Making use of a track-trackmaker association: locomotor inference of an early amniote with help of "fossilized behavior"

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Abstract:

A deeper understanding of an extinct species' paleobiology is a common goal of studies into the functioning of the musculo-skeletal system which is only fragmentarily preserved in fossil tetrapod remains. The combination of a body fossil and ichnofossils stemming from the same species offers the chance to link fossilized anatomical features with "fossilized behavior". In a recent project, a unique combination of an articulated complete specimen of *Orobates pabsti* (Diadectidae) and *Ichniotherium sphaerodactylum* tracks to which *O. pabsti* has previously been assigned as the trackmaker was exploited for an in-depth reconstruction of the locomotion of this species. Phylogenetic analyses place *O. pabsti* close to the crown group node of amniotes and often recover the diadectids as the fossil sister taxon to modern amniotes. Early amniotes became increasingly independent of aquatic habitats and this key evolutionary transition is reflected in the reconstructed locomotor behavior of *O. pabsti*. Research into the fossil's anatomy, the fossil's potential joint mobility and potential movements within the *I. sphaerodactylum* tracks, a comparative analysis of extant tetrapod locomotor mechanics, and finally into a fossil-inspired walking machine (OroBOT) will be summarized.

Keywords: *Orobates*, locomotion, *Ichniotherium*, robot, simulation

Introduction

Early four-limbed vertebrates (i.e., early tetrapods) evolved the salient capability to move on land. It has been argued that the transition from fully aquatic ancestors to fully terrestrial forms was not completed before the appearance of the amniote egg accompanying terrestrial reproduction (e.g., Romer 1957). Soon after the appearance of the first amniotes, the clade underwent a rapid radiation which has previously been linked to the evolution of advanced terrestrial locomotion (Sumida & Modesto 2001). An understanding of locomotor capabilities of early amniotes (both stem representatives and basal members of the crown group) indicative of how well a species was adapted to an terrestrial lifestyle thus has the potential to elucidate further this key event of tetrapod evolution. New, integrative and interdisciplinary approaches allow for reconstructions of locomotor characteristics grounded on quantified empirical evidence (McInroe et al. 2016; Nyakatura 2016).

In the study summarized here, a unique combination of a pristinely preserved, complete and articulated specimen of *Orobates pabsti* (MNG 10181), a basal diadectid (Berman et al. 2004), and fossil tracks of the ichnospecies *Ichniotherium sphaerodactylum* (MNG 1840) assigned to *O. pabsti* as the trackmaker (Voigt et al. 2007) was used to study the locomotor capabilities of this species (Fig. 1). Both utilized fossil specimens stem from the same locality of the Thuringian forest in central Germany, the Early Permian Tambach Formation of the Bromacker quarry near Tambach-Dietharz (Martens 2018). The Tambach Formation of the Bromacker locality has produced dozens of articulated, partially or completely preserved tetrapod body fossil specimens several of which are diadectids including the here used holotype specimen (MNG 10181) and paratypes of *O. pabsti* (Berman et al. 1998; Berman & Henrici 2003; Berman et al. 2004; Martens 2018). The locality has also yielded hundreds of vertebrate tracks including the MNG 1840 tracks of *I. sphaerodactylum* (Eberth et al. 2000; Voigt 2005; Voigt et al. 2007). The Bromacker is furthermore the type locality of the Tambach Sandstone, which in part forms the base of the Upper Rotliegend Group in this area (Eberth et al. 2000; Voigt et al. 2007). All skeletons and tracks stem from a 10m thick stratigraphic interval of this Tambach Sandstone and first fossil finds were exposed in commercial quarries (Voigt et al. 2007). Voigt et al. (2007) were able to establish an association of the tracks of *I. sphaerodactylum* with *O. pabsti* as the trackmaker based on the relative lengths of the digits of the pes imprint and the degree of overstepping of the manus and pes imprints.

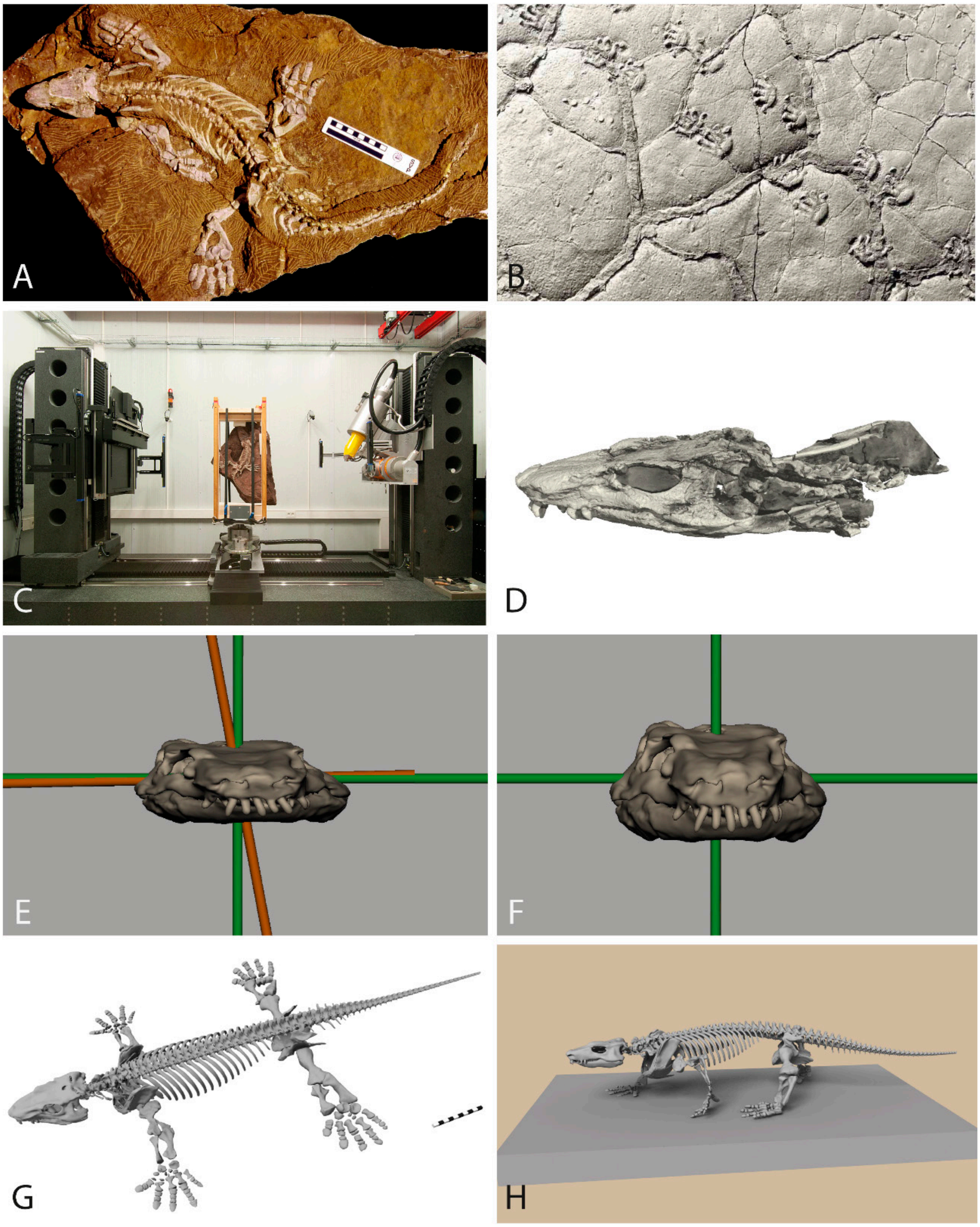

Fig. 1.: Digital reconstruction of *O. pabsti* (figure modified from Nyakatura 2017). A: The holotype specimen of *O. pabsti* MNG 10181; B: The *I. sphaerodactylum* ichnofossil MNG 1840; C: Computed tomography scan of MNG 10181 at the Technical University Dresden, Germany; D: Volume render of the high detail skull scan; E,F: Correcting distortion using symmetry and other evidence (cf. Nyakatura et al. 2015); G: Complete digital reconstruction; H: Virtual mount of MNG 10181.

Thus, the *I. sphaerodactylum* tracks typify "fossilized behavior" of *O. pabsti* and present an intriguing opportunity to study the locomotion of this fossil species. Diadectids are usually recovered as stem amniotes close to the crown group node of amniotes (Laurin & Reisz 1995; Ruta & Coates 2007). However, a couple of recent studies found *O. pabsti* to be an early member of the amniote crown group in at least some of the conducted analyses (Berman 2013; Marjanovic & Laurin 2019). The conjunction of a complete body fossil, assigned tracks, and a key phylogenetic position in the tetrapod tree of life motivated the here summarized investigation into the locomotion of *O. pabsti*.

The methodological approach advocated in this project integrated i) the digital reconstruction of the type specimen of *O. pabsti* MNG 10181, ii) two sets of simulations constrained by the fossil tracks (MNG 1840) and informed by biomechanical insight into sprawling tetrapod locomotion of extant species, and iii) a fossil-inspired, motor-actuated physical replica of *O. pabsti*, a robot dubbed OroBOT (Nyakatura et al. 2019). This combination of empirically grounded quantitative evidence was employed to narrow down the range of plausible locomotor characteristics of *O. pabsti* in a transparent and reproducible way.

A digital reconstruction of *Orobates pabsti*

Despite the superb preservation of the holotype specimen MNG 10181, the fossil was affected by taphonomic and diagenetic processes. As a result the almost 300 million year old specimen is fragmented and suffers from plastic deformation (Nyakatura et al. 2015). Furthermore, the specimen is mostly restricted to a two-dimensional analysis since the skeleton was only superficially prepared out of the surrounding rock matrix to prevent potential damage. To allow a quantitative analysis of the specimen's functional anatomy, it was therefore digitally reconstructed using microfocus computed tomography (µCT) scanning and subsequently virtually repaired. For scanning, the v|tome|x L450 (GE phoenix x-ray systems, Wunstorf, Germany) was used at the Technical University of Dresden, Germany (Fig. 1). For the main slab of MNG 10181 (ca. 1.0 m x 0.8 m x 0.35 m; approx. 35 kg) containing most of the trunk, tail, pelvic girdle, a forelimb and both hindlimbs a resolution of 150 µm was achieved. A slab of MNG 10181, which was separated during preparation (Berman et al. 2004), contained the skull, the cervical vertebrae, the pectoral girdle, and the left forelimb and allowed a more detailed scan with a resolution of 62 µm (Fig. 1).

Taphonomic and diagenetic alterations of the fossil material lead to a high heterogeneity of grey levels between fossil bone and surrounding rock matrix in the µCT images. This prevented the use of automated segmentation algorithms and made a time-consuming manual segmentation necessary. Segmentation was done using the segmentation editor in Amira® 6.0.0 (Thermo Fischer Scientific, Hillsboro, Oregon, U.S.A.). Bone fragments were fused in Autodesk Maya® (Autodesk Inc., San Rafael, California, U.S.A.) and subsequently plastic deformation was corrected using symmetry criteria and circumstantial evidence from additional material (specifically an isolated vertebra MNG 8966) as explained in detail in a previous publication (Nyakatura et al. 2015). It was not possible to virtually reconstruct in sufficient quality large parts of the trunk and tail. These parts were modelled according to the detailed descriptions provided in the literature (Berman et al. 2004). Only the left limbs were reconstructed and were subsequently simply mirrored to obtain right limbs assuming perfect bilateral symmetry. Finally, this idealized digital reconstruction of the holotype specimen of *O. pabsti* was mounted in Maya® (Fig. 1), was made publically available (http://dx.doi.org/10.17880/digital-reconstruction-of-orobates-pabsti-mng10181), and served as the basis for the estimation of body mass (ca. 4kg), the body segments' centers of mass, the mobility in the hip and shoulder joints (Nyakatura et al. 2015), and was the basis for a digital marionette that was used for subsequent simulations of the locomotion (Nyakatura et al. 2019).

Simulating the locomotion using constraints posed by fossil tracks

To identify common principles of sprawling tetrapod locomotion that can also be assumed to have pertained to *O. pabsti*, an in-depth comparative analysis of the locomotor mechanics of a sample of extant species was conducted. Previous work demonstrated the importance of lateral bending of the spine, of retraction in the shoulder and hip joints, and of long-axis rotation of the stylopodial limb elements (humerus and femur) for the generation of propulsion in sprawling gaits (BARCLAY 1946, EDWARDS 1977; ASHLEY-ROSS 1994; KARAKASILIOTIS et al. 2013; NYAKATURA et al. 2014). These kinematic properties were thus quantified in metamorphic Mexican salamanders (*Ambystoma mexicanum*), blue-tongued skinks (*Tiliqua scincoides*), green iguanas (*Iguana iguana*) and spectacled caimans (*Caiman crocodilus*) using x-ray motion analysis (NYAKATURA et al. 2019). Synchronously, ground reaction forces for individual limbs in contact with the ground were recorded (Fig. 2).

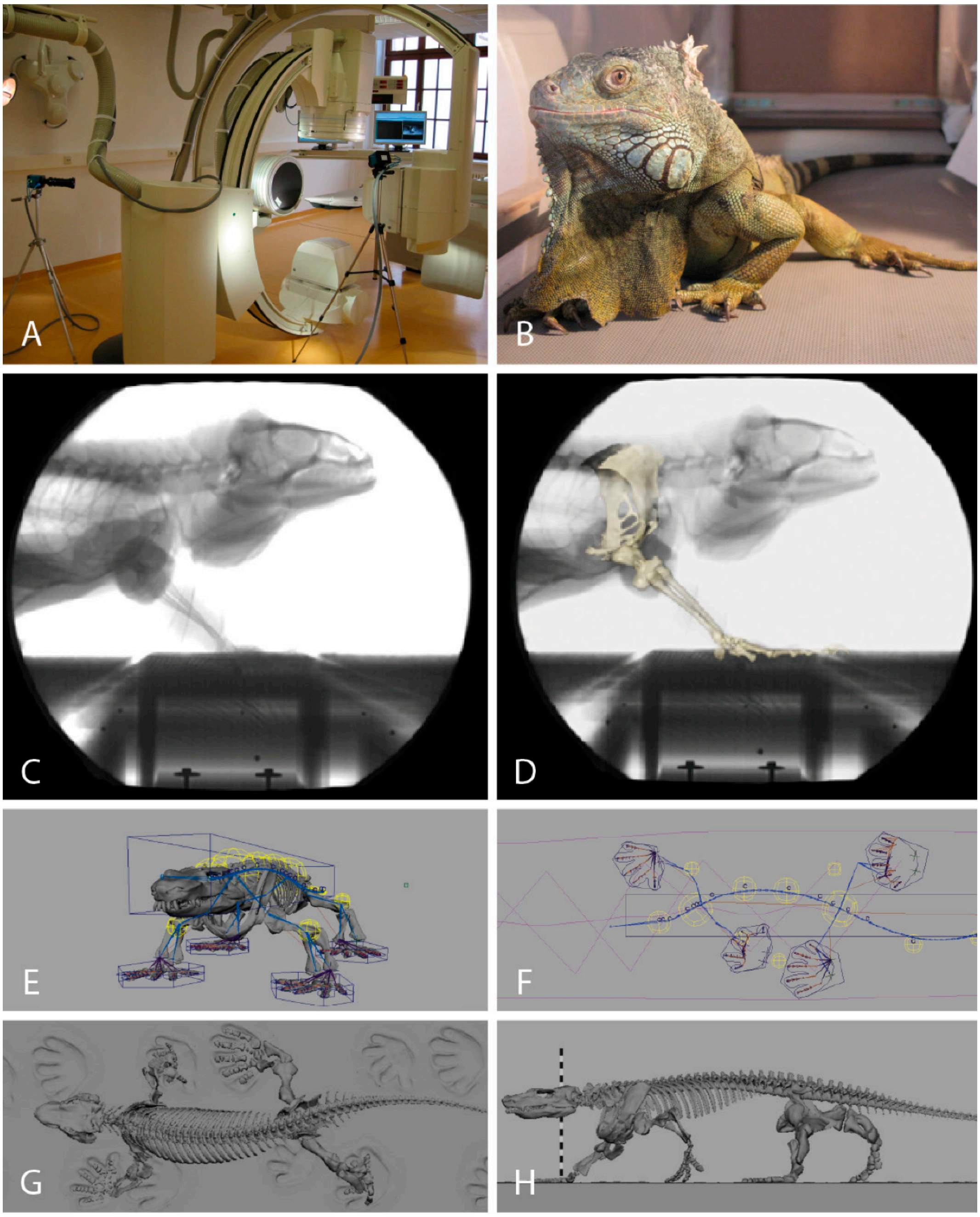

Fig. 2: Kinematic simulation of *O. pabsti* (figure modified from NYAKATURA 2017). A: The biplane high-speed x-ray facility of the Friedrich Schiller University Jena, Germany, where all x-ray motion analyses have been conducted; B: Green iguana on a treadmill; C, D: Video stills from x-ray motion analysis that involves superimposition of three-dimensional bone models on x-ray images to visualize and quantify three-dimensional kinematics (cf. NYAKATURA et al. 2014; NYAKATURA et al., 2019); E: Digital marionette of *O. pabsti*; F: Locomotion is constrained within the MNG 1840 tracks; G, H: The kinematic simulation allows systematic variation of kinematic variables to test for anatomical plausibility.

The sampled extant animals covered a reasonable portion of the mechanical diversity in extant sprawling tetrapods due to differing morphology (e.g., body length to limb length ratio) and different ecologies (terrestrial, semi-aquatic, arboreal). The extant sample also phylogenetically bracketed the anamniote to amniote transition (Witmer 1995). In brief (this data is detailed in Nyakatura et al. 2019), this comparative analysis revealed significant differences between more erect limb postures (fore- and hindlimbs in the caiman and forelimbs in the iguana) and hyper-sprawled limb postures (fore- and hindlimbs in the salamander and the skink, hindlimbs in the iguana). More erect limb postures were accompanied by less long-axis rotation and increased stylopodial retraction. The most important kinematic properties were visualized in a three-dimensional plot, that was termed the sprawling gait space. These plots allow for the direct comparison of the complex gait characteristics. Despite the observed differences between more erect and hyper-sprawled limb postures, the patterns of the vertical ground reaction force component was remarkably similar within our sample of diverse extant taxa, which indicates that dynamic similarity is maintained across extant sprawling taxa (Nyakatura et al. 2019).

The *I. sphaerodactylum* tracks MNG 1840, as "fossilized behavior" of *O. pabsti*, preserved information about stride length, stride width, and pace angulation for a locomotor sequence of the fossil. The fossil's trackway information was thus compared to the tracks of extant species, too (Curth et al. 2014). The MNG 1840 tracks were intermediate to those of the extant species implying that locomotor mechanics of *O. pabsti* likely did not deviate substantially from those of the extant sampled species (Nyakatura et al. 2019). In accordance with the kinematic principles observed in the comparative analysis of extant sprawling tetrapods, the digital marionette of the digitally reconstructed holotype specimen MNG 10181 was animated in Maya® (Fig. 2). The skeleton's movements were hard constrained by the tracks of MNG 1840 (i.e., the autopodia of the digital marionette were forced to contact the ground within the MNG 1840 tracks), which were also digitized and imported into Maya® together with the digital marionette.

The animated digital marionette of *O. pabsti* walking within the MNG 1840 tracks allowed for a systematic variation of the most important kinematic variables (lateral spine bending, long-axis rotation/retraction, body height) in a virtual experiment. 100 parameter combinations were tested for each the forelimb and the hindlimb (Nyakatura et al. 2019). For each parameter combination of *O. pabsti* anatomical plausibility was evaluated and by this regions within the sprawling gait space plot were identified that were characterized by no or just minimal bone collisions or joint de-articulations. These anatomically plausible gaits exhibited little-to-moderate humeral and femoral long-axis rotation, intermediate-to-high body height and moderate lateral spine bending (Nyakatura et al. 2019).

OroBOT – an actuated physical replica of *Orobates pabsti*

A physical walking machine, dubbed OroBOT, was built to mimic the fossil reconstruction of *O. pabsti* and to test reconstructed plausible gaits under realistic conditions (real-world physics). For the construction, three-dimensionally printed parts that were designed after the morphology of *O. pabsti* were used together with off-the-shelf actuators. OroBOT was based on a previous robotic platform, Pleurobot (Karakasiliotis et al. 2016), but was designed to closely mimic properties of *O. pabsti* (e.g. positioning of the girdles along the spine, position of the center of mass, limb lengths etc.; cf. Nyakatura et al. 2019). Pleurobot already was a tetrapod walking machine that was able to replicate salamander stepping locomotion, including lateral bending of the spine, long-axis rotation and retraction in the proximal limb joints, and different body heights (Karakasiliotis et al. 2016). Importantly, OroBOT was simulated first in Webots® (Cyberbotics ltd., Lausanne, Switzerland), an open source robotics simulation software. This allowed dynamic simulation of the robot locomotion. Thus, in addition to the anatomic criterion of plausibility (termed a "filter" in Nyakatura et al. 2019) described above, additional dynamic filters were utilized to further narrow down the likely locomotion of *O. pabsti*. These filters were a power expenditure criterion, a balance criterion, a precision criterion, and a ground reaction

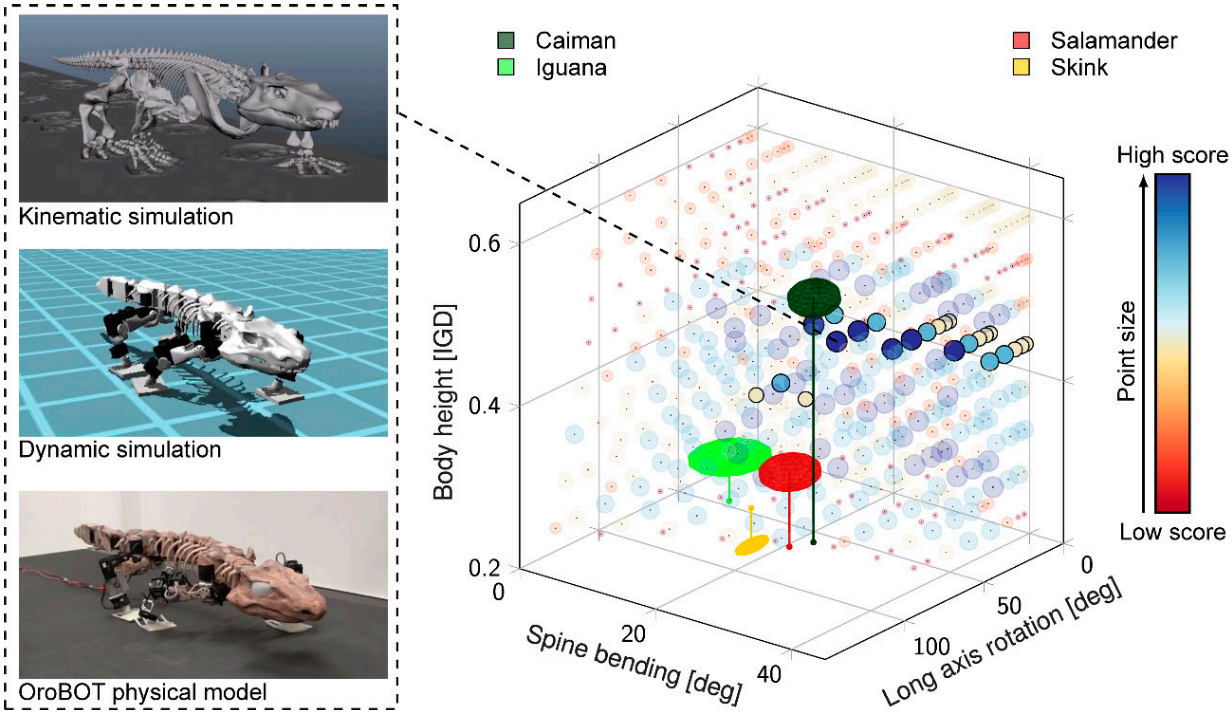

Fig. 3: Several plausible gaits are found after employing all kinematic and dynamic filters and visualized in the three-dimensional sprawling gait space plot (large, dark blue spheres). Pale spheres represent evaluation of dynamic filters only, before being filtered for anatomical plausibility. For comparison, kinematics of extant species are plotted in the sprawling gait space, too. Body height of different species has been normalized by inter girdle distance (IGD). Plausible gaits found for *O. pabsti* resemble the locomotion of the caimans. Figure modified from NYAKATURA et al. 2019.

Finally, it was tested for a number of parameter combinations across the sprawling gaits space whether the physical robot OroBOT matches the simulated gaits in Webots®, which was the case. The robot was able to replicate the track parameters of MNG 1840 in the reconstructed plausible gaits (NYAKATURA et al. 2019).

Discussion and implications

Consistent with previous qualitative assessments of the locomotion of *O. pabsti* (BERMAN & HENRICI 2003; VOIGT et al. 2007), we reconstructed a relatively erect (within the spectrum of sprawling tetrapod locomotion) gait. Locomotion of *O. pabsti* further appeared to be balanced and mechanically power-saving (NYAKATURA et al. 2019). In comparison to earlier tetrapods, this combination points to advanced terrestrial locomotor capabilities. Thus, if diadectids are indeed stem amniotes (e.g., LAURIN & REISZ 1995; but see MARJANOVIC & LAURIN 2019), these results suggest that advanced terrestrial locomotion can be assumed to have evolved before the crown group and predates the subsequent radiation of amniotes.

In addition to the paleobiological insight outlined above, the study summarized here has methodological aspects worth discussing. First, it is important to point out that it was not aspired to find the *one correct solution* for the problem of how has *O. pabsti* has moved. Instead, hard constraints in form of anatomical features of MNG 10181 and track parameters of MNG 1840 were combined with different dynamic filters and together were used to stepwise exclude unlikely parameter combinations (i.e., gaits). This approach was first suggested by GATESY et al. (2009). All data supporting the quantitative assessment of *O. pabsti* locomotion have been made publicly available (NYAKATURA et al. 2015; NYAKATURA et al. 2019) and is aimed to allow future studies to complement and/or revise the current state of knowledge. Additionally, a website was created that allows users to interactively explore the sprawling gait space of *O. pabsti*, give different weights to the filters, and to compare the reconstructed locomotion with that of the analyzed sample of extant sprawling tetrapods (https://go.epfl.ch/Orobates). New insight could lead to completely new filters, that could be used to further narrow down the locomotion of *O. pabsti*. Also, the here advocated approach, coined "robotic paleontology" (Nyakatura et al. 2019), could be transferred to similar problems where a deeper understanding of the functional morphology holds the potential for enabling more fine-grained concepts of key evolutionary transitions (e.g., the origin of active flight in birds and bats or the origin of bipedal locomotion of human ancestors).

Further, this study demonstrates the potential use of robotics for the understanding of biological problems, in contrast to the more common approach of studying biological systems to inform new technical solutions. Compared to motion analyses of living animals, robots allow to systematically test individual parameters similar to computer-aided simulations (Nyakatura 2017). In such simulations, too, systematic analysis of individual parameters provides an opportunity to test the limits of what is plausible and beyond to exhaustingly explore a search space. "Virtual palaeontology" (Cunningham et al. 2014), as utilized in the study summarized here, is a prerequisite for such "virtual experiments" (Nyakatura & Demuth 2019).

Finally, as part of the current study experts from design disciplines concerned with computer generated imagery and computer animation developed together with (paleo-)biologists new tools for the analysis of *O. pabsti*. This constitutes an example of how new technology-driven research strategies in addition to the traditional scientific illustration can increasingly become a means to generate new knowledge rather than "merely" helping to communicate scientific output to peers and the public (Amelung 2019). Consequently, the scientific illustrators were included directly in the author list, instead of being mentioned in the acknowledgements only (cf. Nyakatura et al. 2015; Nyakatura et al. 2019).

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