern species demonstrated that, as has been previously stated (e.g., [10]), lateral bending of the spine, long-axis rotation in the shoulder and hip, and protraction/retraction of proximal limb segments contribute the most to the generation of propulsion. We found differences between more and less athletic species in our sample. Vertical ground reaction forces were very similar across all modern sprawling species. Kinematic simulation revealed that bone collisions and unnatural de-articulations do not occur at certain domains of the search space. Dynamic simulation of the OroBOT further revealed domains of parameter combinations that excel under the proposed metrics for energy expenditure, step precision, and stability. OroBOT finally enables the (re-)construction of actual trackways as well as the measurement and reporting of dynamic parameters like cost of transport and ground reaction forces.

4 Discussion and Outlook

The integrative approach introduced in our study allowed for a reconstruction of locomotor characteristics grounded on quantified empirical evidence [11]. Digital reconstruction of the fragile, fragmented and distorted holotype specimen was a premise for diverse subsequent biomechanical investigations. The model is made available from a public database and received a digital object identifier (http://dx.doi.org/10.17880/digital-reconstruction-of-orobates-pabsti-mng10181). The step-wise argumentation for the reconstruction of locomotor characteristics allows the integration of future insights. Modeling approaches used in the current study potentially can be updated or amended, new approaches can be incorporated in the analysis. The methodology presented here could function as a paragon for similar research problems.

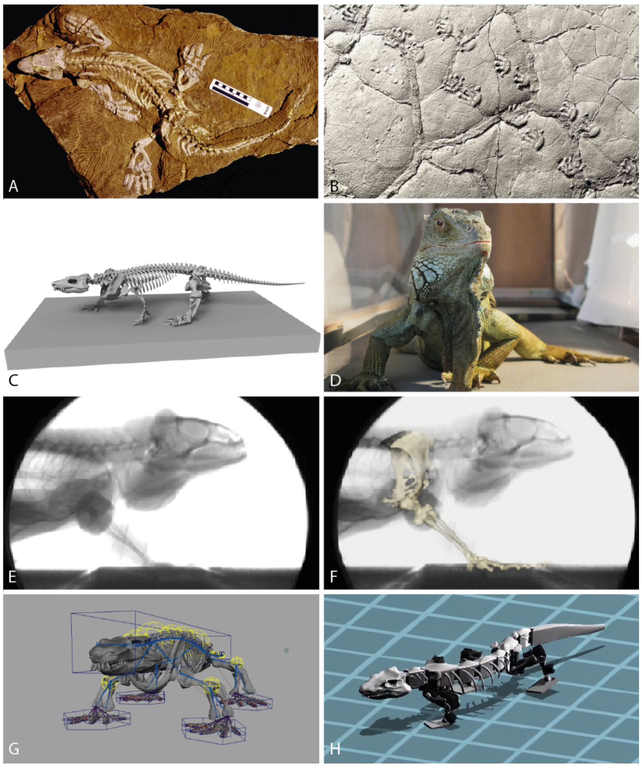

Figure 1: A: The holotype specimen of *Orobates pabsti* (MNG 10181). B: Fossil trackways assigned to *Orobates* as the trackmaker. C: A digital model of the fossil. D-F: X-ray motion analysis of modern sprawling species (here the green iguana) to visualize and quantify skeletal kinematics in-vivo. G: The manipulable simulation of *Orobates* in MAYA® allows to control kinematic parameters. H: WEBOTS™ simulation of OroBOT.

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