A new role for joint mobility in reconstructing vertebrate locomotor evolution

Armita R. Manafzadeh\textsuperscript{a,1,}  Robert E. Kambic\textsuperscript{b,c}, and Stephen M. Gatesy\textsuperscript{a}\textsuperscript{d}

\textsuperscript{a}Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912; \textsuperscript{b}Center for Movement Studies, Kennedy Krieger Institute, Baltimore, MD 21205; and \textsuperscript{c}Department of Neuroscience, Johns Hopkins University School of Medicine, Baltimore, MD 21205

Reconstructions of movement in extinct animals are critical to our understanding of major transformations in vertebrate locomotor evolution. Estimates of joint range of motion (ROM) have long been used to exclude anatomically impossible joint poses from hypothesized gait cycles. Here we demonstrate how comparative ROM data can be harnessed in a different way to better constrain locomotor reconstructions. As a case study, we measured nearly 600,000 poses from the hindlimb joints of the Helmeted Guineafowl and American alligator, which represent an extant phylogenetic bracket for the archosauromorphan ancestor and its pseudosuchian (crocodilian line) and ornithodiran (bird line) descendents. We then used joint mobility mapping to search for a consistent relationship between full potential joint mobility and the subset of joint poses used during locomotion. We found that walking and running poses are predictably located within full mobility, revealing additional constraints for reconstructions of extinct archosaurs. The inferential framework that we develop here can be expanded to identify ROM-based constraints for other animals and, in turn, will help to unravel the history of vertebrate locomotor evolution.

Results

Our resulting ROM maps are displayed as Fig. 1. As expected based on previous findings (6, 7), locomotor (here, steady forward walking and slow running) poses comprise only a subset of each joint’s full ROM. However, our improved methodology and comparative approach uncovered three consistent pose usage patterns. First, in all joints studied, pooled locomotor poses are approximately centered along the cosine-corrected flexion–extension (FECC) axis of mobility (see ref. 11), occupying roughly the middle 60 to 75% of the possible range in guineafowl joints, and the middle 50 to 55% in alligator joints. Second, although both animals’ hip joints remain abducted during locomotion, these poses are biased toward the more adducted side of their ROM envelopes, particularly during the weight-bearing stance phase. Finally, all hinge-like joints studied (knees of both species and guineafowl ankle) are biased toward abduction.

Discussion

We propose that the pose usage patterns revealed by our comparative analysis of extant archosaurian hindlimbs can be translated into constraints for reconstructions of extinct archosaur locomotion. Specifically, we most parsimoniously infer that only the middle 75% of all possible hindlimb FECC excursions should be considered for inclusion in locomotor reconstructions. We also conclude that the pooled set of poses from all reconstructed stride cycles should be centered along the FECC axis of mobility in all joints, and biased toward adduction in hip joints but abduction in hinge-like knees and ankles.

Author contributions: A.R.M. and S.M.G. designed research; A.R.M., R.E.K., and S.M.G. performed research; A.R.M. analyzed data; and A.R.M., R.E.K., and S.M.G. wrote the paper.

The authors declare no competing interest.

Published February 8, 2021.
These ROM-based constraints create a substantially narrowed search space within which to reconstruct archosaurian walking and running cycles. The resulting locomotor hypotheses can then be tested using other parameters such as bone strain, energy expenditure, balance, and/or similarity of ground reaction forces to those of extant species (following refs. 1, 13, and 14), ultimately improving our understanding of the locomotion of individual extinct archosaurs and reshaping analyses of archosaurian locomotor evolution (e.g., ref. 12).

Future studies that adopt the inferential framework we establish here will help to determine whether similar constraints can also be applied to other joints (e.g., forelimb joints), taxa (e.g., stem mammals), and modes of locomotion (e.g., flying). When the results of these studies are viewed within a phylogenetic context and integrated with existing evidence from morphology, kinematics, and kinetics, they will inform a broader range of locomotor reconstructions from across the vertebrate tree. We suggest that, in this way, the discovery of additional ROM-based constraints will better illuminate major transformations such as the origins of terrestriality, bipedality, and flight.

**Materials and Methods**

Marker-based XROMM analysis was used to measure hindlimb joint poses (simultaneous excursions measured in all three rotational degrees of freedom; Fig. 1) from both in vivo behaviors (15) and intact cadaveric manipulations (8) of the Helmed Guineafowl (Numida meleagris) and American alligator (Alligator mississippiensis). Procedures conducted with live animals were approved by the Brown University Institutional Animal Care and Use Committee.
Manafzadeh et al.
A new role for joint mobility in reconstructing vertebrate locomotor evolution

Fig. 2. Hindlimb joint coordinate systems for the (A) Helmeted Guineafowl and (B) American alligator. Both species are shown in their reference pose (all joint rotations equal zero). (Scale cubes, 1 cm³.) Rotation about the blue z axis represents flexion–extension, about the green y axis represents abduction–adduction, and about the red x axis represents long-axis rotation. Conventions for positive rotation follow the right-hand rule; note that, whereas abduction is positive at hips and ankles, it is negative at knees.

All measured joint poses were used to create a polygonal ROM envelope representing full potential joint mobility for each joint. Locomotor (steady forward walking and slow running) poses were then plotted within each envelope to create a ROM map (10) in cosine-corrected Euler joint pose space (11). In this space, $\Psi_{EC}$ incorporates information about both flexion–extension and abduction–adduction, resolving the distortion of uncorrected Euler pose space (e.g., refs. 7 and 8) and enabling a quantitative and qualitative assessment of the relationship between joint mobility and the poses used during locomotion.

See SI Appendix for extended materials and methods. All calibration images, X-ray videos, and computed tomography (CT) files are available at http://xmaportal.org/webportal (BROWN20, BROWN58, and BROWN71).

Data Availability. Calibration images, X-ray videos, and CT files have been deposited in XMAPortal, http://xmaportal.org/webportal (BROWN20, BROWN58, and BROWN71).

ACKNOWLEDGMENTS. We thank D. Baier for XROMM MayaTools; J. Hermanson, S. Nesbitt, T. Owerkowicz, K. Roorda, M. Stocker, and R. Wilhite for specimens; J. Lomax, P. Falkingham, T. Roberts, H. Tsai, and M. Turner for assistance with data collection; B.-A. Bhullar, E. Brainerd, and T. Roberts for helpful conversations; and two anonymous reviewers for their constructive reviews. This work was supported by the Bushnell Research and Education Fund, US NSF (Grants IOS-0925077, DBI-0552051, IOS-0840950, DBI-1262156, EAR-1452119, GRFP), Sigma Xi Grant-in-Aid of Research, Society of Vertebrate Paleontology Cohen Award for Student Research, Association of Women Geoscientists/Paleontological Society Winifred Goldring Award, and Brown University Presidential Fellowship.

1. S. E. Pierce, J. A. Clack, J. R. Hutchinson, Three-dimensional limb joint mobility in the early tetrapod Ichthyostega. Nature 486, 523–526 (2012).
2. J. A. Nyakatura et al., Reverse-engineering the locomotion of a stem amniote. Nature 565, 351–355 (2019).
3. S. M. Gatesy, M. Bäker, J. R. Hutchinson, Constraint-based exclusion of limb poses for reconstructing theropod dinosaur locomotion. J. Vertebr. Paleontol. 29, 535–544 (2009).
4. H. P. Tsai, K. M. Middleton, J. R. Hutchinson, C. M. Holliday, Hip joint articular soft tissues of non-dinosaurian Dinosauria and early Dinosauria: Evolutionary and biomechanical implications for Saurischia. J. Vertebr. Paleontol. 38, e1427593 (2018).
5. J. D. Hutson, K. N. Hutson, A test of the validity of range of motion studies of fossil archosaur elbow mobility using repeated-measures analysis and the extant phylogenetic bracket. J. Exp. Biol. 215, 2030–2038 (2012).
6. P. Arnold, M. S. Fischer, J. A. Nyakatura, Soft tissue influence on ex vivo mobility in the hip of Iguana: Comparison with in vivo movement and its bearing on joint motion of fossil sprawling tetrapods. J. Anat. 225, 31–41 (2014).
7. R. E. Kambic, T. J. Roberts, S. M. Gatesy, 3-D range of motion envelopes reveal interacting degrees of freedom in avian hind limb joints. J. Anat. 231, 906–920 (2017).
8. A. R. Manafzadeh, A practical guide to measuring ex vivo joint mobility using XROMM. Integr. Organismal Biol. 2, obaa041 (2020).
9. B. J. Knörlein, D. B. Baier, S. M. Gatesy, J. D. Laurence-Chasen, E. L. Brainerd, Validation of XMALab software for marker-based XROMM. J. Exp. Biol. 219, 3701–3711 (2016).
10. A. R. Manafzadeh, K. Padian, ROM mapping of ligamentous constraints on avian hip mobility: Implications for extinct ornithodirans. Proc. Biol. Sci. 285, 20180727 (2018).
11. A. R. Manafzadeh, S. M. Gatesy, A coordinate-system-independent method for comparing joint rotational mobilities. J. Exp. Biol. 223, jeb.227108 (2020).
12. J. R. Hutchinson, The evolution of locomotion in archosaurs. C. R. Palevol 5, 519–530 (2006).
13. P. J. Bishop, A. R. Cuff, J. R. Hutchinson, How to build a dinosaur: Musculoskeletal modeling and simulation of locomotor biomechanics in extinct animals. Paleobiology, 10.1017/pab.2020.46 (2020) In press.
14. M. T. Carrano, Locomotion in non-avian dinosaurs: Integrating data from hindlimb kinematics, in vivo strains, and bone morphology. Paleobiology 24, 450–469 (1998).
15. E. L. Brainerd et al., X-ray reconstruction of moving morphology (XROMM): Precision, accuracy and applications in comparative biomechanics research. J Exp Zool A Ecol Genet Physiol 313, 262–279 (2010).