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The Dimetrodon dilemma: Reassessing posture in sphenacodontians and related non-mammalian synapsids

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The *Dimetrodon* dilemma: Reassessing posture in
sphenacodontians and related non-mammalian synapsids

A thesis submitted in partial fulfillment of the requirement for
the degree of Bachelor of Science in the Department of
Geology from The College of William and Mary

by

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ABSTRACT

Historically, the early synapsid *Dimetrodon* has been reconstructed with sprawling posture. However, referred trackways are narrower than most sprawling taxa and its spine lacks lateral flexibility, implying that this animal carried its body higher above the ground. The goal of this research was to re-evaluate the posture of *Dimetrodon* and other synapsids, by comparing body and trace fossil measurements to present-day analogues.

I collected linear measurements from limb and girdle bones of museum collections for *Dimetrodon*, other extinct synapsids, and extinct relatives of early amniotes. I also collected pace angles from the literature for taxa with associated trackways, where available. I compared these data with analogous measurements for 45 modern mammalian, reptilian, and amphibian species, which were collected from museum specimens or the literature. I analyzed these data using three multivariate statistical analyses to estimate posture in *Dimetrodon* and other fossil taxa in this study.

The results of this study suggest that *Dimetrodon* and its immediate relatives had a hindlimb abducted to 30°, similar to a Savannah monitor lizard or Virginia opossum. This study and previous work also suggest they had a unique style of locomotion compared to all other tetrapods. *Dimetrodon* lacks true modern functional analogues, likely due to the huge temporal and phylogenetic distance separating early synapsids from modern tetrapods. Additionally, *Aulacephalodon*, a more derived synapsid, was estimated to have a similar to more sprawling posture than *Dimetrodon*. This indicates that locomotor transitions in synapsids followed a process of mosaic evolution, rather than a continuous gradient from sprawling to upright posture.

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INTRODUCTION

   Dimetrodon (Fig. 1) was the apex terrestrial predator during the early to middle

Permian (Romer and Price, 1940). This genus was a "pelycosaur"-grade synapsid, and

a member of Sphenacodontidae, the most-derived family of basal, non-mammalian

synapsids (Reisz et al., 1992) . This "sail"-backed precursor of mammals is

conventionally depicted with sprawling posture, but this may be inaccurate. Its

trackways have a narrower gauge than most sprawling taxa, implying that this animal

was capable of some limb adduction and carried its body higher above the ground (Hunt

and Lucas, 1998). Additionally, mediolateral flexion of the sphenacodontid vertebral

column was likely reduced, similar to modern crocodilians and in contrast to sprawling

tetrapods, such as squamates (Kemp, 2005; Hopson, 2015).

   Through this study, I sought to **1) reconstruct posture in *Dimetrodon*, related

basal and derived non-mammalian synapsids, and stem amniotes**; **2) compare the

posture of fossil synapsids with extant species**, to identify modern analogues for

synapsid posture; and **3) describe transitions in synapsid posture**, to explore the

number and sequential order of these events.

Significance

   Historical reconstructions of many terrestrial vertebrates display sprawling

posture, but it is now accepted that some of these organisms, such as dinosaurs and

some pseudosuchians, had upright posture, as reflected in modern reconstructions

(Charig, 1972; Parrish, 1983; Bonaparte 1984). It is likely that early synapsids, like

Dimetrodon, were also reconstructed inaccurately. Such a finding would affect how

paleobiologists interpret the evolution, life history, and functional anatomy of

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"pelycosaurs" and basal therapsids, forming a more holistic understanding of their overall biology. If basal synapsids are found to have evolved elevated postures earlier than previously thought, or multiple times in different lineages, this could provide insight into how, when, and in which taxa major "mammalian" locomotor characters began to arise. Identifying and understanding these structures, their function, and their evolution from the Permian through to present could reveal strategies that promoted the long-term success and eventual dominance of mammals. Additionally, the techniques I use are widely applicable to other taxa and associated research questions, such as broad analyses of archosaurian locomotion and human joint biomechanics.
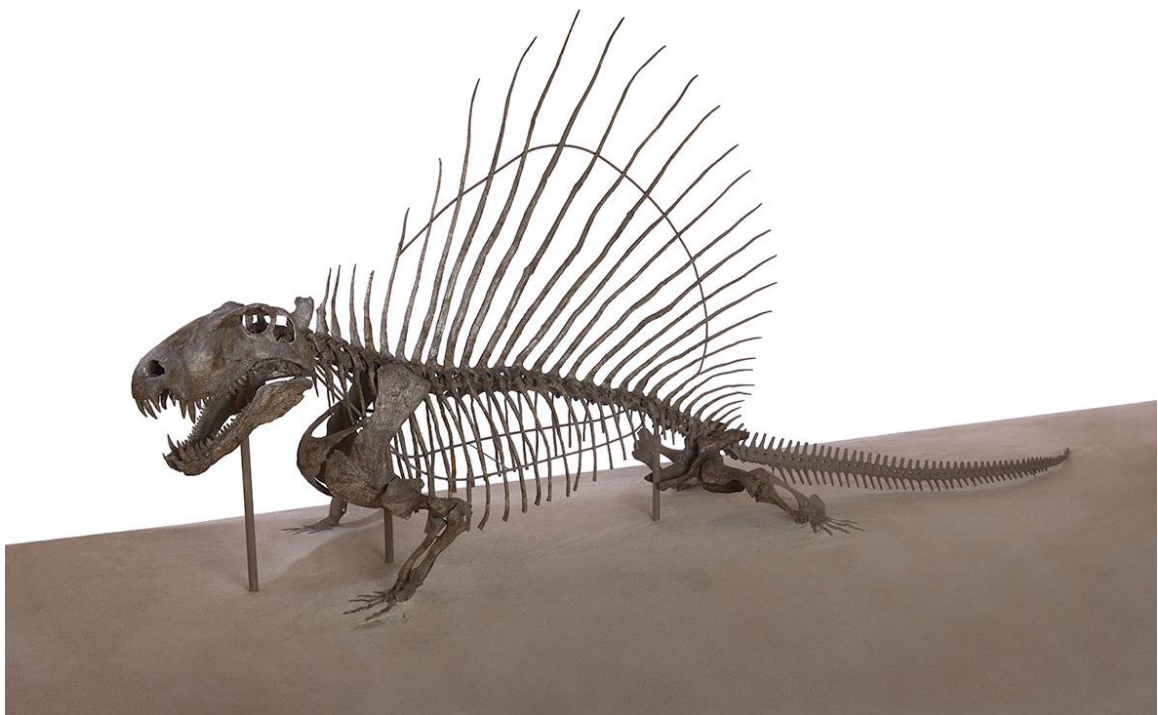

Figure 1. *Earlier* Dimetrodon grandis *mount from the Smithsonian National Museum of Natural History, photo courtesy of Donald E. Hurlbert and James Di Loreto, Smithsonian.*

Synapsida

Dimetrodon, other non-mammalian synapsids, and mammals are part of the clade Synapsida (Fig. 2). Synapsids are one of the main groups of the Amniota, which includes all tetrapods that lay an amniotic (terrestrial) egg, such as extant mammals, birds, and reptiles (Carroll, 1988; Kemp, 2005). Synapsids and their ancestors are phylogenetically distinct from all other amniotes. Most notably, they possess a single temporal opening that is located under the eye orbit, unlike sauropsids (the clade of modern reptiles, birds, and their ancestors), which traditionally have two temporal fenestrae (Kemp, 2005). Non-mammalian synapsids are commonly referred to as "mammal-like reptiles," but this is a misleading term. Referring to synapsids as "reptiles" suggests they are phylogenetically related to sauropsids, and promotes the idea that mammal ancestors "evolved" from reptiles (Angielczyk, 2009). However, the two groups have been evolutionarily distinct for hundreds of millions of years, having diverged from one another in the mid-Carboniferous, around 310-333 Ma (Benton,1990; Kumar & Hedges, 1998; Benton et al., 2014).

The earliest, most basal synapsids are traditionally grouped into a paraphyletic group, called the "Pelycosauria" (Fig. 2) (Romer and Price, 1940; Kemp, 2005). Earliest examples of "pelycosaurs" occur in the Early Pennsylvanian (323-315 Ma) of North America and the group persisted into the late Permian. They were most prolific in the early Permian. Up to 70 percent of early Permian amniote genera were members of the "pelycosaur" group (Carroll, 1988; Lucas, 2006). These early tetrapods were incredibly diverse; developing a wide variety of body plans and inhabiting a range of niches, some

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of which were filled for the first time (Rubidge and Sidor, 2001). Due to a poor fossil record during the Carboniferous, the exact relationships amongst "pelycosaurian" clades are difficult to distinguish, but it is largely agreed that Caseasauria (which includes families such as Caseidae) is the most ancestral, while Eupelycosauria is more derived (Carroll, 1988; Kemp, 2005). Within Eupelycosauria, the family Ophiacodontidae (of which *Ophiacodon* is a member) is most basal, while the family Sphenacodontidae (of which *Dimetrodon* is a member) is considered most derived (Kemp, 2005).

Therapsids are more derived than the "pelycosaurs", and include mammals in addition to all their ancestors more derived than sphenacodonts. Therapsids are distinguished by a variety of "mammal-like" features, including loss of certain skull elements, reduction of palatal teeth, and changes in the postcranial skeleton, specifically in the girdle bones (Carroll, 1988; Rubidge and Sidor, 2001; Kemp, 2005). Therapsids are widely considered to have had intermediate posture (Walter, 1986; Blob, 2001). Of the therapsids, suborders Anomodontia (specifically the subclade Dicynodontia) and Gorgonopsia were particularly diverse. Gorgonopsids, such as *Lycaenops*, were the dominant carnivores of the late Permian, and possessed highly conserved postcranial body plans (Rubidge and Sidor, 2001; Kemp, 2005). Dicynodonts, such as *Aulacephalodon*, were the most successful and diverse group of therapsids. They were the dominant herbivores of the late Permian, and are thought to have been capable of both hindlimb adduction and abduction, or holding their limbs close to or further out from the body, respectively (Rubidge and Sidor, 2001).
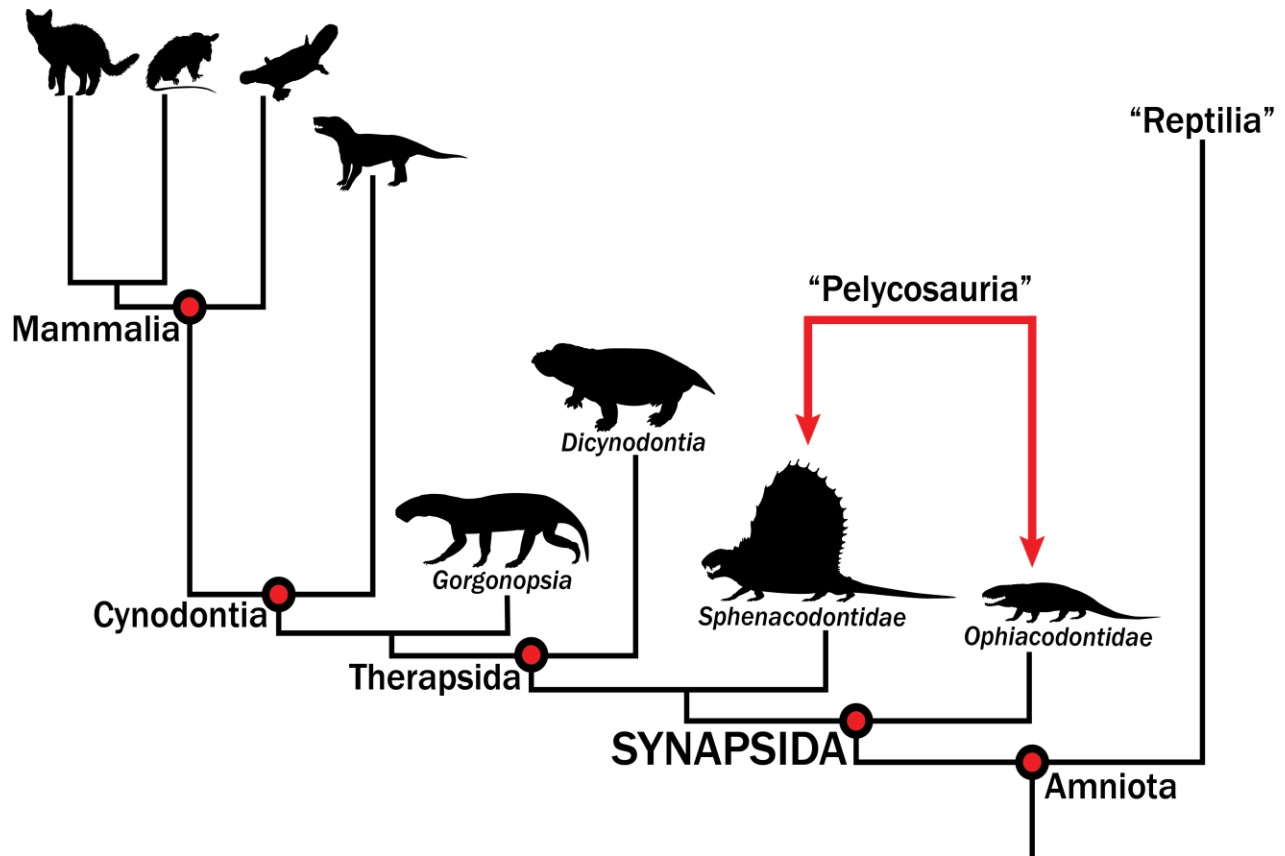
Figure 2. *Cladogram of synapsid relationships after Kemp (2005).*

<u>*Dimetrodon* and the Phylogenetic Importance of Sphenacodontidae</u>

    Dimetrodon is a member of the family Sphenacodontidae (Fig. 2), the most derived family of "pelycosaurs." This genus is one of the most easily recognizable synapsids, due to its tall neural spines (Romer and Price, 1940). It is named for its "two-measure" teeth, as it is the first synapsid known to exhibit canines. *Dimetrodon* is also considered to be one of the first large terrestrial carnivores to prey on animals of similar size (Romer and Price, 1940; Rubidge and Sidor, 2001). Approximately a dozen species of *Dimetrodon* are currently recognized, with the largest species, *Dimetrodon*

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angelensis, reaching 4.6 m and 250 kg and the smallest, *Dimetrodon teutonis*, measuring under 1 m and 14 kg (Romer and Price, 1940; Reisz, 1986; Rubidge and Sidor, 2001).

Dimetrodon body fossils are mostly found in the early Permian rocks of the southwestern United States (New Mexico, Texas, and Oklahoma) except for *D. teutonis*, which is found in Germany (Romer and Price, 1940; Berman et al., 2001). The ichnogenus, or trackway classification, attributed to sphenacodontians, *Dimetropus*, has a much broader stratigraphic and geographic range. *Dimetropus* is found in the late Carboniferous to early Permian of the above mentioned states to as far north as Nova Scotia in North America, France, Germany, Poland, and Russia in Europe, and Morocco in northwest Africa (Lucas et al., 1999; Hunt et al., 2004; Voigt et al., 2011, 2012).

The model sphenacodont-grade postcranial skeleton, which is based on *Dimetrodon*, retains many ancestral amniote characters but also exhibits notable derived characters. As noted by Kemp (2005), the prezygapophyses of each vertebra face inwards at an angle of 45° from the horizontal, an increase of 15° from more basal pelycosaurs, indicating a limited lateral flexibility of the vertebral column. The humerus of *Dimetrodon* fits into a screw-shaped glenoid fossa, signifying a more limited range of motion at the glenohumeral joint (Jenkins, 1969). The acetabulofemoral joint, on the other hand, is shallow and simple, likely allowing for a greater range of motion (Kemp, 1982, 2005)

Tetrapod Posture

<u>Qualitative Measures - Posture Grade</u>

Posture grades are discrete categories of tetrapod locomotion defined on the basis of relative orientations of the proximal limb bones and elevation of the trunk above the ground. Earliest descriptions of posture in tetrapods were based on the notion of a "primitive, reptilian" condition, characterized by *abd*ucted limbs (perpendicular to the parasagittal plane) and slow movement, and an "advanced, mammalian" condition, characterized by *add*ucted limbs (parallel to the parasagittal plane) and rapid movement (Jenkins, 1971). It has been popular in the past forty years to classify tetrapods into three broad posture grades: sprawling, semi-erect/dual-gait, and upright (Fig. 3). Reptiles and amphibians are broadly considered "sprawling," crocodilians are considered "dual-gait," and mammals are considered "upright" and "cursorial" (Bakker, 1971; Charig, 1972; Gatesy, 1991; Kubo and Benton, 2009). These groups can be problematic, however, as they assume that "upright" locomotion is the "improved" or "advanced" condition and "sprawling" locomotion is "primitive. The discrete binary between sprawling and upright carries a high degree of phylogenetic bias and ignores the broad spectrum of tetrapod locomotion in favor of discrete categories (Jenkins, 1971; Jenkins and Camazine, 1977; Gatesy, 1991). Monotremes for example, do not fit the "cursorial" model, as they almost fully abduct their proximal limb bones in a manner that resembles sprawling posture, although their form of locomotion is quite different from that of a reptilian "sprawler" (Jenkins, 1970). Other mammals, both placentals and marsupials, also show a wide range in limb abduction, with some "cursorial" types, such as felids, canids, and ungulates, fully adducting the limb, and "non-cursorial" types holding their proximal limb bones as much as 50° outside of the parasagittal plane (Jenkins, 1971; Jenkins and Camazine, 1977). It is important then, when describing

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posture based on these discrete grades, to be more specific in terms of how they are

defined, to better encompass the variation within mammalian and reptilian groups.
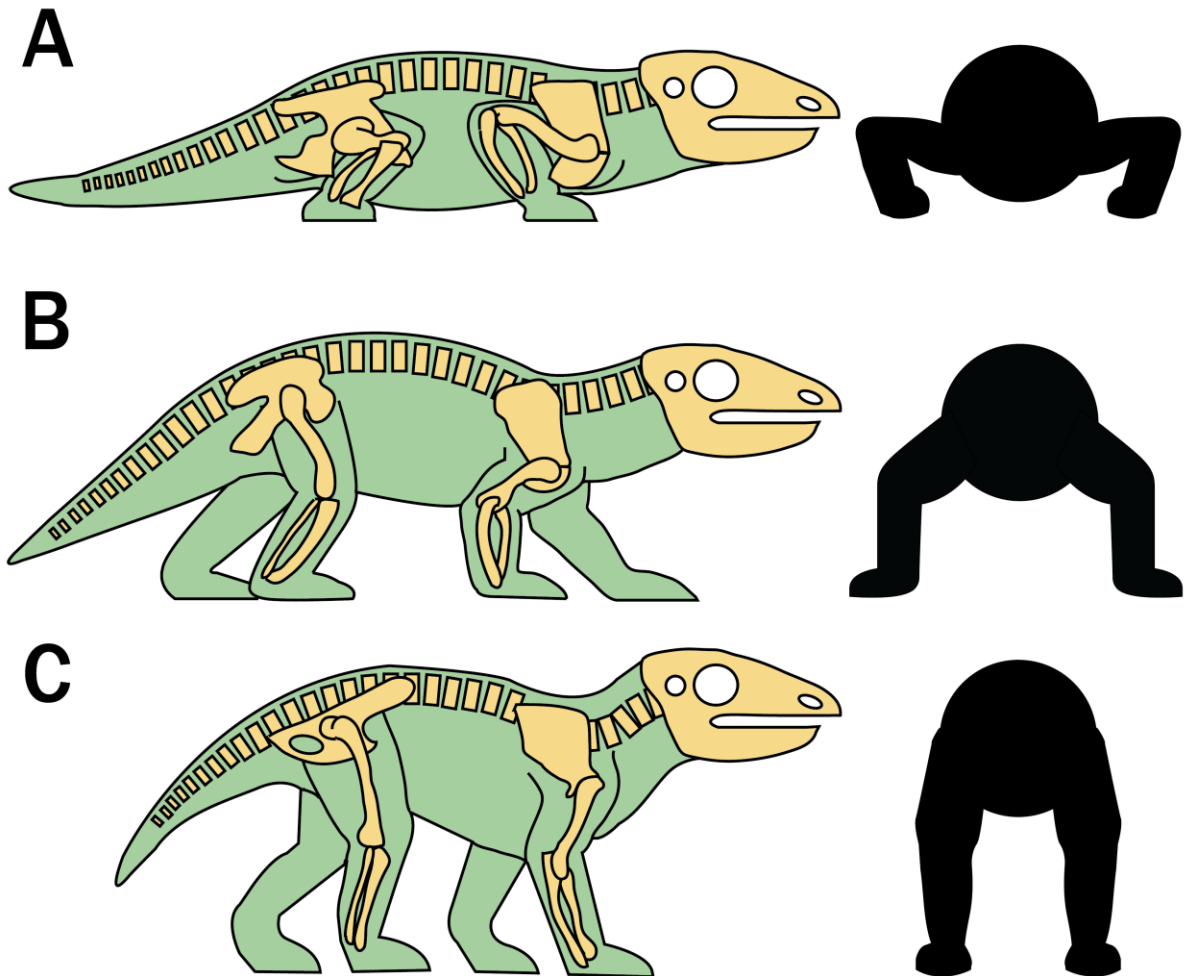
Figure 3. Diagram of three discrete posture grades sprawling (A), dual-gait (B), and upright (C) viewed in the sagittal plane (left) and frontal plane (right), after Gatesy (1991).

Quantitative Measures – Femoral Abduction Angle

In contrast to the discrete categories provided by posture grades, the femoral

abduction angle (FABA) provides a continuous scale to describe posture. The femoral

abduction angle is defined as the smallest angle between the long axis of the femur and

parasagittal plane (Fig. 4) (Kubo and Ozaki, 2009). The benefit of this method of

describing posture is that it operates outside of the generalizations by posture grades, and is independent of assumptions made based on phylogenetic relationships (i.e., mammals must be upright and reptiles must be sprawling) (Gatesy, 1991; Kubo and Ozaki, 2009). Femoral abduction angle is by no means a replacement for posture grade, but it is another useful tool to comprehensively describe an organism's posture.
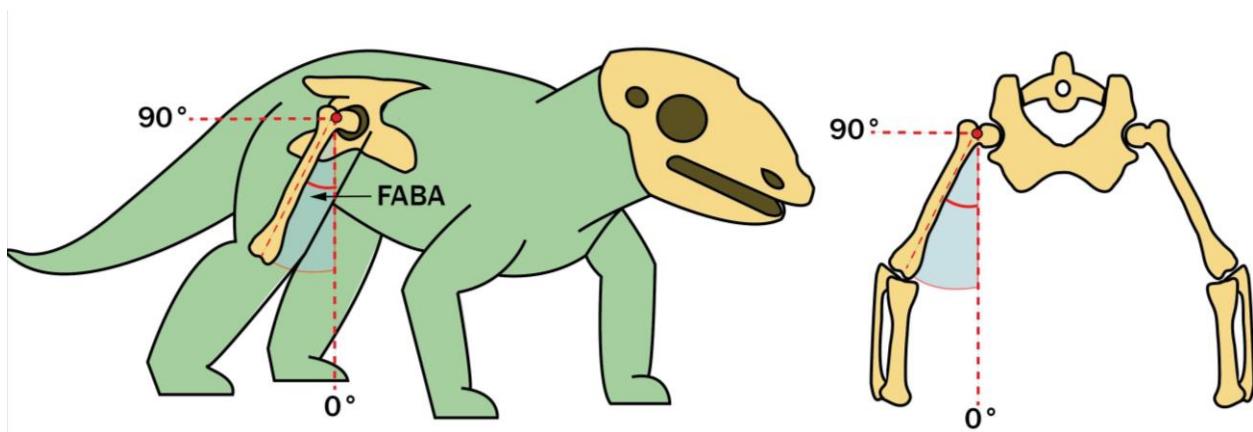
Figure 4. *Visualization of femoral abduction angle in the tetrapod hindlimb in angled lateral view (left) and frontal view (right)*

METHODS

Many studies show that bone morphology and trackway pace angle correlate with limb posture since bone form directly reflects limb function and posture (Biewener, 1983, 1989; Blob & Biewener, 1999) Postcranial skeletal dimensions have long been thought to correlate with tetrapod posture, but it is unclear which characters are most important for determining an organism's posture (Jenkins and Camazine, 1977; Beck, 2004). Trackway pace angulations also correlate with an organism's posture, as wide pace angulations (~120°-180°) indicate non-sprawling posture and narrow pace angulations (<108°) indicate sprawling posture (Kubo and Ozaki, 2009). Previous

studies using linear skeletal dimensions to predict posture generally focus on a small set of characters that are ineffective for describing posture on their own, because a small sample of variables cannot effectively describe complex locomotor systems. However, increasing the quantity of characters measured per specimen provides more information about an organism's skeleton, and may increase the ability to describe and predict posture in fossil tetrapods (Beck, 2004). Trackways are also an incomplete predictor of posture, as pace angle is frequently influenced by mediolateral flexion of the axial skeleton in organisms with a larger FABA (more sprawling) (Kubo and Ozaki, 2009). Because of this, trackway data are likely most effective when combined with other information, such as skeletal dimensions. Because of this, I compared a wide range of postcranial skeletal characters and trackway pace angles of extant tetrapods with analogous measurements from fossil synapsids and stem-amniotes, using three multivariate statistical analyses. Permian synapsids have an extensive postcranial skeletal and trackway record, providing abundant material that can be compared with extant vertebrates.

Taxonomic Sampling

<u>Extant Species</u>

I collected data from 45 species of extant tetrapod taxa, including 21 mammal, 22 reptile, and 2 salamander species (Table 1). I selected taxa that practice near-obligate terrestrial locomotion, with few exceptions, from a range of families and orders within each class to maximize phylogenetic diversity. I categorized posture grades of these taxa based on descriptions in the literature. Broad posture grades are defined as sprawling, upright, or dual-gait. Narrower posture grades, which are more descriptive of

locomotion style as well as posture, include groups such as "cursorial" and "non-cursorial" therian mammals and "elevated sprawling" and "fully sprawling" squamates.

Class	Order	Genus/Species	Common name	No. Spec
Mammalia	Marsupialia	*Didelphis virginiana*	Virginia opossum	3
		Vombatus ursinis	Common wombat	3
		Sarcophilus harrisii	Tasmanian devil	3
		Thylacinus cynocephalus	Thylacine/Tasmanian wolf	3
	Carnivora	*Herpestes ichneumon*	Egyptian mongoose	3
		Canis lupus	Grey wolf/dingo	3
		Vulpes vulpes	Red fox	3
		Felis silvestrus	Domestic cat/wildcat	3
		Ursus americanus	American black bear	3
		Procyon lotor	Common raccoon	3
		Lontra canadensis	North American river otter	3
		Mephitis mephitis	Striped skunk	3
	Ungulata	*Capra hircus aegagrus*	Domestic goat	3
		Odocoileus virginianus	White tailed deer	3
		Pecari tajucu	Collared peccary	3
	Edentata	*Dasypus novemcinctus*	Nine-banded armadillo	3
	Lagomorpha	*Lepus californicus*	Black-tailed jackrabbit	3
	Rodentia	*Hydrochoerus hydrochaeris*	Capybara	3
		Castor canadensis	American beaver	3
	Monotremata	*Ornithorhynchus anatinus*	Platypus	3
		Tachyglossus aculeatus	Short-beaked echidna	3
Reptilia	Crocodilia	*Alligator mississippiensis*	American alligator	3
		Alligator sinensis	Chinese alligator	3
		Paleosuchus trigonatus	Smooth fronted caiman	3
		Paleosuchus palpebrosus	Cuvier's dwarf caiman	2

		Caiman crocodilus	Common caiman	3
		Crocodylus porosus	Saltwater crocodile	2
		Crocodylus rhombifer	Cuban crocodile	2
	Squamata	*Varanus komodoensis*	Komodo dragon	3
		Varanus exanthematicus	Savannah monitor	3
		Varanus salvator	Asian water monitor	3
		Tupinambis teguixin	Gold tegu	3
		Heloderma suspectum	Gila monster	3
		Corucia zebrata	Monkey tail skink	3
		Tiliqua scincoides	Northern blue tongue skink	3
		Iguana iguana	Green iguana	3
		Cyclura cornuta	Rhinoceros iguana	3
		Furcifer pardalis	Panther chameleon	1
		Trioceros jacksonii	Jackson's chameleon	3
		Trioceros melleri	Meller's chameleon	3
		Calumma parsonii	Parson's chameleon	2
	Testudinata	*Terrapene carolina*	Common box turtle	3
		Rhinoclemmys pulcherrima	Painted wood turtle	1
Amphibia	Urodela	*Andrias japonicus*	Japanese giant salamander	3
		Cryptobranchus alleganiensis	Hellbender	1
			TOTAL	125

 Table 1. Extant species used in study with higher taxonomic classifications, binominal names, common names, and number of specimens used per taxon.

Fossil Genera

    I focused on sampling from *Dimetrodon*, since this genus is one of the most common tetrapods of the early Permian and the most easily recognized "pelycosaur". I studied additional synapsid and stem-amniote taxa based on the completeness of postcranial material available and phylogenetic relationship to *Dimetrodon* (Table 2). As a more basal taxon to *Dimetrodon*, I included *Ophiacodon*, a "pelycosaur" of the family

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Ophiacodontidae. To sample from more derived synapsids to *Dimetrodon*, I incorporated three therapsid genera, including *Lycaenops* (Gorgonopsidae), as well as the dicynodonts *Aulacephalodon* (Geikiidae) and *Dinodontosaurus* (Kannemeyeriidae). I also included two stem-amniotes of the Diadectomorpha, *Diadectes* and *Diasparactus* (Diadectidae), as a basal outgroup for Synapsida.

Class	Order/ Suborder	Genus	No. Specimens
Synapsida	"Pelycosauria"	*Ophiacodon*	6
		Dimetrodon	11
	Therapsida	*Aulacephalodon*	1
		Dinodontosaurus	1
		Lycaenops	1
--	Diadectomorpha	*Diadectes*	3
		Diasparactus	1
		Total Specimens	**24**

Table 2. Fossil species used in study with higher taxonomic classifications, genus, and number of specimens observed.

Data Collection

Postcranial Morphology

For all 45 species of extant vertebrates, I measured postcranial skeletal specimens from collections of the National Museum of Natural History (NMNH, Washington, DC), and Field Museum of Natural History (FMNH, Chicago, IL). I collected data from an average of three specimens per taxon, with 125 specimens total, to account for some temporal, regional, and subspecies variation. A full list of extant museum specimens is provided in Appendix A. I avoided specimens with obvious wear, breakage, and/or pathological changes (unless restricted to a single side) to prevent collecting inaccurate representations of standard skeletal morphology for each species.

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I examined cleaned, disarticulated specimens when available to increase ease of measurement; however, long bones were frequently still articulated on older specimens. Juvenile specimens were avoided for mammals, and only the largest specimens available were used for reptiles and amphibians, to ensure adult/sub-adult specimens were measured rather than juveniles.

For the seven extinct genera, I measured postcranial fossil elements from collections of the NMNH, FMNH, and Museum of Comparative Zoology (MCZ, Cambridge, MA). A full list of fossil museum specimens is provided in Appendix B. I selected specimens with the most complete postcrania, focusing first on specimens with complete appendicular skeletons, and then measuring those with less complete material. I avoided specimens that were disintegrating, obviously deformed, roughly prepared, and/or composed of several individuals. Where specimens contained broken/missing elements, and/or elements buried in matrix, but otherwise well-preserved material, I collected data from the complete parts of the skeleton, and did not measure damaged or missing elements.

I measured appendicular skeletal elements of both extant and extinct taxa using digital calipers. I took 57 measurements from the bones of the shoulder girdle (scapula and coracoid) and pelvic girdle (ilium, ischium, and pubis), as well as the proximal and distal long bones of the forelimb (humerus, radius, and ulna) and hindlimb (femur and tibia) (Fig. 5). I focused on bone length, long bone diameter in the craniocaudal and mediolateral directions, shape of articular surfaces (lengths of long and short axes), and size and position of major muscle attachment surfaces (after Beck, 2004).
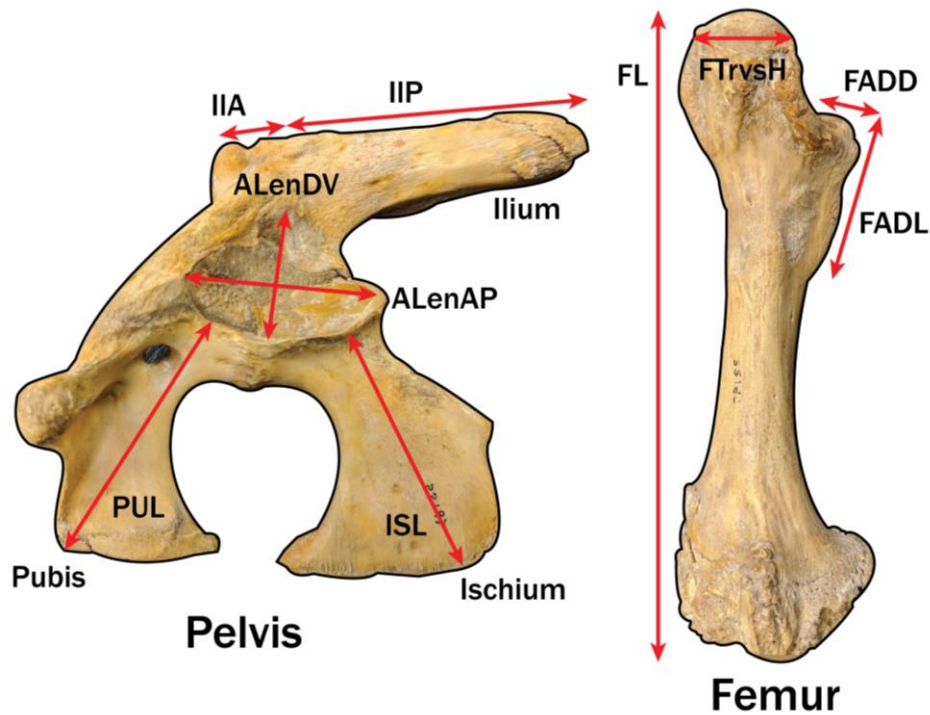
Figure 5. *Illustrations of selected linear dimensions of the pelvis and femur of* Varanus komodoensis*.*

Trackway Morphology

    I recovered pace angles (Fig. 6) for extant taxa from trackways in the literature, and recorded values as published, or in the absence of that data, measured angles from aerial photos and/or scale drawings in papers or guidebooks. There was a great deal of variability in the sample size of data available per species. Some taxa, such as *Crocodylus porosus* (n=8) and *Tiliqua scincoides* (n=13), had several associated trackways in the literature, but for most species only one or two were available. Because of this variability, I averaged the pace angle for the trackways for each species, and used that as a species average value. To differentiate between the high walk and sprawling gait of crocodilians, when a species had values for both, I took an

average of each gait rather than an average of all pace angles at both postures. I only collected pace angles from tracks of animals that were moving at slow, even gaits, such as a walk or slow trot. I was unable to recover trackway data for nine extant species: two mammals (*Thylacinus cynocephalus, Sarcophilus harrisii*), five reptiles (*Varanus salvator, Cyclura cornuta, Trioceros jacksonii, T. melleri, Calumma parsonii*), and the two cryptobranchid amphibians (*Andrias japonicas, Cryptobranchus alleganiensis).*

For extinct taxa, I also compiled pace angles from published trackways in the literature. I used three ichnogenera, *Ichniotherium cottae*, *Dimetropus*, and *Dicynodontipus* in this study. *Ichniotherium cottae* is the only ichnogenus known in the fossil record to have a verified track maker, as body fossils of *Diadectes* have been found with an *I. cottae* trackways in the same horizon and locality (Voigt et al., 2007). The track maker of *Dimetropus* is assumed to be a member of Sphenacodontidae or Edaphosauridae, so for this study I attributed it to *Dimetrodon,* as sphenacodontids share conserved postcranial morphology (Fröbisch et al., 2011, Romano et al., 2016). Similarly, *Dicynodontipus* is assumed to have been made by a large dicynodont like *Aulacephalodon* or a close relative (de Klerk, 2002). All other fossil taxa were excluded from analyses incorporating pace angle, due to a lack of attributed ichnogenus. Analyses that incorporated pace angle used the following fossil specimens (n=4): *Dimetrodon milleri* (MCZ 1365), *Dimetrodon "incisivus"* (FMNH UC-1), *Diasparactus zenos* (FMNH UC-679), and *Aulacephalodon peavoti* (FMNH UC-1532). Analyses that omitted pace angle used the same four specimens but also included *Ophiacodon mirus* (FMNH UC-671) (n=5).

When measuring tracks in Adobe Illustrator, I used photos of tracks taken in aerial view normal to the ground, or scale drawings of tracks. I measured pace angle as the angle between three consecutive pes prints from the middle digit (Fig. 6). Chameleon tracks were the exception to this and were measured from the center of the pes print, as their modified foot results in a highly derived print (Kubo, 2010).
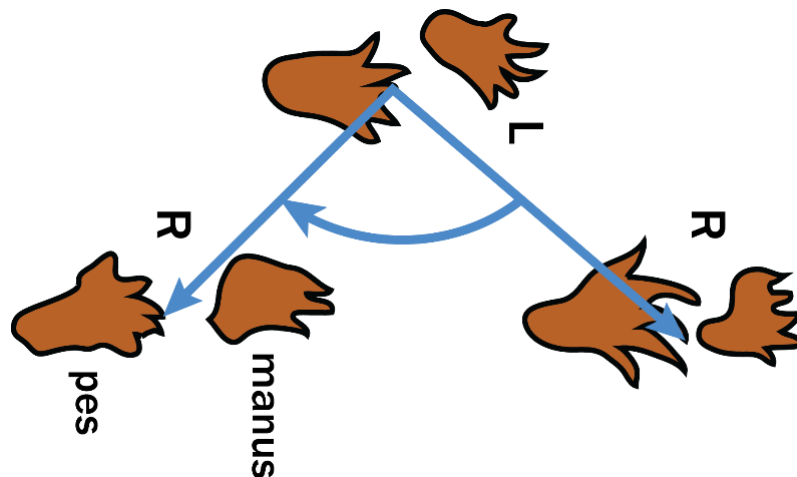
Figure 6. *Illustration of pace angle, measured as the angle between three consecutive pes prints from the middle digit.*

Extant FABA

I collected femoral abduction angles (FABA) for extant taxa from the literature, where available. I was able to recover FABA for 19 of the 45 species, because biomechanical analyses tend to favor copious repeat analyses within a single species rather than fewer analyses with phylogenetically diverse taxonomic samples. I expanded some estimates of FABA based on the literature, to increase the number of taxa with associated FABA. First, the FABA of *Vulpes vulpes* (~5°) is recognized as a general angle for canids, so I applied it to *Canis lupus* as well (Jenkins and Camazine, 1977). No quantitative studies have been done on the limb abduction/adduction capabilities of artiodactyl ungulates, but I have listed the three species I use as having a

FABA of ~0° as other biomechanical studies of different aspects of their limbs state that they are restricted to flexion/extension movement strictly within the parasagittal plane (Hildebrand and Goslow, 2001; Clifford, 2010). Finally, the only chameleon for which limb biomechanical analyses exist in the literature, *Trioceros jacksonii*, has a humeral abduction angle, but not a FABA (Peterson, 1984). However, this angle is similar to the FABA value for chameleon species not included in this study, so the humeral abduction angle has been substituted for FABA for this specific taxon (Fischer et al., 2010).

Statistical Analysis

All data were analyzed in RStudio using three multivariate statistical methods: discriminant function analysis (DFA) principal component analysis (PCA), and multiple regression analysis (MRA). DFA and PCA were used to explore posture grade in fossil taxa, and MRA was used to predict FABA in fossil taxa. The data used in these analyses included limb dimensions, pace angle, estimated body mass, and FABA.

Sparse Discriminant Function Analysis – *Estimating posture grade*

I used a sparse discriminant function analysis (DFA) with the R package "sparseLDA" to group extant taxa into their assigned posture grades, to which extant taxa can be compared (Clemmensen and Kuhn, 2016). Due to the high dimensionality of this dataset, the sparse DFA is useful for identifying variables that best estimate posture and estimate the optimal number of variables to maximize performance. DFA is useful for discriminating preassigned groups into their respective categories, by defining axes that maximize distance among the groups. Each axis, called a linear discriminant axis (LD), is made up of the variables that increase disparity between groups. I

conducted two separate DFA analyses, one including pace angle and the other

excluding it, so that more extant taxa could be incorporated, as well as the synapsids

Ophiacodon and *Lycaenops*, which lack an attributed ichnogenus. Both DFA included

all variables associated with skeletal dimensions.

I next used leave-one-out cross validation (LOOCV) to determine the optimal

number of variables for each analysis (to maximize accuracy) and optimal smoothing

parameters (to reduce bias in the dataset). Finally, in the actual DFA, extant specimens

in the modern dataset were discriminated into their respective posture grades using

variables selected in the LOOCV along each axis. I then incorporated fossil specimens

into the analysis and explored their posture grades, based on relative proximity to or

distance from extant specimens of known posture grade. DFA cannot handle missing

data, so any taxa with missing data were eliminated. The nine extant taxa and

Ophiacodon mirus specimen mentioned above were omitted from the DFA incorporating

pace angle for this reason, but incorporated into the DFA without pace angle.

Principal Component Analysis – *Estimating posture grade*

I used principal component analysis (PCA) to further explore the data in a less

discriminatory fashion. Like DFA, PCA determines which variables contain the most

information when combined, and then converts them into axes. In PCA, the axes are not

related to particular classifications of the data, but instead represent the direction of

highest variation in the data. Each axis is called a principal component (PC), where PC1

is the axis that accounts for most of the variability, PC2 the second-most, PC3 the third-

most, and so on. Because it takes a less forceful approach to the data than DFA, PCA

is a complementary way to explore posture grade. PCA also cannot handle missing

data, so it also excluded the same nine extant taxa, and included the four fossil taxa in the DFA with pace angle.

Multiple Regression Analysis – *Estimating FABA*

I used sparse multiple regression analysis (MRA) to estimate FABA in fossil specimens, based on the known FABA of extant taxa using the package "glmnet" (Friedman et al., 2010). MRA explores the relationship between a set of predictor variables, which in this study includes limb and trackway dimensions, and a response variable, which is FABA. I used the modern dataset to generate the model that best estimated the known response (FABA) in extant specimens, and then used that model to estimate the unknown response in fossil specimens.

I used a similar approach to the sparse DFA in the sparse MRA, starting with a LOOCV to choose the smoothness penalty, most useful variables, and their coefficients in the model. I used the same variables in the DFA and PCA, including pace angle, and incorporated extant FABA. MRA also cannot handle missing data, so the extant and fossil taxa excluded in previous analyses were also excluded here. 50% confidence intervals for the FABA of fossil specimens were obtained by bootstrapping the modern data (n=1000).

Interpretation of Loadings

I interpreted variables that had high loadings in two or more of the four analyses. In each analysis, I selected variables with coefficients greater than the absolute value of ±0.3 for DFA and ±0.2 for PCA. The multiple regression incorporated few variables, so a cutoff for interpretation wasn't applied or necessary.

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RESULTS

Interpreted Anatomy

The 13 variables that were interpreted as predictors of posture across all four analyses are listed in Tables 3 & 4. Five variables are associated with the forelimb and six are associated with the hindlimb, and pace angle has a large coefficient in all analyses in which it was included.

The LOOCV for the DFA with pace angle results in a model using 23 variables along each linear discriminant axis (Fig 7). For the DFA without pace angle, the LOOCV resulted in a model with 13 variables along each linear discriminant axis. In both of the DFA analyses, clusters of extant taxa are well-defined and well separated in a triangle (Fig 8, 9). This indicates that all three clusters represent distinct locomotor grades, rather than a gradational scale from sprawling to dual-gait to upright posture. The removal of pace angle allows for the additional taxa mentioned in the methods to be incorporated, but also reduces the length of the linear discriminant axes, likely because the analysis with pace angle incorporates 23 variables while the other uses 13.

In the principal component analysis, the first PC axis (PC1) explains 77.3% of the variation, but is not particularly informative because it is highly correlated with size, since all variables are loaded around 0.1 (Fig 11). The second principal component axis (PC2) accounts for 11.6% of the variation in the data, and separates mammals from all other taxa making it somewhat informative of locomotion, but more so of phylogeny and the derived skeletal anatomy of mammals. The third axis (PC3) accounts for 2.2% of the variation in the data, and exhibits a continuum between "squatted" and cursorial

locomotion in the mammal morphospace, and sprawling and dual-gait locomotion in the reptile morphospace (Fig 12).

The LOOCV for the multiple regression, resulted in a model with 10 variables. In the FABA plot, posture grades are not well defined amongst extant taxa. Sprawling taxa do represent the highest FABA, and upright taxa do represent the lowest FABA, but boundaries between the groups are not distinct (Fig. 13A).

Classification of Posture and Estimates of FABA

Both *Dimetrodon* specimens were assigned into the upright cluster in both of the DFA's (Table 5). Both specimens plot quite far from the cluster, however, and are better described as plotting between the sprawling and upright clusters. In the PCA, both specimens recover in the morphospace of large squamates (varanids, teiids, and iguanids like *Tupinambis teguixin*) in the graph with both PC2 and PC3 (Fig 12). Along PC2, they have similar values to large squamates and small crocodilians (like *Paleosuchus palpebrosus*), while along PC3, they align with large squamates and shorter-limbed therian mammals, such as *Lontra canadensis*. In the multiple regression, *Dimetrodon milleri* was estimated to have a FABA of 37.26° with 50% confidence intervals ranging from 31° to 46°. *Dimetrodon incisivus* was estimated to have a FABA of 25.45° with 50% confidence intervals of 19° to 40° (Fig 13B). These FABA align with taxa such as the Virginia opossum (*Didelphis virginiana,* 38°), raccoon *(Procyon lotor,* 30°), saltwater crocodile (*Crocodylus porosus,* 27° in high-walk), and Savannah monitor (*Varanus exanthematicus*, 28°).

Diasparactus recovers as sprawling in both of the discriminant function analyses, but also appears to be intermediate with dual-gait in the DFA with pace angle (Table 5, Fig 8). In the PCA, *Diasparactus* recovers close to the edge in the morphospace of large squamates. Along PC2, it shares a similar location to *Dimetrodon*, as well as large squamates and small crocodilians, and along PC3, it shares a similar location to monotremes (like *Ornithorhynchus anatinus*) and "squat"-legged therian mammals (like *Vombatus ursinus*) (Fig 12). In the MRA, *Diasparactus* was estimated to have a FABA of 47.24° with 50% confidence intervals of 34° and 53°, aligning it with extant taxa like *Paleosuchus trigonatus* (48° in low-walk) and *Tachyglossus aculeatus* (43°).

Aulacephalodon is surprisingly assigned to the sprawling cluster in the DFA with pace angle (Fig 8. When pace angle is removed, it is still assigned as sprawling, but with a much lower probability and plots closer to both *Dimetrodon* (Fig 9, Table 5). In the PCA, it recovers well apart from any of the morphospaces of extant tetrapods. It falls in the same position along PC2 as the other fossil specimens, with large squamates and small crocodilians, but along PC3 it falls at a far more positive value than any of the other taxa, although it is closest to the monotreme *Tachyglossus aculeatus*. In the MRA, *Aulacephalodon* was estimated to have a FABA of 69.18° with 50% confidence intervals of 56° and 87°, aligning it with *Iguana iguana* (70°).

Ophiacodon mirus is only incorporated in the discriminant function analysis with pace angle omitted. In this analysis it recovers firmly within the sprawling cluster (Fig 9).

Interestingly, none of the fossil specimens recover with dual-gait taxa in any of the analyses of posture grade (DFA and PCA). Overall, synapsid taxa in the DFA seem to fall between the sprawling and upright clusters, while *Diasparactus* plots distally from

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all three groups, but recovers as closer to sprawling. Because of this, their form of "intermediate" posture may be poor analogue for a transitional posture between sprawling to upright tetrapod locomotion (Parrish, 1987; Gatesy, 1991). With this in mind, I conducted another sparse DFA with the dual-gait taxa dropped, which plotted the data along a one-dimensional linear discriminant axis equivalent to LD1 in the DFA with pace angle (Fig 10). The histogram shows a similar pattern in the fossil taxa to the DFA, with both *Dimetrodon* specimens recovering intermediately between sprawling and upright, but more proximal to upright, and both *Aulacephalodon* and *Diasparactus* recovering within sprawling.

		Sparse DFA w/ p.a.		Sparse DFA w/out p.a.		PCA			MRA
		LD1	LD2	LD1	LD2	PC1	PC2	PC3	
Forelimb	SCL	0.000	**0.928**	0.000	**1.029**	0.152	0.123	0.010	
	CB	0.229	0.000	**-0.308**	-0.084	0.070	**-0.305**	0.029	
	DPCmom	0.144	0.000	-0.130	0.000	0.100	**-0.225**	**-0.402**	**-2.141**
	RL	**-0.464**	0.000	**0.395**	0.000	0.154	0.100	-0.171	
	OL	**-0.382**	-0.112	0.260	-0.244	0.124	**0.207**	**0.241**	**-5.795**
Hindlimb	FADD	0.027	**-0.304**	0.000	**-0.503**	0.112	-0.141	**0.428**	**3.393**
	FABD	0.000	0.078	0.000	0.000	0.108	**0.279**	**0.230**	**11.974**
	FABDV	0.000	0.026	-0.008	0.000	0.064	**-0.329**	-0.094	**5.074**
	FABDH	-0.009	**-0.756**	0.000	**-0.452**	0.134	**0.231**	0.177	
	ALenDV	**0.410**	0.381	**-0.306**	0.241	0.152	-0.142	-0.080	
	IIDVL	**-0.302**	-0.069	**0.475**	0.000	0.124	0.187	0.139	**11.819**
Trackway	Pace Angle	-0.018	**0.503**			0.067	**0.327**	**-0.361**	**-15.787**

Table 3. *Loadings/coefficients of 13 variables across all four analyses that were significant for two or more analyses.*

Forelimb	**SCL**	Vertical length of scapula
	CB	Length of coracoid (in diapsids) or coracoid process (in mammals)
	DPCmom	Vertical distance between the top of the deltopectoral crest to the humeral head
	RL	Length of radius
	OL	Vertical height of olecranon process of ulna
Hindlimb	**FADD**	Horizontal depth of femoral adductor attachment
	FABD	Horizontal depth of femoral abductor attachment
	FABDV	Vertical distance of the top of the femoral abductor attachment to the top of the femoral head
	FABDH	Horizontal distance from the lateral margin of the femoral abductor attachment to the center of the femoral head (when femur is oriented in frontal view)
	ALenDV	Dorsoventral height of acetabulum
	IIDVL	Distance from dorsal margin of acetabulum to dorsal border of the ilium (in line with where it meets the sacrum)
Trackway	**Pace angle**	Angle measurement between three consecutive steps in a trackway

Table 4. *Descriptions of interpreted variables from Table 3, taken from Appendix C.*
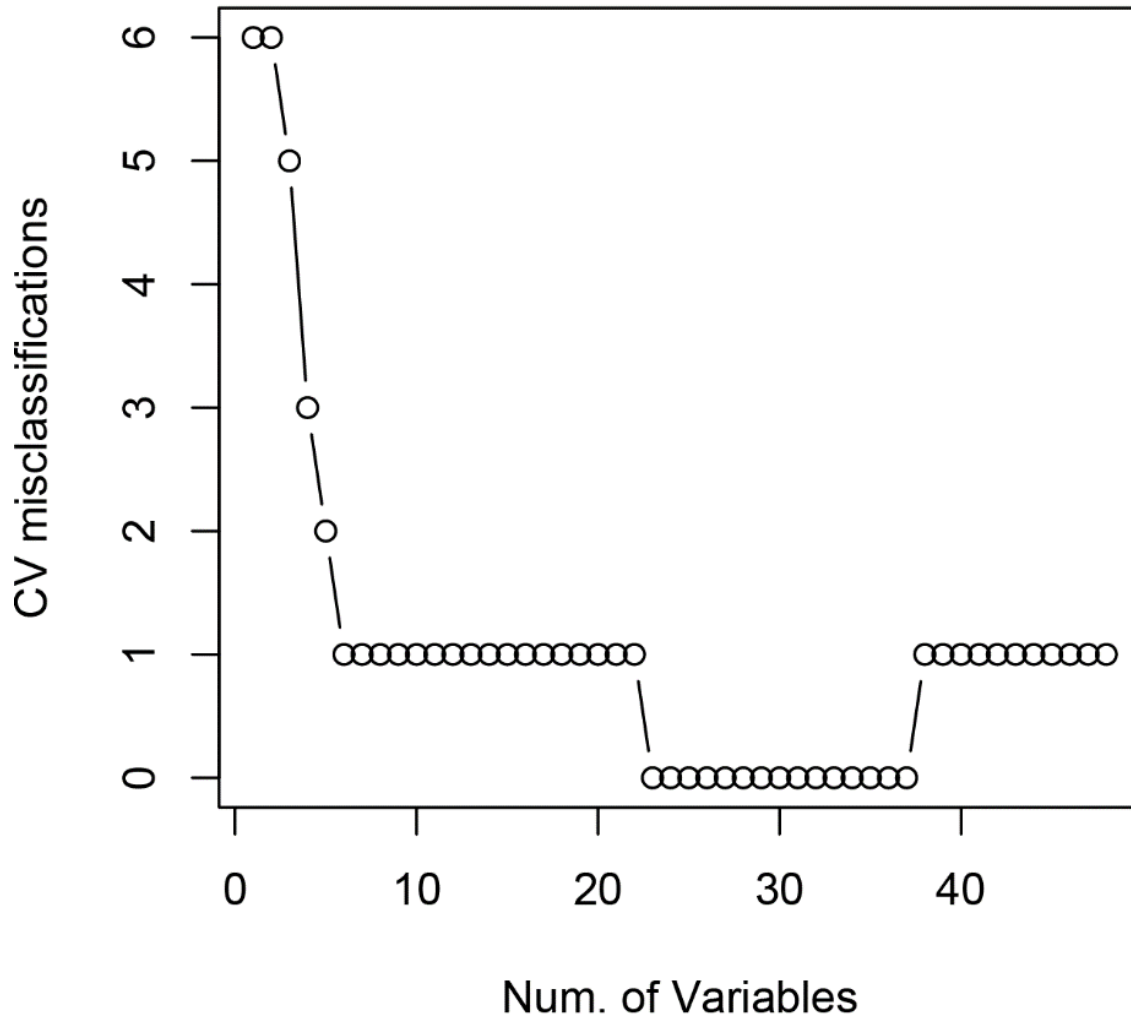
Figure 7. *Plot of number of misclassifications during LOOCV of sparse DFA versus the number of variables included*
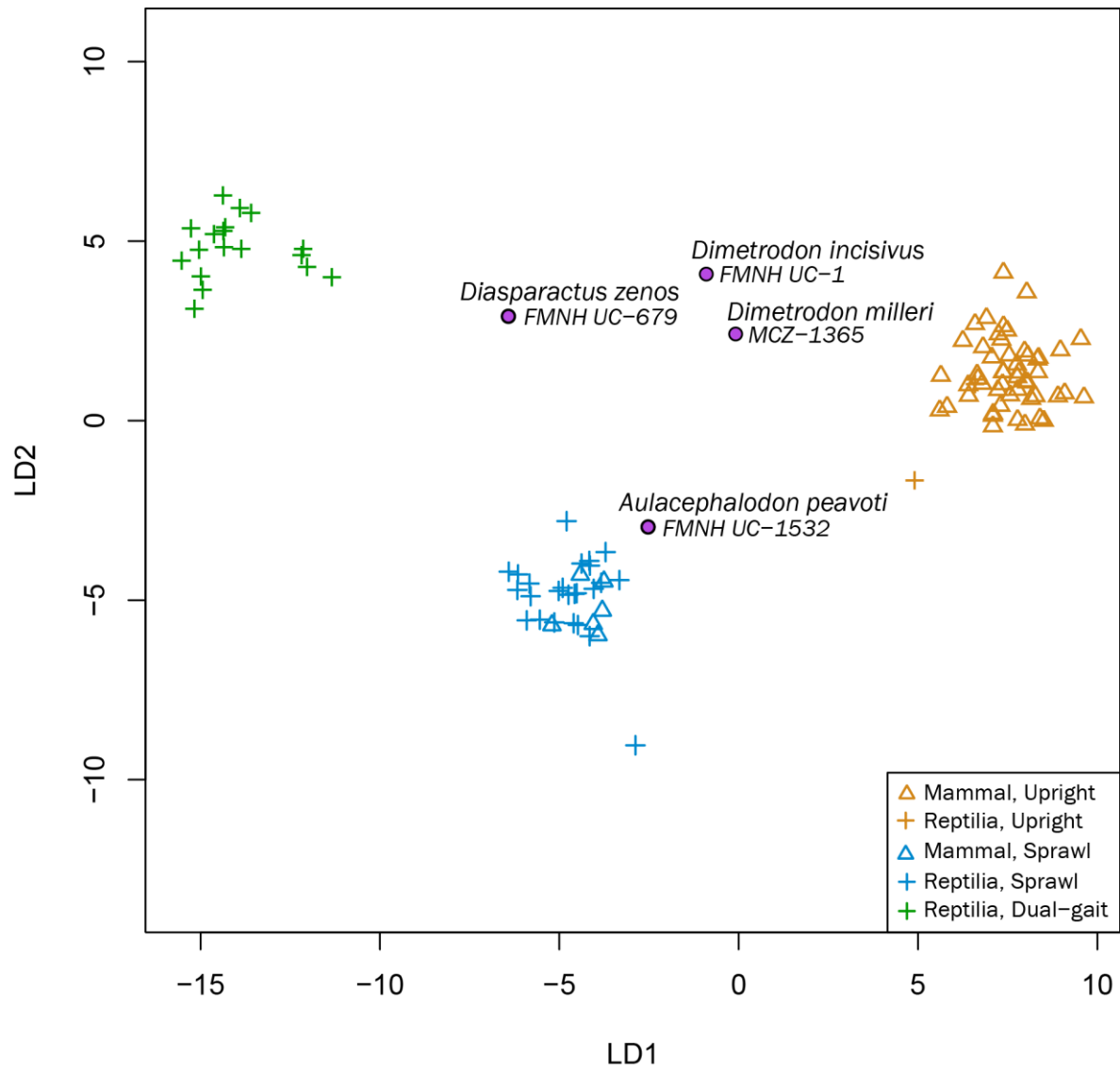
Figure 8. *Sparse discriminant analysis plot of 36 extant taxa (102 specimens total) and 4 fossil specimens. No specimens with missing data were included.*
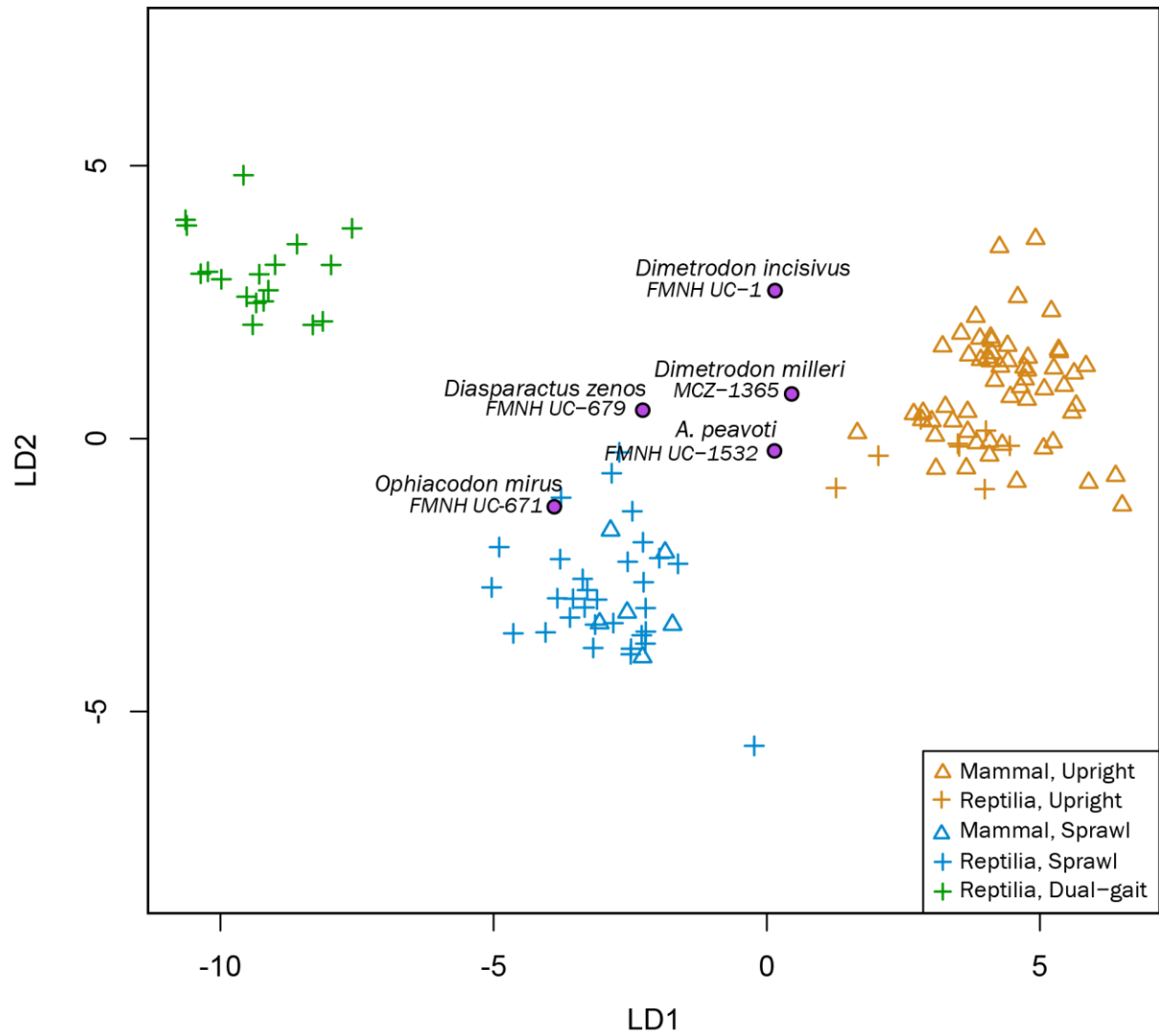
Figure 9. *Sparse discriminant analysis plot omitting pace angle, using 45 extant taxa (125 specimens total) and 5 fossil specimens. No specimens with missing data were included.*
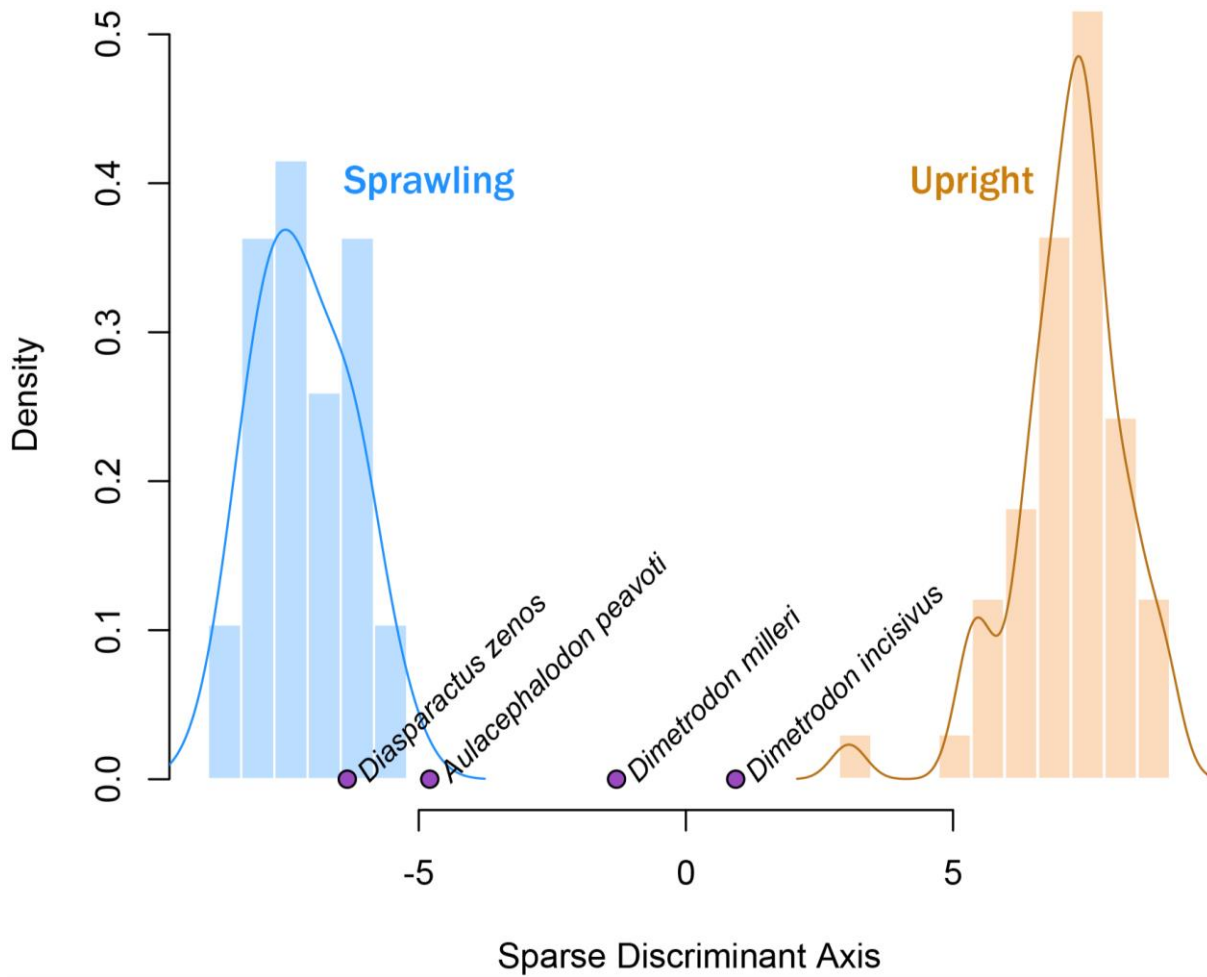
Figure 10. *Histogram of one dimensional DFA using most parsimonious model again (n=23 variables).*

Taxon	Sparse DFA w/ pace ang			Sparse DFA w/o pace ang		
	Dual-gait	Sprawling	Upright	Dual-gait	Sprawling	Upright
Aulacephalodon peavoti	0.0000	1.0000	0.0000	0.0000	0.5547	0.4453
Dimetrodon incisivus	0.0000	0.0004	0.9996	0.0000	0.0000	1.0000
Dimetrodon milleri	0.0000	0.0003	0.9997	0.0000	0.0031	0.9969
Diasparactus zenos	0.3488	0.6512	0.0000	0.0000	1.0000	0.0000
Ophiacodon mirus	----------			0.0000	1.0000	0.0000

Table 5. *Proability of classification into each grade for both DFA analyses. Grey boxes highlight classification (highest probability) for each taxon.*
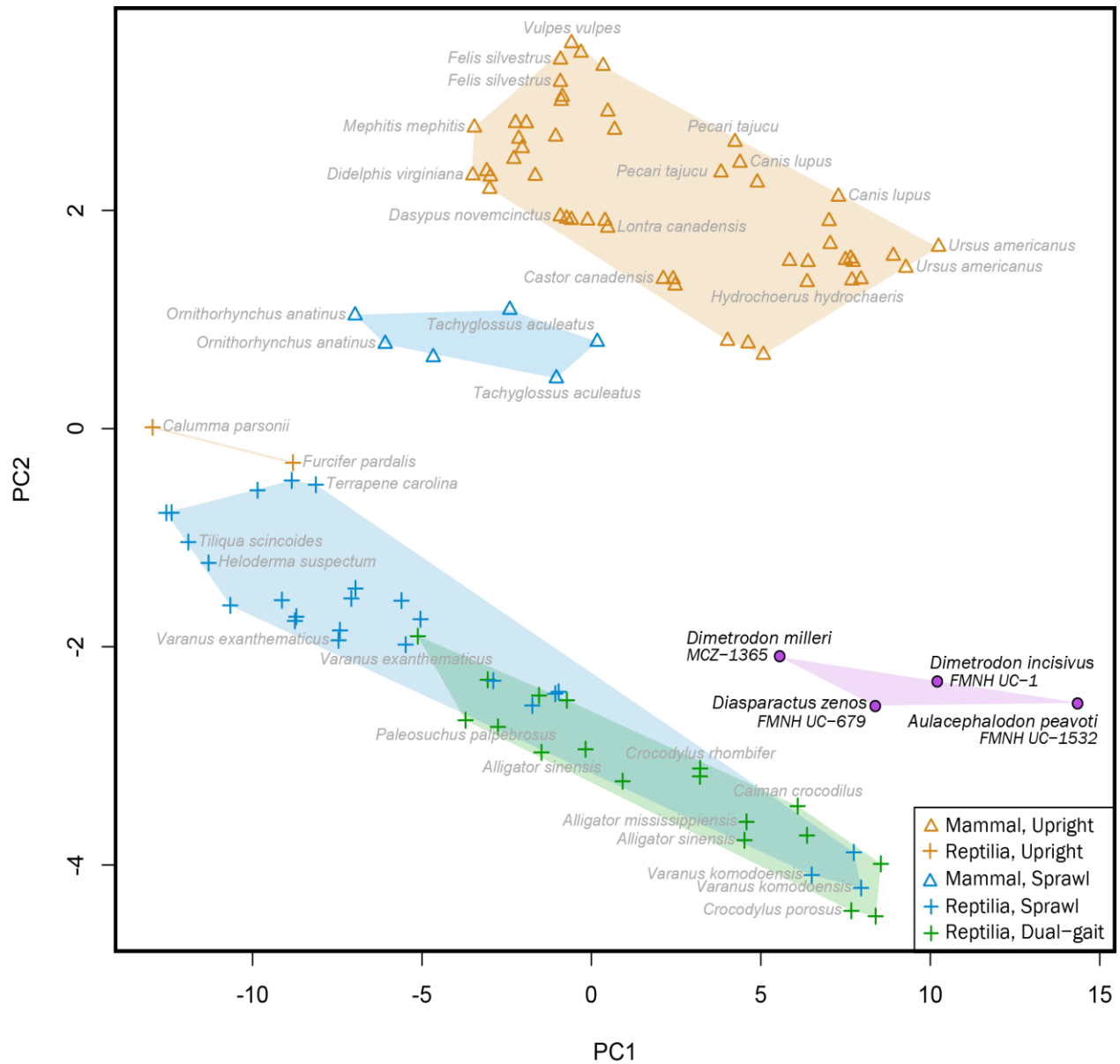
Figure 11. *Plot of PC1 and PC2 (102 extant specimens, 4 fossil specimens with complete data. PC1 (77%) is correlated with size, while PC2 (12%) separates out mammals from non-mammalian tetrapods*
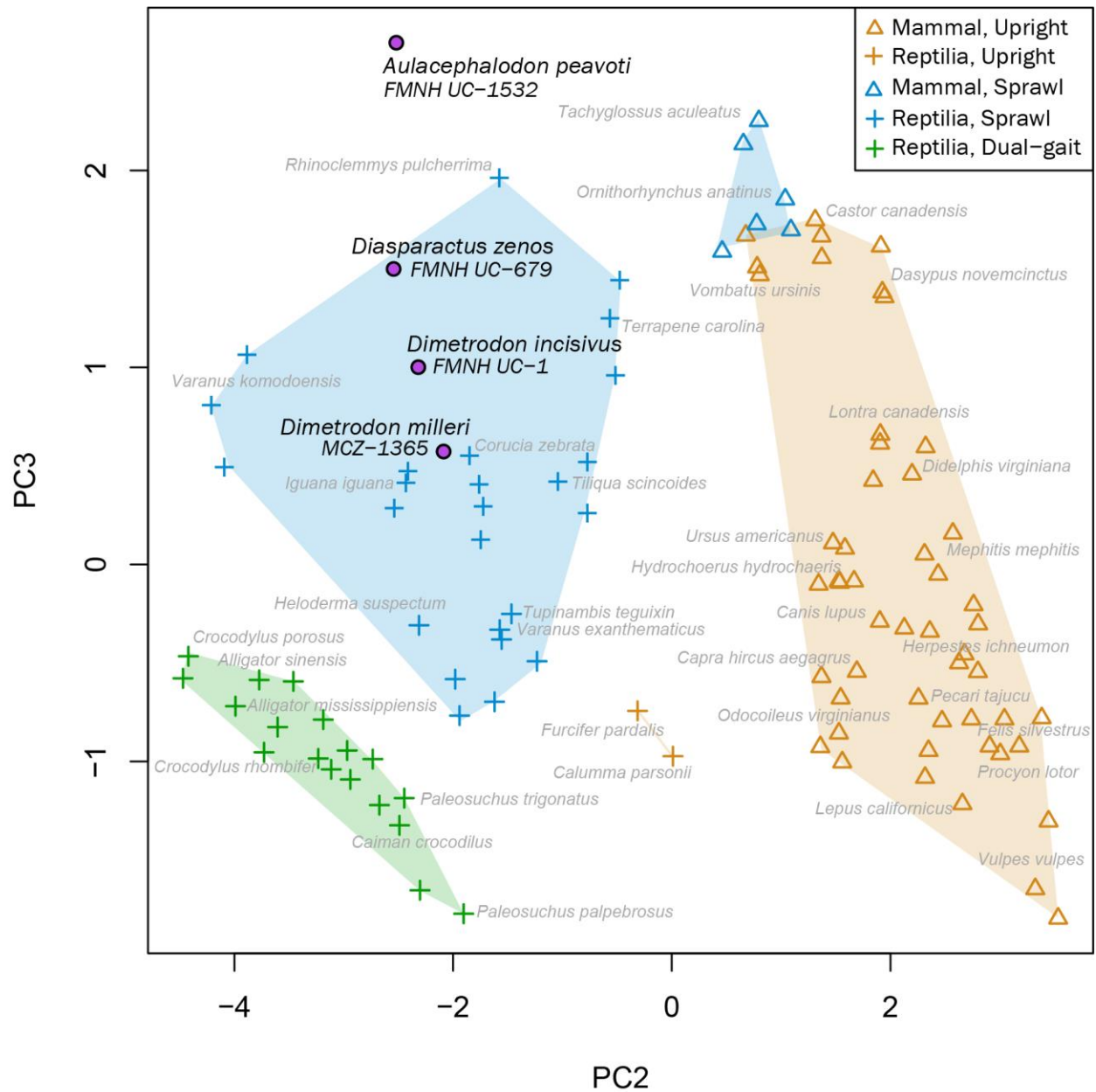
Figure 12. *Plot of PC2 and PC3 (102 extant specimens, 4 fossil specimens with complete data). PC2 (12%) is correlated with size, while PC3 (2.2%) is associated with posture*
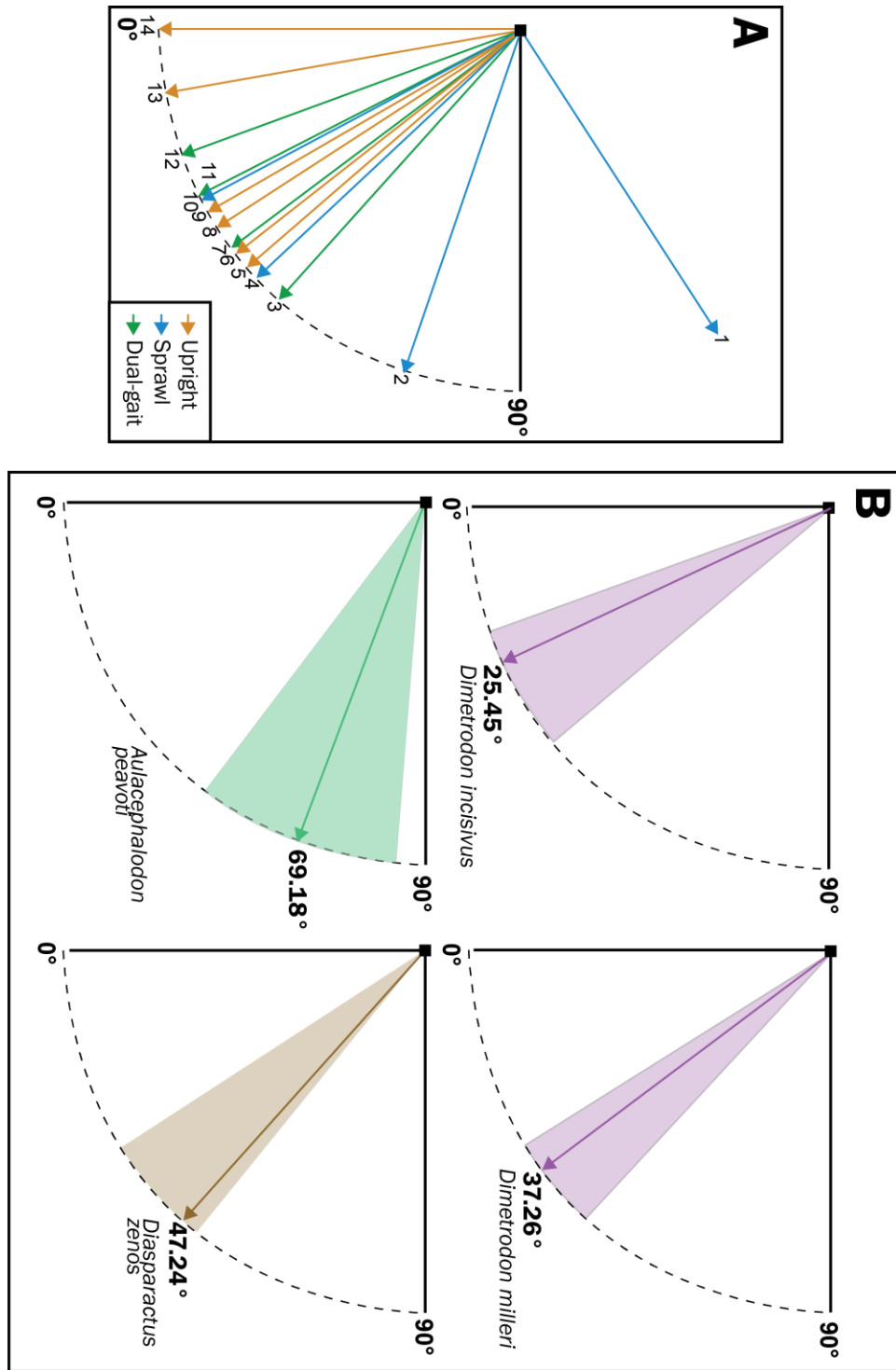
Figure 13A. FABA of 18 extant taxa. 1) Tiliqua scincoides, 2) Iguana iguana, 3) Paleosuchus trigonatus, 4) Tachyglossus aculeatus, 5) Trioceros jacksonii, 6) Didelphis virginiana, 7) Alligator mississippiensis, 8) Mephitis mephitis, 9) Procyon lotor, 10) Varanus exanthematicus, 11) Crocodylus porosus, 12) Caiman crocodilus, 13) Vulpes vulpes, Canis lupus, 14) Pecari tajucu, Odocoileus virginianus, Felis silvestrus, Capra hircus aegagrus. **Figure 13B.** Predicted FABA of four fossil taxa. Arrows indicate predicted FABA and translucent cones are 50% confidence intervals.

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DISCUSSION

Posture in Extinct Synapsids

Estimation and analogues of sphenacodontian locomotion

Posture estimates for *Dimetrodon* are consistent in both DFA, in the MRA, and along PC3 (Fig 8, 9, 12, 13B). In both DFA, *Dimetrodon* recovers intermediately between sprawling and upright clusters. In the MRA, *Dimetrodon* has an intermediate FABA (*D. milleri* = 37°, *D. incicivus* = 25°), similar to non-cursorial mammals, varanid lizards, and high-walking crocodilians, (Fig 13A, B). Along PC3, both *Dimetrodon* again recovers with varanid lizards and non-cursorial therians, but distally from crocodilians (Fig 12). Two themes arise from these results: 1) sphenacodontians, like *Dimetrodon*, were not sprawling or upright in a traditional sense, but had an intermediate hindlimb posture, and 2) sphenacodontian locomotion was distinct from any extant tetrapods and lacks a singular modern analogue.

Previous reconstructions of sphenacodontian posture suggest a highly sprawling, abducted hindlimb, close to 90° (Jenkins, 1969; Kemp, 1982, 2005; Hopson, 2015). However, the results of this study suggest that the hindlimb of sphenacodontians was adducted to 30° (Fig. 14). However, despite this adducted hindlimb, the forelimb of *Dimetrodon* was likely far more sprawling (Fig 15). Similar to most "pelycosaurs", the sphenacodontian shoulder features a highly constrained, "screw-shaped" glenoid fossa that is quite dorsoventrally flattened, restricting the humerus to protraction/retraction in the transverse plane (Jenkins, 1969; Kemp, 2005; Hopson, 2015). The combination of a highly constrained forelimb with a freer, adducted hindlimb produces a posture quite

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unlike traditional representations of sphenacodontian locomotion that is entirely unique and distinct from all extant tetrapods, basal synapsids, stem-amniotes, and therapsids. Sphenacodontian locomotion, while highly derived from more basal synapsids, is still likely more similar to other "pelycosaurs" than therapsids. Therapsids have much greater diversity in functionality of the forelimb, due to higher humeral morphological disparity when compared to "pelycosaurs", especially at the shoulder joint (Lungmus and Angielczyk, 2019). The adducted femur and primitive, "pelycosaurian" humerus in sphenacodontians may represent a precedent locomotor form within "pelycosaurs" to more gracile, cursorial locomotion seen in early therapsids, like biarmosuchians, as well as other unique forms across Therapsida (Carroll, 1988). Since the sphenacodontian hindlimb was already adducted, morphological transitions of the humerus at the shoulder joint were perhaps the final steps towards the radiation of locomotor capabilities of therapsids.

No locomotor analogues exist for *Dimetrodon* and other sphenacodontians, due to their phylogenetic and temporal distance of over 270 million years from extant mammals. Singular modern analogues are useful in shallow temporal ranges, with less phylogenetic distance, or in cases of extreme homoplasy, such as between basal and extant carnivorans, or homoplasy between ceratopsians and ungulates (Carrano, 1999, 2000, 2001 ; Paul and Christiansen, 2000, Argot, 2010) Using a single extant taxon as a comparative reference to highly basal taxa results in "over-fitting" to a qualitative model. Comparisons of basal synapsids with extant tetrapods can however still be informative, if a suite of taxa that reflect different aspects of the synapsid locomotor system are employed rather than a single analogue.

Extant groups that are informative to synapsid posture include: varanid lizards, non-cursorial/ambulatory therians, and monotremes. Varanids, unlike many other squamates, are highly active pursuit predators and capable of a considerable degree of limb adduction (Wang et al., 1997; Clemente et al., 2009; Kubo and Ozaki, 2009, Clemente et al., 2011). *Varanus exanthematicus*, the Savannah monitor*, has a FABA very similar to *Dimetrodon* in this study, and is also more sprawling in the forelimb than the hindlimb, using anteroposterior protraction/retraction to move the humerus (Jenkins, 1983; Kubo and Ozaki, 2009). Like large varanids, *Dimetrodon* was probably a highly active pursuit predator, despite lacking a fully upright posture (Florides et al., 2001). Ambulatory therian mammals, such as *Didelphis* (possums), *Procyon* (raccoons), or *Lontra* (New World river otters), while having far more mobility at the pelvic and pectoral girdle than sphenacodontians, are comparatively similar in having a "squatted" psoture and abducting their proximal limb bones out of the parasagittal plane, unlike traditional descriptions of upright posture represented by cursorial mammals (Jenkins, 1971; Jenkins and Camazine, 1977). Monotremes are often considered functionally sprawling based on the posture of their proximal limb bones, but have a spinal column with greatly reduced mediolateral flexion. Unlike therian mammals, monotremes like *Tachyglossus* have a highly constrained shoulder girdle and glenoid, and use humeral rotation and adduction to progress the forelimb, rather than flexion and extension (Kemp, 2005; Regnault and Pierce, 2018). While sphenacodontians likely used more of a protraction/retraction movement to progress the humerus through the glenoid, they share a similar, U-shaped shoulder girdle that results in highly restricted movement.

A note on crocodilians

Crocodilians an often cited analogue for intermediate posture in both archosaurian and stem-mammalian lineages, but this "intermediate" posture does not reflect an actual transitional, intermediate posture acquired from a sprawling ancestor (Gatesy, 1991; Reilly and Elias, 1998). Fossil taxa do not recover with extant dual-gait taxa in any of the analyses, with the exception of the MRA (only because it estimates one continuous measure of posture), which may be due to a couple of factors. First, Crocodylia is a phylogenetically conserved group that is highly derived from other orders of amniotes. Second, the ancestors of crocodilians were upright and cursorial. Because of this, their form of "intermediate" posture may be poor analogue for a transitional posture between sprawling to upright tetrapod locomotion (Parrish, 1987; Gatesy, 1991).

Estimates of posture in other fossil specimens

Estimates of posture in *Diasparactus* and *Ophiacodon* specimens are more sprawling than in *Dimetrodon*. Neither of these results is surprising due to the phylogenetic position of both of these taxa, as *Ophiacodon* is one of the most basal synapsids and *Diasparactus* is a sister taxon to Amniota (Benson, 2003; Benson, 2012; Nyakatura et al., 2019). Recent studies integrating data from trackways, body fossils, and robotic reconstructions of the diadectid *Orobates* have shown that derived, intermediate locomotion may have first evolved in stem-amniote groups, like Diadectomorpha, (Nyakatura et al., 2019). The results of this study support this, as *Diasparactus*, a close relative of *Orobates*, is also shown to have had a more intermediate hindlimb posture (FABA = 47°, Fig 13B) than would be expected for a tetrapod outside crown amniotes, although not as adducted as *Dimetrodon*.

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Aulacephalodon recovers as quite sprawling (FABA = 69°) in all of the analyses that include pace angle; however, when pace angle is excluded, *Aulacephalodon* recovers as far more intermediate, closer to the *Dimetrodon* specimens. While it is surprising that a derived therapsid has a more sprawling limb posture than a basal synapsid, in some studies large dicynodonts are estimated to have held their femora in a sprawling to intermediate posture. A study by Fröbisch (2006) noted that the FABA of *Tetragonias* was likely 35-50°. However other studies have shown that kannemeyerid dicynodonts likely held their limbs in a parasagittal stance (Walter, 1986). An explanation for this could be that pace angle confounds posture estimates, resulting in a large FABA for *Aulacephalodon*. A wide variety of morphological and environmental constraints outside of FABA contribute to pace angle, such as lateral undulation of the spine in many extant squamates (Kubo and Ozaki, 2009). In the case of *Aulacephalodon*, trunk width may also play a role in reducing pace angle by increasing stride width (Kubo and Benton, 2009). For example, *Pecari tajucu*, an ungulate with a FABA of 0° has a pace angle of 145°, and has a wider trunk than *Vulpes vulpes*, which has a FABA of 10° but a pace angle of 176°. Compared to other taxa in this study *Aulacephalodon* appears to have had a wider trunk, which may be reflected in trackways and thus skew reconstructions of limb posture. In the near future, I will run an additional MRA without pace angle, to see whether this changes estimates of FABA.

Mosaic Evolution in the Synapsid Locomotor System

Even if pace angle is a confounding variable to estimating posture in large dicynodonts like *Aulacephalodon*, it is odd, based on traditional models of synapsid evolution, that *Dimetrodon* would have a more adducted hindlimb. Even without pace

angle, *Aulacephalodon* appears to be slightly more sprawling or crouched than both of the *Dimetrodon* specimens. This is surprising considering how derived anomodont therapsids are from sphenacodontians (Sidor, 2001). The traditional model of the evolution of synapsid locomotion is a gradual but direct transition from sprawling "pelycosaurs" to upright mammals. Evidence of mosaic evolution throughout synapsid lineages has become increasingly prevalent in recent decades, such as therian-like forelimbs but primitive hindlimbs in some early mammals, and plesiomorphic skull characters retained in synapsids but lost in sauropsids (Gauthier et al., 1989; Qiang et al., 1999). The results of this study present further support for this pattern. Synapsid locomotor evolution should not just be understood along a continuum from sprawling to upright, but as a complex narrative of locomotor patterns that reflect phylogeny, ecological niche, and morphological novelty.

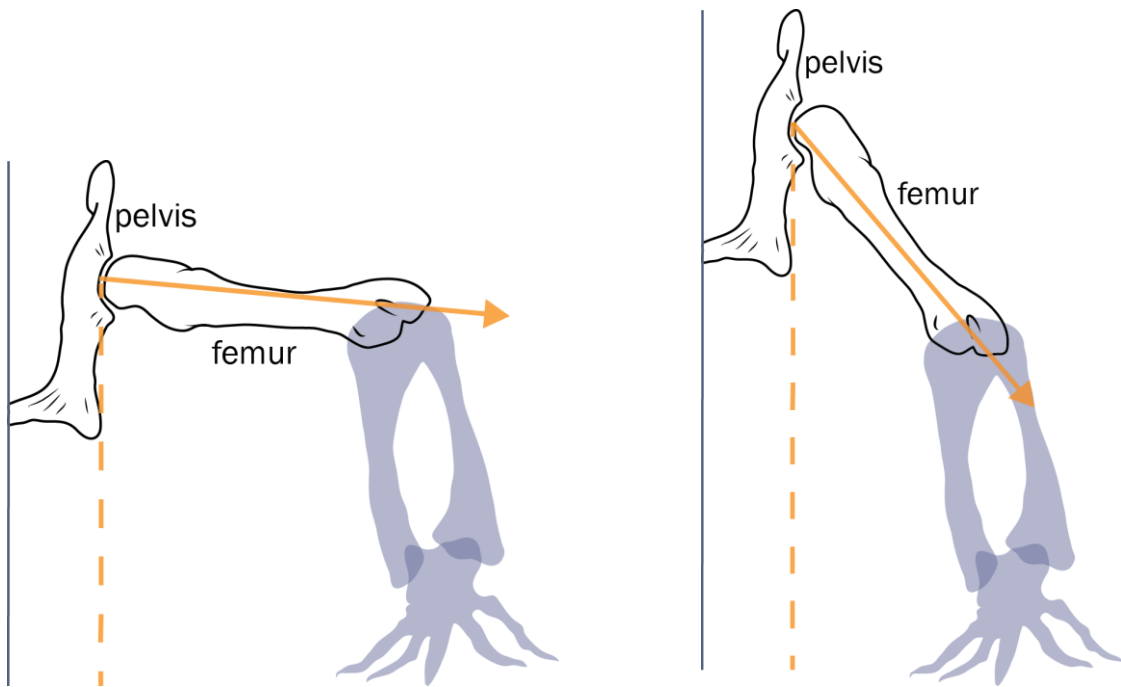*Figure 14. Left: previous reconstruction of the spenacodontian hindlimb, in frontal view. Right: reconstruction of sphenacodontian hindlimb posture with the results of this study. Modified from Jenkins (1969) and Kemp (1982, 2005).*
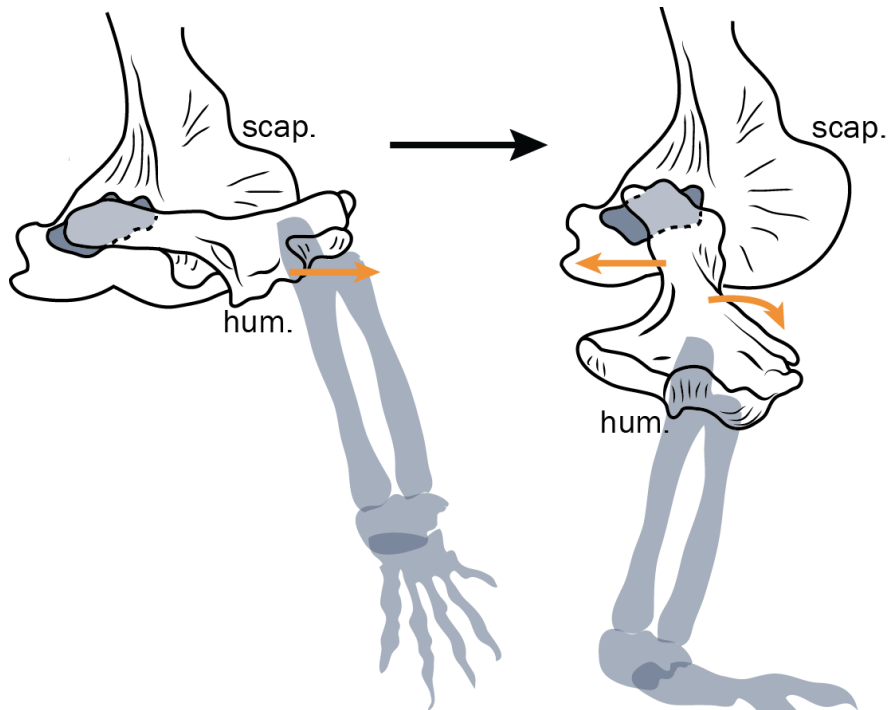

Figure 15. Sphenacodontian shoulder girdle in lateral view, left: swing phase of step cycle, right: stance phase of step cycle. Modified from Jenkins (1969) and Kemp (1982, 2005).
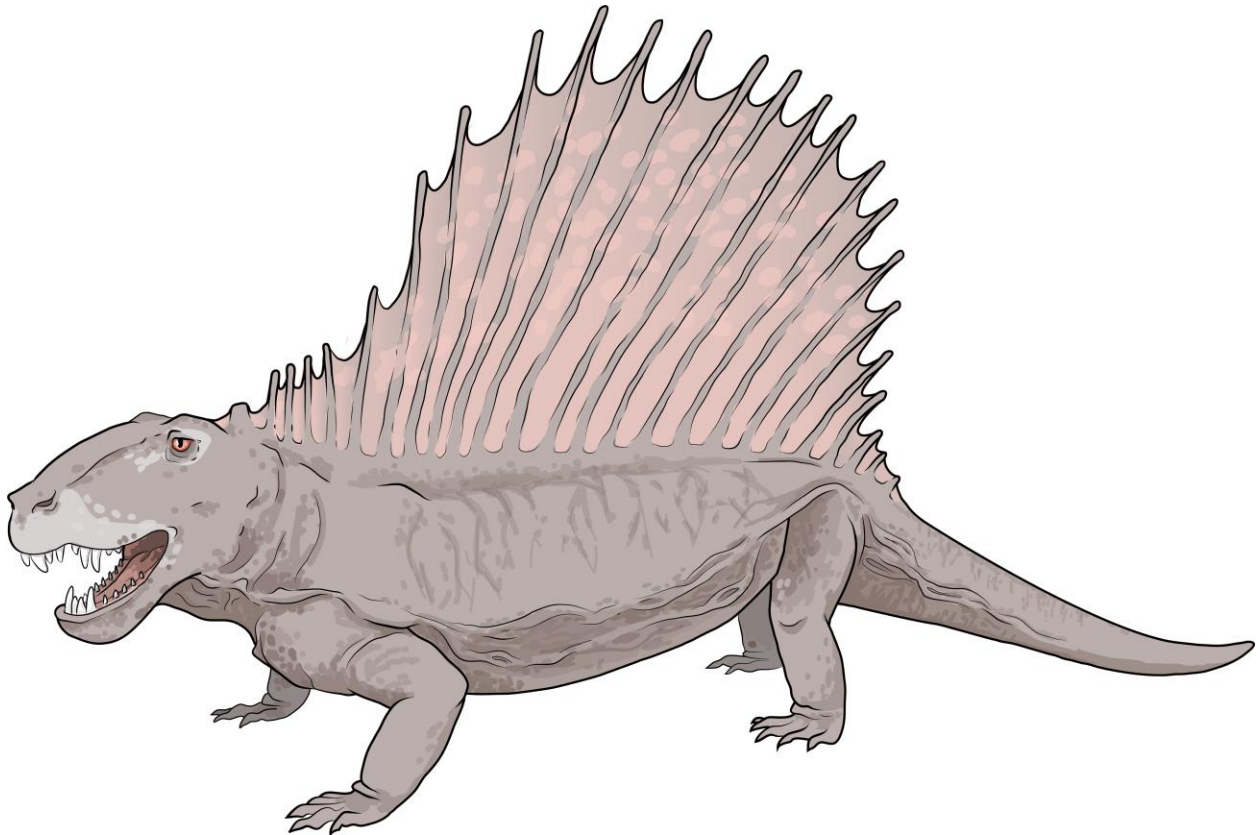
Figure 16. *Reconstruction of Dimetrodon with adducted hindlimb and sprawling forelimb.*

Describing Posture in Tetrapods

<u>Discrete vs. Continuous measures of femoral abduction</u>

Historically, posture has been described in discrete grades, which were defined

by how "improved" a taxon's posture was, and assumed a gradual, direct transition from

sprawling "primitive" to an upright "fully-improved" posture in tetrapod lineages (Charig,

1972). One of the major criticisms of describing posture by grades is the bias inherent in

assuming more upright organisms are superior to more sprawling ones. This was first

addressed with "thecodonts", once thought of as a morphological grade but now

recognized as a highly diverse, paraphyletic group (Gauthier, 1986). At the same time,

many pseudosuchians, including the ancestors of modern crocodilians, were discovered

to have had an upright posture, marking the "semi-improved" (dual-gait) posture of extant crocodilians as a secondary acquisition of from a highly cursorial ancestor (Parrish, 1987). Within "upright" mammals, there is a wide range of locomotion styles, highlighting that posture grades are far from discrete (Jenkins, 1971). Because of this, quantitative measures like FABA have become a more accepted way of describing posture, because they provide a continuously and quantitative measure of what posture grades describe discretely, supposedly removing the bias of posture grades. However, this study shows that posture grades that can be supported by a unique suite of characters and in context with quantitative data are actually quite useful. Using only discrete grades masks variation, and using singular quantitative measures can make it difficult to recognize meaningful comparisons. Locomotor grades that are informed by and used in conjunction with continuous data can synthesize patterns in tetrapod posture in a broadly applicable manner.

Influence of phylogeny

One of the major reasons previous studies have cautioned against using posture grades, along with over-generalizing locomotor modes, is that they carry phylogenetic assumptions (Gatesy, 1991). Posture grades used in the DFA and defined in the PCA are largely defined by class-level phylogenetic designations, with some exceptions. Assumptions made on the basis of phylogeny alone confound our understanding of locomotion. For example, extant squamates are all considered to have a general sprawling posture, and while many squamates have a large degree of femoral abduction, examples such as *Varanus exanthematicus* have a comparatively small FABA (Fig 13A). Varanid lizards are more metabolically and behaviorally active than

other squamates, which their locomotion reflects (Clemente et al., 2009). Lumping

varanids under the broad label of "sprawling" assumes shared morphology results in

shared locomotion, rather than shared morphology simply indicating a shared

phylogenetic history. On the other hand, when used to contextualize, rather than

generalize posture, phylogeny can be an informative tool. The posture of particular

lineages is only understood relation to their ancestors and close relatives. Crocodilians,

for example, long thought to be remnants of sprawling, "thecodont"-grade archosaurs

seemed to be an appropriate analogue for a transitional posture between sprawling and

upright locomotion (Charig, 1972). However, now that basal crocodylomorphs are

understood to have had a fully upright, cursorial posture, crocodilian dual-gait posture

does not make sense as an analogue for a "transitional" posture. Without the context of

phylogeny, information that is critical to understanding crocodilian posture is lost.

<u>Considering the entire tetrapod locomotor system</u>

Both posture grade and FABA are discrete and continuous measures used to

describe a similar feature, the degree of femoral limb bone abduction. While femoral

abduction is quite informative for posture, it fails to capture other important information

to classify tetrapod locomotion and posture. Describing tetrapod locomotion by focusing

on the femur and/or hindlimb may result in missing important information from other

regions of the locomotor system. Many studies of tetrapod locomotion examine isolated

portions of the locomotor apparatus as independent systems, looking at the forelimb

apart from the hindlimb or vice versa (Jenkins and Camazine, 1977; Brinkman, 1981;

Jenkins, 1983; Parrish, 1983; Blob and Bieweiner, 1999; Paul and Christiansen, 2006;

Baier and Gatesy, 2013; Lungmus and Angielczyk, 2019). Most of these studies focus

on the contribution of the hindlimb and overlook the contribution of the forelimb (Jenkins and Camazine, 1977; Brinkman, 1981; Parrish, 1983, Baier and Gatesy, 2013). However, the forelimb and hindlimb of tetrapods are far from independent systems (apart, perhaps, from obligate bipeds) and the forelimb offers a significant (and often ignored) contribution to locomotion in obligate quadrupeds. As mentioned in the previous section, major changes in the morphology of the synapsid forelimb, particularly early therapsids, correlate with increased locomotor disparity, indicating that evolutionary novelties of the forelimb are vital to understanding transitions in synapsid locomotion (Lungmus and Angielczyk, 2019). While studies examining discrete regions of the tetrapod locomotor system are important for independently understanding specific functional structures, these data must be contextualized with studies of the entire locomotor system of that taxon, to fully understand its contribution to locomotion and relation to other functional structures.

Additionally, other measures of locomotion commonly recorded in cineradiographic/ XROMM studies, such as flexion and rotation at the shoulder, hip, elbow, and knee, and mediolateral flexion of the spinal column could explain the additional variation between locomotor habits not explained by FABA. Mediolateral flexion (or pelvic rotation) in particular is important to sprawling locomotion, as can be seen in both squamates and salamanders, and to a lesser extent, crocodilians (Kemp, 2005; Kubo and Ozaki, 2009; Hopson, 2015). For fossil taxa for which we are unable to observe *in vivo* locomotion, any kind of quantitative estimate of posture or locomotion is greatly informative, but further descriptors of extant synapsid posture outside of femoral abduction are needed to build a quantitative framework for fossil synapsid locomotion.

Morphological Predictors of Posture: *Anatomical and functional implications*

<u>Forelimb and Pectoral Girdle</u>

Scapular length (SCL), the length of the coracoid/coracoid process (CB), and distance between the deltopectoral crest and humeral head (DPCmom) all relate to movement at the shoulder joint. Muscles that attach at the shoulder girdle and insert on the deltopectoral crest, such as *M. deltoideus*, are involved in stabilizing the shoulder girdle and produce flexion/extension of the humerus contributing to the mechanical advantage of the forelimb during the swing phase of the step cycle (Table 6) (Leach, 1977; Klinkhamer et al., 2017). In both discriminant function analyses, SCL separates dual-gait and upright clusters from sprawling along LD2 (Fig 8, 9). In upright taxa, particularly therian mammals, the upper portion of the scapular blade acts like a "high fulcrum" about which the humerus can swing (Fischer, 1994). Crocodilian scapulae share a similar shape with mammalian taxa, which could be a function of the high-walk gait or a relic of ancestral cursoriality (Parrish, 1987). This tall scapular blade is also seen in extinct, cursorial quadrupeds such as hadrosaurid dinosaurs (Egi and Weishampel, 2002; Carpenter and Wilson, 2008). In squamates, the scapula is broader and shorter, lowering the "high fulcrum" seen in more upright taxa, and aiding in anteroposterior protraction/retraction of the humerus during the propulsive portion of the step cycle, rather than flexion/extension in the parasagittal plane (Jenkins and Goslow, 1983, Freitas et al., 2017). CB aids in separating mammals from other tetrapods along PC2 and along LD1 of the DFA without pace angle (Fig 9, 12). Therian mammals, unlike other tetrapods, lack a distinct coracoid and instead have a small coracoid process off the scapula. The coracoid of monotremes is distinct but highly reduced. Synapsids all

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the way to non-mammalian cynodonts retain their coracoid, but it becomes greatly reduced in crown group mammals (Crompton and Jenkins, 1973; Sereno, 2006). DPCmom increases towards squamates and crocodilians along PC2, but increases towards cursorial mammals and crocodilians along PC3 (Fig 12). It also has a negative coefficient in the MRA, meaning it decreases estimates of FABA (Table 3). The conflicting signals along PC2 and PC3 may be because, cursorial taxa (such as ungulates, felids, canids, and lagomorphs) have a deltopectoral attachment that extends above the humeral head, while in crocodilians and squamates it starts and ends below the humeral head (Jenkins and Goslow, 1983; Freitas et al., 2017; Klinkhamer et al., 2017). The height of the olecranon process of the ulna (OL) and the length of the radius (RL) relate to the mechanical advantage of the forelimb at the elbow joint. The major muscle of the olecranon process is *M. triceps,* which extends the elbow, and flexors and extensors of the manus extend the length of the radius, from the elbow joint to the carpals. OL separates mammals from squamates along LD1 of the DFA with pace angle, increases along PC2 towards mammals and PC3 towards monotremes and testudines, and decreases FABA estimates in the MRA (Fig 8, 12; Table 3). For increasingly upright taxa, a larger olecranon process indicates a greater degree of elbow flexion and forelimb adduction. The elbow joint of upright taxa is also restricted to a simple hinge joint in the direction of flexion and extension, making it reliant on muscles like *Triceps* to swing the limb (Beck, 2004; Fujiwara, 2009; Fujiwara and Hutchinson, 2012). Sprawling and dual-gait taxa tend to have a shorter olecranon, and greater freedom of movement about the elbow joint than upright taxa (Jenkins and Goslow, 1983 (?); Meers, 2003; Baier and Gatesy, 2013). RL appears to separate dual-

gait and upright clusters along LD1 in both DFA analyses (Fig 8, 9). Longer distal limb bones contribute to a longer stride length in upright taxa, while sprawling taxa are thought to invest in mediolateral trunk flexion and protraction/retraction of the humerus to increase stride length in the forelimb (Romer, 1956; Hildebrand, 1974; Beck, 2004; Kubo and Ozaki, 2009; Heckert et al. 2010).

<u>Hindlimb and Pelvic Girdle</u>

The depth of the proximal femoral adductor scar (FADD) is associated with adduction of the femur, and extension and stabilization of the hip. In both DFA, it aids in separating the sprawling cluster from the other two (Fig 8, 9). It increases in increasingly sprawling/"squatted" taxa along PC3, and increases estimates of FABA (Fig 12, Table 3). Major adductors and extensors of the hip insert at FADD, including *M. quadratus femoris* in mammals, and *M. caudifemoralis* in reptiles, and *M. adductor* group muscles in both groups (Rowe, 1986; Carlon and Hubbard, 2012; Klinkhamer et al., 2017). Sprawling taxa actively use hip adductors during the propulsive phase of the step cycle, to depress and rotate the femur, unlike cursorial, taxa, which rely on flexion/ extension of the femur to propel the limb (Jenkins and Camazine, 1977; Brinkman, 1981) The depth of the proximal femoral abductor scar (FABD) and its vertical and horizontal distance from the femoral head (FABDV, FABDH) and the dorsoventral height of the ilium (IIDVL) are associated with abduction of the femur as well as flexion and stabilization of the hip. FABD increases towards mammals along PC2 and sprawling/ "squatted" taxa along PC3, and increases estimates of FABA (Fig 12, Table 3). FABDV increases in sprawling and dual-gait taxa along PC2 and increases estimates of FABA (Fig 12, Table 3). FABDH aids in separating dual-gait and upright clusters in both DFA

and increases in mammals along PC2 (Fig 8, 9, 12). IIDVL helps separate dual-gait and sprawling clusters from upright along LD1 of both DFA, and increases estimates of FABA in the MRA (Fig 8, 9, Table 10). Muscles associated with these structures include *M. iliofemoralis* in reptiles and the *M. gluteus* muscles in mammals (Rowe, 1986; Carlon and Hubbard, 2012; Klinkhamer et al., 2017). In mammals, the proximal femoral abductor scar extends more laterally from the shaft but more proximally to the femoral head (↑ FABDH, ↓ FABDV) while the opposite is true for more sprawling taxa. Similar to the adductor scar, the abductor scar is likely closer to the femoral head in upright taxa because it mainly functions to stabilize the hip, rather than aid in limb propulsion, whereas the opposite is true for more sprawling taxa (Jenkins and Camazine, 1997). The dorsoventral height of the acetabulum (ALenDV) relates to the range of motion of the femur at the hip. ALenDV helps separate the upright cluster from sprawling and dual-gait in along LD1 of both DFA, and separates dual-gait and upright clusters from sprawling along LD2 (Fig 8, 9). The shape of the acetabulum constrains the movement of the femur through the step cycle of the hindlimb, and the acetabulum tends to be rounder in more upright taxa. However, the acetabulum is also constrained by a great deal of cartilage and connective tissue, not preserved on bone alone (Tsai et al., 2018).

Pace Angle

Pace angle separates upright and dual-gait taxa from sprawling along LD2, increases along PC2 and decreases along PC3 towards cursorial mammals, and has a strong influence on decreasing estimates of FABA in the MRA (Fig 8, 12, Table 3). Pace angle has shown to be a strongly correlated with FABA in extant taxa and is commonly used to infer the posture of extinct taxa (Marsicano and Barredo, 2004; Paul and

Christiansen, 2006; Kubo and Benton, 2009; Kubo and Ozaki, 2009). Pace angle

reflects posture as a relative measure of the degree of proximal limb flexion/ extension

(stride length) and limb adduction/ abduction (stride width) (Kubo and Benton, 2009).

Action	Variable(s)	Relevant Musculature		
		Mammal (Leech, 1977; Carlon and Hubbard, 2012)	**Crocodilian** (Meers, 2003; Klinkhamer et al., 2017)	**Squamate** (Jenkins and Goslow, 1983; Freitas et al., 2017)
Shoulder flexion/ extension, stabilization	SCL, CB, DPCmom	*M. deltoideus, M. coracobrachialis M. pectoralis*	*M. deltoideus, M. coracobrachialis M. pectoralis*	*M. deltoideus, M. coracobrachialis M. pectoralis*
Elbow extension, humerus stabilization	RL, OL, CB	*M. triceps*	*M. triceps*	*M. triceps*
Hip adduction/ extension, stabilization	FADD	*M. adductor group, M. quadratus femoris, M. pectineus, M. iliopsoas*	*M. adductor group, M. caudifemoralis, M. pubo-ischio-femoralis internus medialis*	*M. adductor group, M. caudifemoralis*
Hip abduction/ flexion, stabilization	FABD, FABDH, FABDV, IIDVL	*M. gluteus, M. vastus lateralis*	*M. iliofemoralis, M. pubo-ischio-femoralis internus dorsalis*	*M. iliofemoralis*
Hip flexion/ extension	ALenDV	--		
Position of prox limb bones	Pace Angle			

Table 6. *Interpreted variables and their locomotor contribution, including action and relevant musculature*

CONCLUSIONS

This study provides evidence that sphenacodontians, like *Dimetrodon*, had a much more adducted hindlimb posture (FABA = ~30°) than shown in previous reconstructions, and an entirely distinct locomotion mode compared to extant tetrapods. Using three different multivariate statistical techniques to analyze quantitative comparative anatomical data, I estimated posture in four extinct synapsids and a stem-amniote, and provided further evidence for mosaic evolution of diverse synapsid locomotor modes. I find further support that evolutionary novelties of the synapsid forelimb are correlated with increased diversity in locomotor modes of therapsids, as the sphenacodontian shoulder is highly constrained in comparison to the adducted hindlimb (Lungmus and Angielczyk, 2019). This study shows that an adducted hindlimb, characteristic of many active, terrestrial tetrapods, proceeds the evolution of crown-group Therapsida, and further supports a similar trend found in diadectomorphs (Nyakatura et al., 2019). Future studies, also considering phylogeny and additional continuous measures of posture are needed to fully describe the locomotion of basal amniotes. However, this study suggests that the functional capabilities of basal synapsids have been greatly underestimated, which has significant implications for the life history and ecologic significance of these organisms, as well as the evolution of "mammalian" traits in stem-mammalian lineages.

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