

Introduction

Dimetrodon, a “pelycosaur” grade synapsid, was the apex predator of the Early to Middle Permian. Easily recognized by tall neural spines and large caniniform teeth, this ancient relative of therapsids, and later mammals, is widely categorized with sprawling posture despite how derived it is from basal synapsids. (Romer, 1940) The spine of *Dimetrodon* exhibits limited lateral flexibility and trackways attributed to the organism lack body dragging marks, implying our understanding of its locomotion is outdated. (Kemp, 2005; Hunt and Lucas, 1998) By studying the functional morphology of the forelimb and hindlimb of *Dimetrodon* compared to that of extant reptiles and mammals, I seek to better quantify its locomotion across the spectrum of sprawling to upright posture.

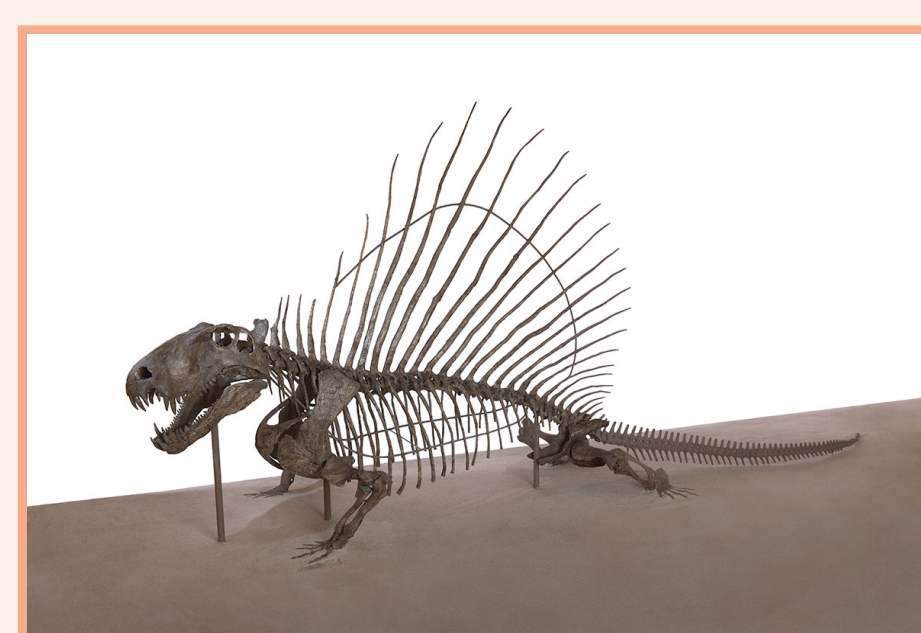


Photo by Donald E. Hurlbert and James Di Loreto, Smithsonian.

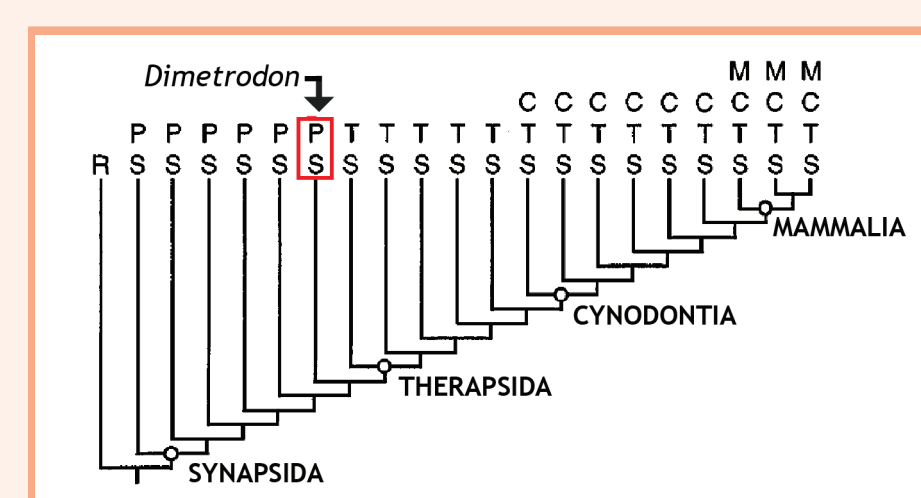


Figure 1 from Rubidge and Sidor, 2001.

Questions

Did *Dimetrodon* truly have sprawling posture?

Can postural grade and/or femoral abduction angle be estimated for fossil taxa from limb dimensions and pace angulation?

Does femoral abduction angle rather than discrete postural grade better inform transitions in locomotion? (Gatesy, 1991)

Describing Posture in Tetrapods

Postural grade

Grade	Description	Traditionally sorted taxa
Sprawling	proximal limb bones held near perpendicular to parasagittal plane	Squamate reptiles, turtles, amphibians, pelycosaur
Dual-gait	capable of holding proximal limb bones intermediately or in sprawling condition	Crocodylians, therapsids
Upright	proximal limb bones held near parallel to parasagittal plane	Mammals, dinosaurs, birds

Postural grades sort taxa into discrete categories and assume “upright” is improved condition. (Gatesy, 1991)

Femoral Abduction Angle (FAA)

Describes far away from the body the femur is held in reference to the parasagittal plane. At 90° an posture is considered fully sprawling and at 0° posture is considered fully upright, as shown in the figure to the right.

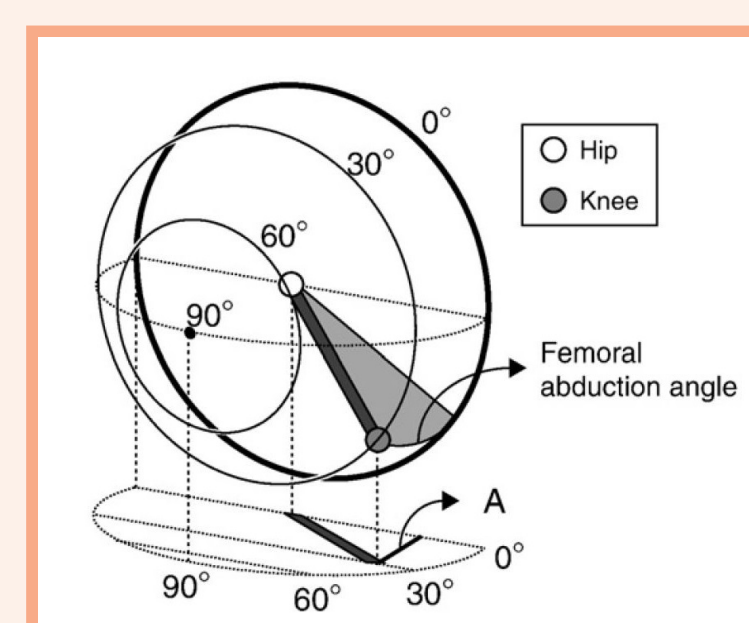
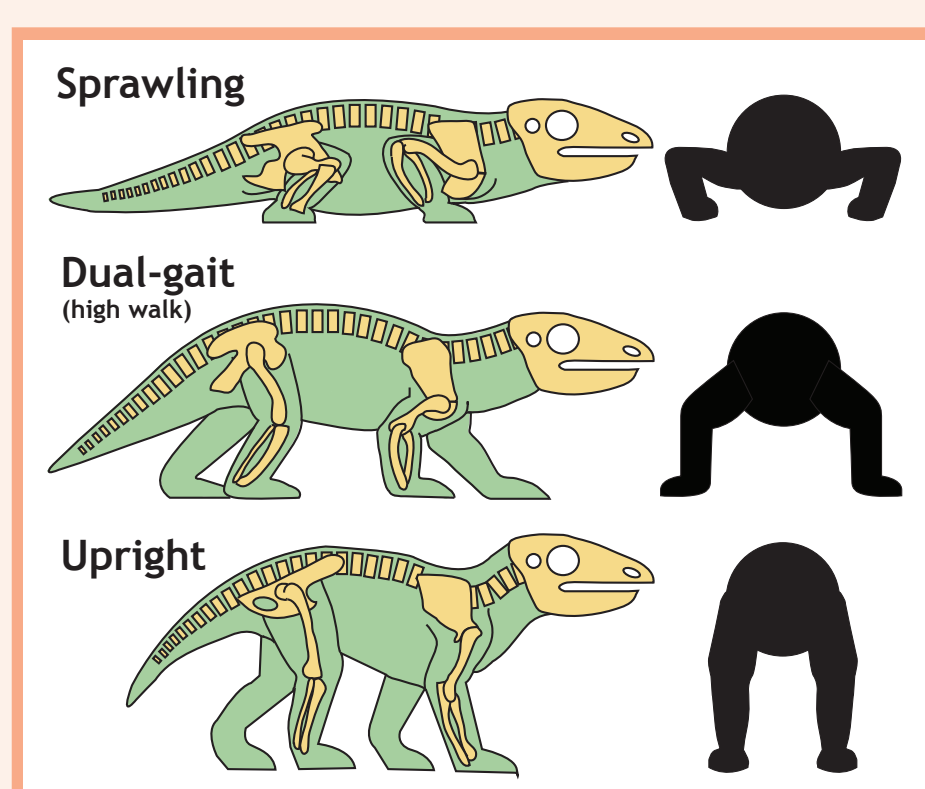


Figure 2 from Kubo and Ozaki, 2009.

Methods

Collected data:

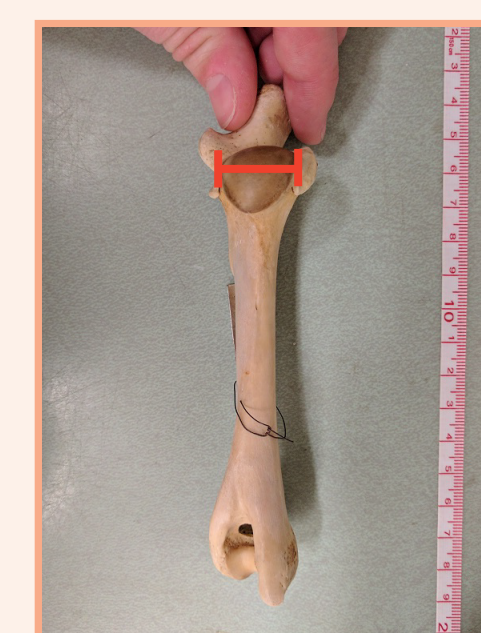
1. Linear measurements of 58 continuous variables of girdles, zeugopodia, and stylopodia of 23 extant taxa (11 mammals, 12 reptiles) and *Dimetrodon* (Beck, 2004)
2. Pace angulations for same 23 extant species and ichnogenus *Dimetropus* (Kubo and Benton, 2009)
3. Femoral abduction angles for 7 extant species

Stats:

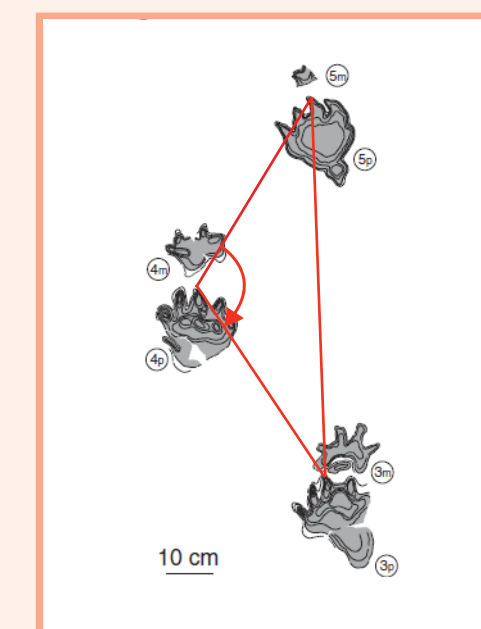
1. Discriminant function analysis (DFA) on limb dimensions and pace angulation of extant species to predict that of *Dimetrodon*
2. Multiple regression of 7 extant taxa with known femoral abduction angles to predict that of *Dimetrodon*



Femur of *Varanus komodoensis* (USNM 101444) in dorsal view with FemAbDist labeled (see chart below)



Humerus of *Pecari tajacu tajacu* (USNM 261026) in anterior view with HumHWMMax labeled (see chart below)



Dimetropus tracks from Sacchi et al. 2014 with pace angle labeled (see chart below)

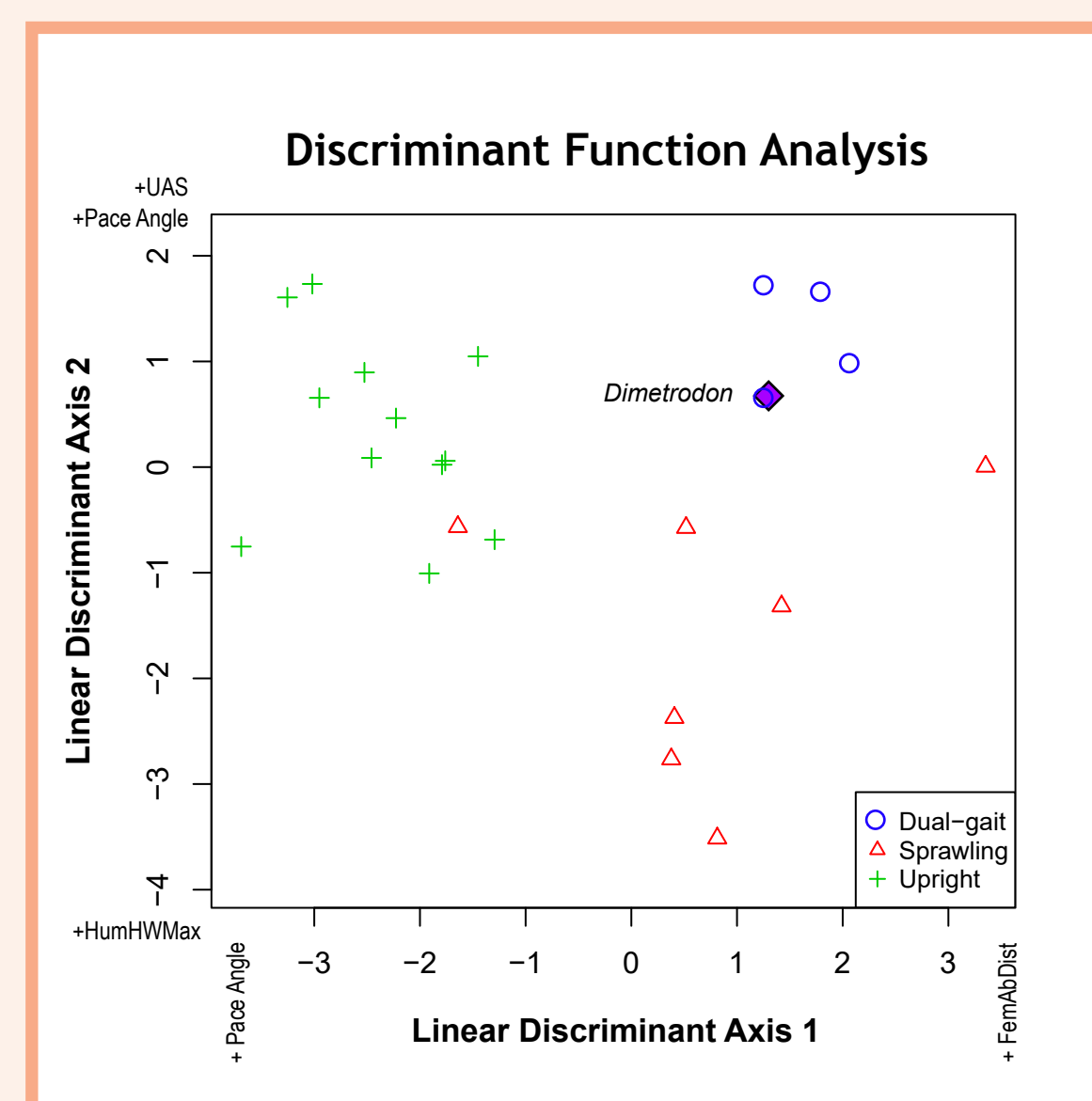


Ulna of *Alligator sinensis* (USNM 292078) with UArW labeled (see chart below)

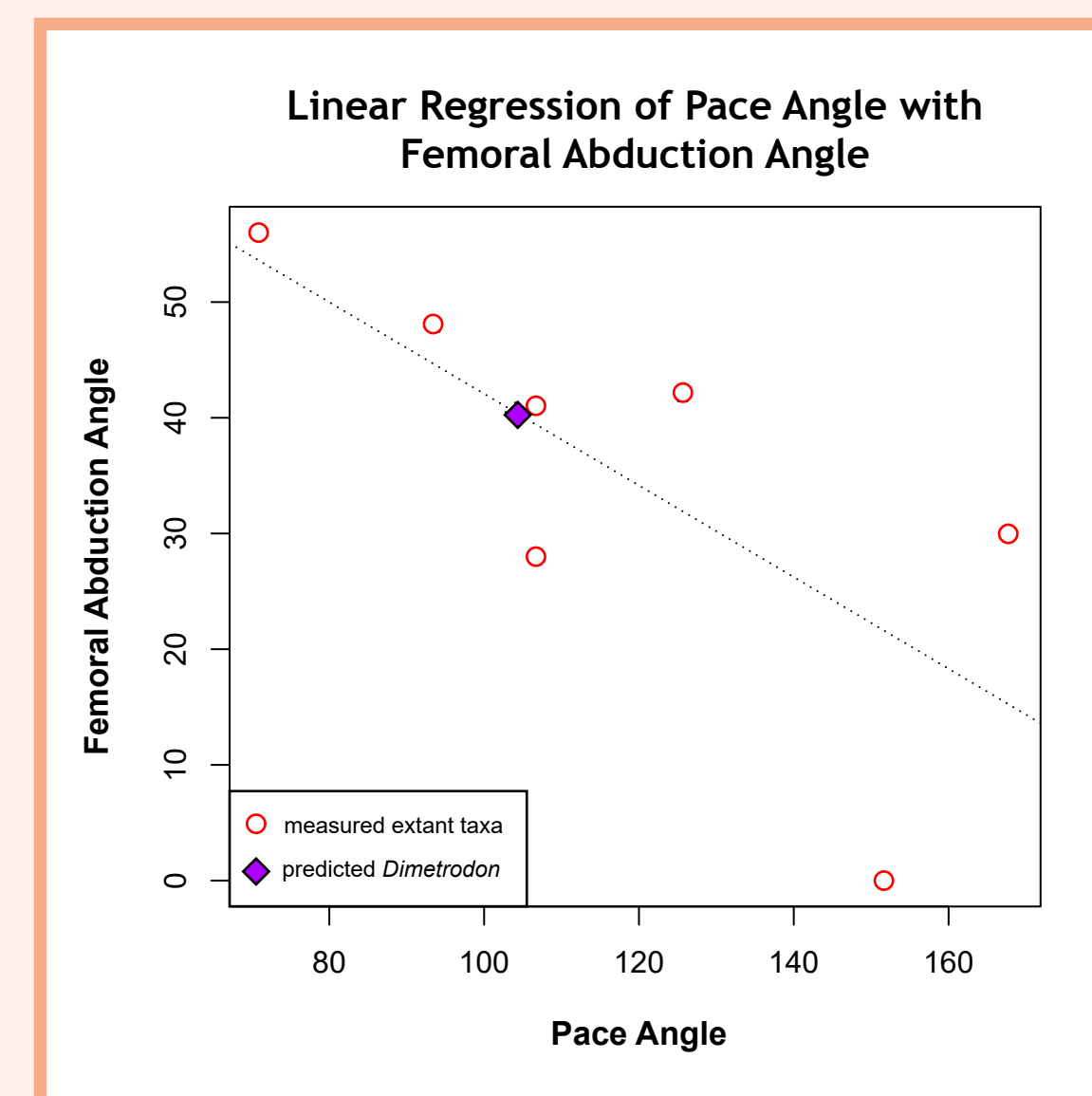
Results

Measurement #	Name	Description	Correlation to posture
1	FemAbDist	Distance between femoral head and abductor scar	Increases in sprawling and dual-gait taxa, decreases in upright taxa
2	Pace Angle	Angle between three consecutive steps in a trackway	Increases in upright taxa, decreases in sprawling taxa
3	HumHWMMax	Width of humeral head in anterior-posterior direction	Increases in sprawling taxa, decreases in dual-gait and upright taxa
4	UArW	Width of proximal articular surface of the ulna	Increases in upright and dual-gait taxa, decreases in sprawling taxa

Table elaborating the variables that best sorted extant taxa by assigned posture category during discriminant function analysis (DFA). Variables chosen by cross-validation.



Graph of 4 variable DFA of extant taxa with *Dimetrodon*. Variables shown are best predictors of postural grade. Plot shows *Dimetrodon* grouping with dual-gait taxa, overlapping directly over *Caiman crocodylus*. Sprawling taxa are loosely clustered, dual-gait are well clustered, and upright taxa are fairly clustered. The sprawling taxon within the upright taxa is the monotreme *Tachyglossus aculeatus*. The two sprawling taxa closest to the dual-gait taxa are *Tupinambis teguixin*, *Varanus komodoensis*, and *Varanus exanthematicus*.



Preliminary regression of pace angle with FAA of extant taxa, predicting an FAA of 40° for *Dimetrodon*. Only 7 taxa from the larger set of 23 had a known abduction angle, so results should be treated with caution. In this initial regression, only pace angle was shown to have a strong correlation with FAA.

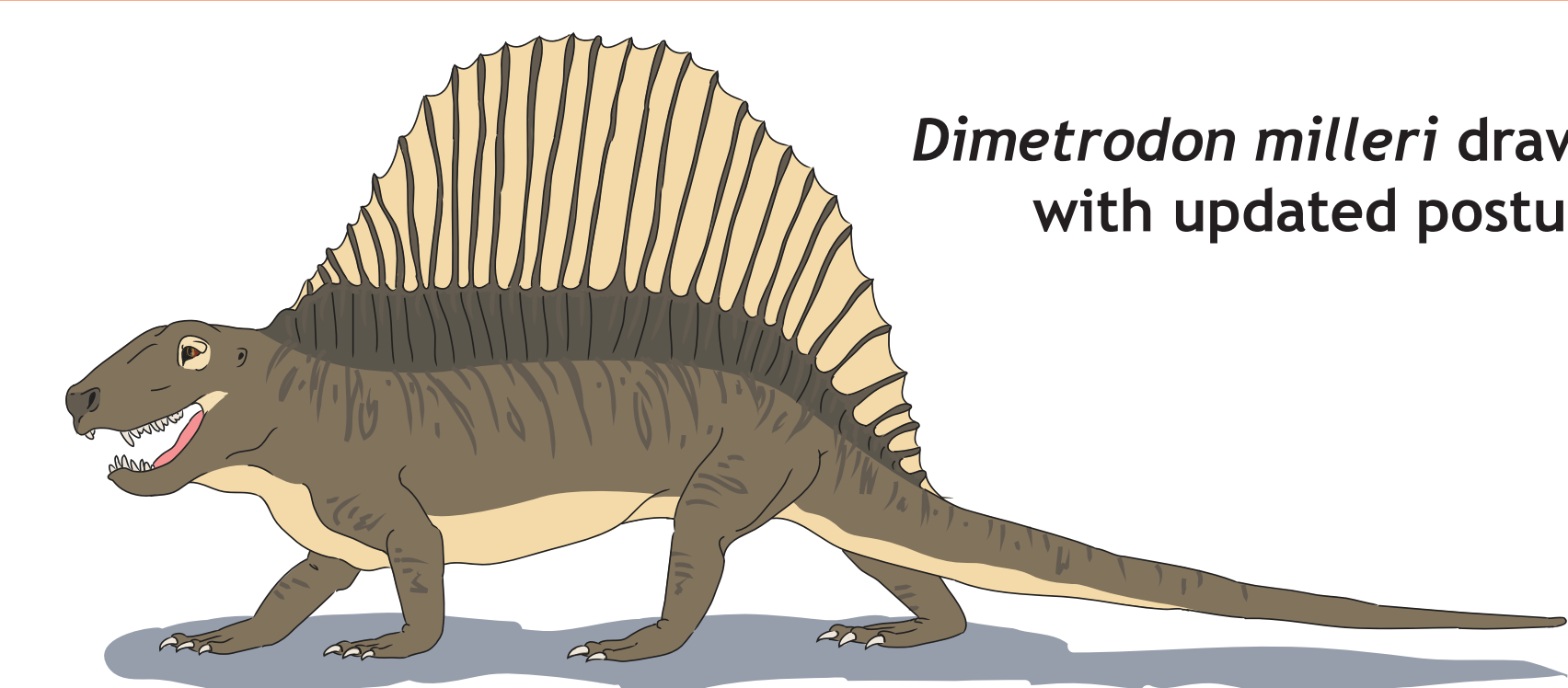
Conclusions

I. *Dimetrodon* is likely not a true sprawling tetrapod as it overlaps with dual-gait taxa in the DFA

- a. DFA was sensitive to how many variables were used, due to the limited sample size of extant taxa
- b. DFA is useful in sorting taxa based on postural grade, but provides little context for the range of tetrapod locomotion styles
 - i. Arboreal, cursorial, semi-aquatic, and other specialist taxa are masked by broad postural grades
- c. Dual-gait taxa may cluster tightly due to phylogenetic similarity, as they are all are crocodylians

II. 40° is a reasonable FAA estimate for *Dimetrodon* based on its DFA proximity to crocodylians with similar FAA

- a. Larger sample size needed to better define determinants of FAA
- b. Pace angle was the best predictor of FAA in this dataset, but other variables are shown to contribute in previous studies as well
 - i. Lateral trunk bending and pelvic rotation has a significant impact on increasing pace angle in sprawling taxa (Kubo and Ozaki, 2009)



Dimetrodon milleri drawn with updated posture

Future Work

- Collect data from a wider number and variety of modern taxa and reduce the number of variables
- Expand list of taxa with known femoral abduction angles
- Take phylogenetic relationships of taxa into account during further analysis
- Expand fossil taxa to basal “pelycosaur” and therapsids
- Apply these methods to other groups such as extinct archosaurs

References

Beck, A.L., 2004. The locomotor evolution of the non-mammalian synapsids: The University of Chicago, 343 p.
 Gatesy, S.M., 1991. Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. *Journal of Zoology*, v. 224, p. 577-588.
 Hunt, A.P. and Lucas, S.P., 1998. Vertebrate tracks and the myth of belly-dragging: Tail-dragging tetrapods of the Late Paleozoic. in *Permian Stratigraphy and Paleontology of the Robledo Mountain, New Mexico*. Bulletin 12, p. 67-70.
 Kemp, T.S., 2005. Evolution of Mammalian Biology: Locomotion, in *Origin and Evolution of Mammals*, p. 342 p.
 Kubo, T. and Ozaki, M., 2009. Does pace angulation correlate with limb posture? *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 275, p. 54-58. doi: 10.1016/j.palaeo.2009.02.001.
 Kubo, T. and Benton, M.J., 2009. Tetrapod postural shift estimated from Permian and Triassic trackways. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 275, p. 1029-1037. doi: 10.1016/j.palaeo.2009.02.007.
 Romer, A.S. and Price, L.I., 1940. *Review of the Pelycosauria*. Baltimore, MD, Waverly Press Inc., 538 p.
 Rubidge, B.S. and Sidor, C.A., 2001. Evolutionary patterns among Permian-Triassic Therapsids: Annual Review of Ecology, Evolution, and Systematics, v.32, p. 449-480.
 Sacchi, E., Cifelli, R., Clifton, P., Nicolson, U., and Romano, M., 2014. *Dimetropus osageorum* n. sp. From the Early Permian of Oklahoma (USA): A Trace and Its Trackmaker. *Ichnos*, v. 21, p. 175-195.

Acknowledgements

We would like to thank Gene Hunt, Liz Cottrell, Virginia Power, Addison Wynn, Darrin Lunde, Paula Bohaska, Jessica Candiff, Katherine Turk, Allison Beck, Tai Kubo, Matthew Carrano, and Rowan Lockwood for their advice, support, and guidance over the course of this project, and the Museum of Comparative Zoology for access to their collections. We would also like to thank the National Science Foundation for funding this research through the Natural History Research Experiences program. NSF Grant No. 1560088.

