

1 **Abstract**

2

3 Facultative bipedality is regarded as an enigmatic middle ground in the evolution of obligate  
4 bipedality, and is highly mechanically demanding in extant lepidosaurs. Traits associated  
5 with this phenomenon are largely associated with the caudal end of the animal: hindlimbs  
6 and tails. The articulation of the pelvis with both of these structures suggests a  
7 morphofunctional role in the employment of a facultative locomotor mode.

8 Using a 3D geometric morphometric approach, we examine the pelvic osteology and  
9 associated functional implications of 34 species of extant lepidosaur. Anatomical trends  
10 associated with the use of a bipedal locomotor mode and substrate preferences are  
11 correlated and functionally interpreted based on musculoskeletal descriptions.

12 Changes in pelvic osteology associated with a facultatively bipedal locomotor mode are  
13 similar to those observed in species preferring arboreal substrates, indicating shared  
14 functionality between these ecologies.

15

16 **Keywords**

17 Geometric morphometrics

18 Functional anatomy

19 Ecology

20 Locomotion

21 Facultative bipedality

22

23

## 24 Introduction

25

26 Lepidosauria represents one of the most diverse groups of modern tetrapod, comprising ~~of~~  
27 over 10,000 species inhabiting every continent except Antarctica. In addition to a near  
28 global distribution, they ~~occupy~~ exhibit a variety of adaptations reflective of the ecological  
29 niches they occupy in their preferred environments. These ~~include~~ can relate to varied diets,  
30 differing reproductive strategies and, of most interest to this study, their varied locomotor  
31 capabilities. The adaptability of the lepidosaur body plan to ~~alternative~~ locomotor styles  
32 appropriate to ~~in~~ different environments is evident across the group: ~~repeated~~ iterative?  
33 evolution of a limb-reduced, snakelike body plan (Woltering, 2012); specialisations for  
34 arboreal lifestyles (Higham & Jayne, 2004; Anzai *et al.*, 2014), ~~some of which are even~~  
35 ~~capable of~~ including an ability to ~~gliding~~ between trees (McGuire & Dudley, 2005); and even  
36 pachyostotic postcranial skeletons ~~for to facilitate~~ diving, ~~such as~~ in the case of the marine  
37 iguana (*Amblyrhynchus cristatus*) (Hugi & Sánchez-Villagra, 2012). One of the most  
38 intriguing locomotor styles represented in this group is facultative bipedality – a locomotor  
39 mode during which ordinarily quadrupedal animals temporarily move using only two limbs.

40

41 Multiple avenues of research into vertebrate evolution and anatomy have shown that  
42 animal behaviour can have an impact on ~~the~~ morphology, particularly that related to  
43 navigating their environment. Phenomic integration of anatomy and behaviour, amongst  
44 other traits, are essential to the survival of animals within ecological niches and the  
45 understanding of evolutionary transitions. A classic example is the transition from a  
46 quadrupedal to bipedal locomotor mode in hominins – structural changes are observed in  
47 the pelvic girdle, the vertebral column and the limbs as more upright postures are adopted

48 (Senut *et al.*, 2018). However, the observable phenome in the fossil record is ~~disparate~~  
49 distinct from that in the modern world because of the lack of behavioural observations.  
50 Forging an understanding of fossil species requires a thorough understanding of the  
51 observable in living taxa that create a plausible framework for comparison with, and  
52 interpretation of, extinct forms. For example, a recent study of inner ear morphology in  
53 canids enabled plausible inferences to be made concerning the hunting behaviour in their  
54 fossil relatives (Schwab *et al.*, 2019). The connection between modern phenomic  
55 observations and palaeontological data, based solely upon anatomy, has a substantial  
56 history dating back to early 19<sup>th</sup> Century observations by Georges Cuvier – and the  
57 perceptive commentaries by such as George Lauder (1991). ~~R-and~~ recent technological  
58 advances have done much to improve this connectivity.

Commented [MOU1]: Wrong word! I think you mean either 'distinct' or 'disengaged'

59  
60 The facultatively bipedal locomotor mode observed in some extant squamate species is of  
61 particular interest because of its potential application to the interpretation of locomotor  
62 modes among taxa in the fossil record (Irschick & Jayne, 1999a). It has been hypothesized  
63 that the adoption of facultative bipedality represents an intermediate locomotor mode in  
64 the evolution of hominin bipedality (Senut *et al.*, 2018). In contrast, ~~z~~ the role ~~played by of~~  
65 facultative bipedality in the evolution of archosaurian bipedality is far less well understood  
66 (Grinham, VanBuren, & Norman, 2019). Many studies have ~~also~~ examined the kinematics  
67 and performance ranges of this locomotor mode in modern squamates (Irschick & Jayne,  
68 1999b; Clemente *et al.*, 2008; Clemente & Wu, 2018). However, the core anatomical  
69 understanding is far less extensively explored. Our current understanding of the  
70 morphology linked to locomotor mode in squamates is based almost exclusively on classic  
71 examples of what may now be termed 'historic' research (Snyder, 1952, 1954, 1962) ~~by~~

72 [Richard Snyder](#). These articles ([Snyder, 1949, 1952, 1954, 1962](#)) were based upon ~~out~~dated  
73 methods of observations and interpretative modelling, and would now benefit from the  
74 broadening of such analyses to incorporate a wider range of species and the use of recently  
75 developed shape analysis methods. Fresh research in this

76

77 In this study, we address the current understanding of morphologies associated with  
78 facultative bipedality in extant Lepidosauria, and test a novel hypothesis that locomotor  
79 mode and substrate use in these reptiles can be causally linked to the morphology of the  
80 lizard pelvis. By examining both locomotor mode (obligate quadruped or facultative biped)  
81 and the species' preferred substrate (arboreal, semi-aquatic, terrestrial, rock-climbing) we  
82 will attempt to identify which aspects of ecological behaviour influence pelvic morphology  
83 most significantly in these animals.

84

## 85 **Methods**

86

87 The pelvis was selected as an anatomical structure of interest based on several key factors.  
88 Firstly, the articulation of the pelvis with both the axial and appendicular skeleton,  
89 particularly the tail and hind limbs, means that it plays a central role in locomotor function.

90 Secondly, it is readily identifiable ~~and easily segmented from in~~ microcomputed X-ray  
91 tomography ( $\mu$ CT) scans, [making it a good target for segmentation](#). Finally, due to its link to  
92 locomotor function, it should be subject to evolutionary pressures based on the use of the  
93 axial and hind limb appendicular skeletal structures. Landmark-based 3D geometric  
94 morphometrics were used to analyse the shape of the three bones of the pelvis (ilium,  
95 ischium & pubis) in 34 different species of extant lepidosaur (Figure 1).

96

97 [Figure 1 near here]

98 Prior to specimen analysis, the pelves of 36 extant lepidosaur species representing all major  
99 extant four-legged groups were examined using  $\mu$ CT. These species inhabit a wide range of  
100 substrates and include representatives that are either obligate quadrupeds or facultative  
101 bipeds. These examinations revealed that the pelves of chamaeleon species were so  
102 dissimilar to those of other lepidosaurians in terms of osteological morphology that their  
103 inclusion in this dataset would compromise the analytical protocols used in this study ([see](#)  
104 [supplementary file](#)) (Higham & Jayne, 2004; Fischer, Krause, & Lilje, 2010). As a result,  
105 representatives of ~~the family~~ Chamaeleonidae were removed from the dataset, leaving a  
106 final dataset of 34 specimens. Scans were either collected as primary data and scanned at  
107 the Cambridge Biotomography Centre, or collected from online databases and publication  
108 repositories (Table 1) (Schachner *et al.*, 2014; Regnault, Hutchinson, & Jones, 2017).  
109 Locomotor mode in these specimens was determined based on literature sources or  
110 personal observations, and substrate use based on a large-scale ecological database of  
111 extant squamates (Meiri, 2018). For species known to use multiple substrates, the most  
112 preferred was also noted, based on this database and an extensive literature review.

113 [Table 1 near here]

114 We tested for a phylogenetic signal in substrate use and locomotor mode within our dataset  
115 using the packages *phytools*, *ace* and *phylobase* (Hackathon *et al.*, 2011; Revell, 2017;  
116 Paradis *et al.*, 2018). A recently published molecular-based time-calibrated phylogeny for  
117 Squamata was pared down to match the species in our dataset (Zheng & Wiens, 2016). For  
118 species featured in our database, but not the phylogeny, the most closely related species  
119 was substituted ([see supplementary file](#)). Tuatara (*Sphenodon punctatus*) was also added to

120 the base of the modified tree, expanding the analysis to include extant Lepidosauria. Using  
121 the *phylo4d* function we mapped traits associated with substrate use and locomotor mode  
122 on to our tree. The *phyloSignal* function was used to perform [five statistical tests of](#)  
123 [phylogenetic signal \(Blomberg's K and K\\*, Abouheif's C-mean, Moran's I and Pagel's Lambda](#)  
124 [λ test for phylogenetic signal \)](#). [The results from these different tests can be considered](#)  
125 [together to determine whether phylogenetic signals exist in the traits examined](#) (Table 2).

126 Figure 1 was produced using the *gridplot.phylo4d* function, and serves to illustrate the  
127 relationships between phylogeny and trait values.

128 [Figure 2 near here]

129 [Table 2 near here]

130 MicroCT scans of specimens were processed using the open-source medical imaging  
131 software 3DSlicer (Version 4.10, [www.slicer.org](http://www.slicer.org)) (Fedorov *et al.*, 2012). TIFF image stacks  
132 were scaled using voxel size. The three major bones of one half of the pelvis (pubis, ilium,  
133 ischium) were then segmented using the inbuilt Segmentation toolkit. Bones were  
134 segmented individually when possible, then combined as a composite structure. In species  
135 where the three elements were fused into a single unit, such as in Chinese crocodile lizard  
136 (*Shinisaurus crocodilurus*), bones were segmented as a single unit (Costelli & Hecht, 1971).  
137 3D models were generated with a surface smoothing parameter of 10-20% dependent on  
138 scan resolution, with the intention of preserving maximum shape detail and increasing  
139 workability. These models were saved and then exported for use in landmarking software.  
140 Lateral profiles for a selection of these models are shown in [Figure-Figure 2](#), in order to  
141 represent the morphological variation encompassed by species in this study, and key  
142 morphologies are highlighted in [Figure-Figure 3](#). All specimens were fluid preserved at time  
143 of scanning, except the savannah monitor (*Varanus exanthematicus*) that was scanned

144 during live medical trials (Schachner *et al.*, 2014). Methods of preservation are expected to  
145 have had no impact on scans ~~because we are examining hard tissues~~ only hard tissue is  
146 examined here.

147 [Figure 3 near here]

148 3D models were imported into IDAV Landmark (Wiley *et al.*, 2005) ~~(UC-Davies)~~ software for  
149 application of landmarks. We used a mixture of 25 Type II/III landmarks as defined in Table  
150 3. Using the *LaSEC* function (Watanabe, 2018), the effectiveness of this number of  
151 landmarks was tested, and confirmed to account for at least 95% of shape variation  
152 (~~Figure~~ Figure 4). The multi-scaled forest lizard (*Adolfus africanus*) was used as the atlas  
153 species in Landmark.

154 [Figure 4 near here]

155 [Table 3 near here]

156 Landmark data were imported into the R programming environment (R Core Team, 2017)  
157 for analysis using the *readland.nts* function in *geomorph* ~~for analysis~~ (Adams, Collier, &  
158 Kaliontzopoulou, 2018). These data were then subject to a General Procrustes Analysis  
159 (GPA) using the *gpagen* function. GPA enables mathematical comparison of 3D point clouds  
160 (landmarks previously mentioned) by scaling and rotating all point clouds to match the same  
161 orientation and centroid size. The mathematical output from GPA can then be examined  
162 statistically ~~examined, which was done here using~~ with principal components analysis (PCA)  
163 using the *gm.prcomp* function (Table 4). PCA outputs are displayed in Figure ~~Figure~~s 5-8, and  
164 ~~, that~~ represent the morphospace of the pelvic structure.

165 [Table 4 near here]

166 After examining the results of the shape analysis, functional interpretations regarding the  
167 variable structures present in the pelvises of the species in our dataset were explored. Using

168 historic and modern works regarding the musculoskeletal architecture of the lepidosaur  
169 pelvis, we infer functional interpretations pertaining to limb and axial skeleton relative to  
170 locomotor mode and substrate preference (Snyder, 1954, 1962; Fischer *et al.*, 2010; Diogo &  
171 Molnar, 2014; Dick & Clemente, 2016; Diogo *et al.*, 2018).

172

## 173 **Results**

174

175 We find that there is no phylogenetic signal present for the traits of bipedality, rock-

176 climbing, ~~or~~ semi-aquatic ~~or terrestrial~~ substrate use (most  $p$ -values  $\geq 0.05$ , Table 24).

177 There is a signal present for arboreal ~~and terrestrial~~ substrate use (most  $p$ -values  $\leq 0.05$ ,

178 Table 24). As this study primarily focuses on the employment of a bipedal locomotor mode

179 and a signal is present in only ~~40~~ one of the five% of the substrates tested, we decided not

180 to conduct a phylogenetic correction for subsequent analyses. ~~Additionally, the use of~~

181 ~~phylogenetic correction can lead to complications identifying positive results, particularly~~

182 ~~when examining functional traits as in this study (de Bello *et al.*, 2015).~~

183

184 All PCA results are presented on two-axis scatter graphs with each species represented by a

185 single point in morphospace (Figure ~~Figures~~ 5-8). The colour of the point is based on either

186 locomotor mode or primary substrate, dependent on the result presented. Convex hull

187 polygons were used to represent the range of morphospace utilised by species in each

188 category. Large empty spaces within convex hulls can be indicative of ~~a variety of~~ disparate

189 morphotypes ~~all~~ occupying a similar ecological niche. Scores for each specimen on principal

190 components, as well as cumulative variance, are recorded in Tables 4 and 5. Morphospace

191 maximum and minimum approximations for principal components (PC) 1 and 2 are



192 indicated by warped meshes of the green forest lizard (*Bronchocela cristatella*) pelvis on the  
193 axis of [FigureFigure 5](#).

194 [Figures 5-8 near here]

195 [Table 5 near here]

196 Principal component 1 (30.8% variance) largely accommodates a general robustness in the  
197 pelvis, differences in the size of the acetabulum relative to the whole structure, the length  
198 of the iliac blade and the size of the preacetabular process ([FigureFigures 5 and 7](#)).

199 Additionally, the angle of the iliac blade relative to the ischial base is notably shallower in  
200 negative PC1 values. Highly positive scoring PC1 species are skink species, which tend to  
201 have a gracile pelvis, whereas the negatively scoring species represent a variety of iguanid  
202 and agamid species, alongside tuatara. Facultative bipeds tend to score negatively on PC1,  
203 with the exception of Schreiber's fringe-fingered lizard (*Acanthodactylus schreiberi*, [Figure](#)  
204 [Figure 5](#)).

205

206 Principal component 2 (13.88% variance) accommodates less of a gracility gradient than  
207 PC1, rather accounting for variation in specific pelvic osteologies. The preacetabular process  
208 is hypertrophied and more defined in positive PC2 values. The angle of the iliac blade  
209 remains relatively constant to the ischial base. The orientation of the pubis is more anterior  
210 in positive PC2 values. A longer ischidiac base is also observed in positive PC2 values.

211 Facultative bipeds tend to score positively on PC2 ([FigureFigure 5](#)).

212

213 Principal component 3 (13.79% variance) constrains a large amount of shape variation in the  
214 ilium, in particular ([FigureFigure 6](#)). Negative PC3 values indicate a convexly curving iliac  
215 blade extending well beyond the ischidiac tuberosity, with a lack of any distinguishable

216 preacetabular process. Positive PC3 values, on the other hand, suggest a short and concave  
217 iliac blade, ending vertically short of the ischidial process, with a well-defined preacetabular  
218 process. Facultative bipeds all score positively on PC3 ([FigureFigure 6](#)).

219  
220 Principal component 4 (8.75% variance) accounts for more variance in the iliac blade, but  
221 also in the morphology of the acetabulum ([FigureFigure 6](#)). Positive PC4 values indicate a  
222 slightly dorsoventrally flattened acetabulum, along with an ilium morphology extending well  
223 beyond the ischidial tuberosity with a defined preacetabular process. Negative PC4 values  
224 indicate a sharply angled ilium and a short PT. Facultative bipeds score across a wide range  
225 of PC4 scores ([FigureFigure 6](#)).

226  
227 Regarding substrate use on the PC1 and PC2 plot ([FigureFigure 7](#)), the largest region of the  
228 morphospace is represented by the terrestrial substrate. These reptiles spend their time  
229 primarily on the ground. There is significant overlap between the terrestrial substrate and  
230 all other substrates. The next largest region on this plot is arboreality, with almost all  
231 arboreal species scoring negatively on PC1 and positively on PC2, suggesting a more  
232 constrained pelvic shape relative to terrestrial dwellers. The regions of morphospace  
233 occupied by facultative bipeds and arboreal dwellers are very similar. Semi-aquatic species  
234 occupy the next largest region of morphospace, and includes semi-arboreal species such as  
235 the basilisks (*Basiliscus vittatus* and *B. basiliscus*). They occupy a mostly negative PC1 region  
236 and a variable PC2 region, overlapping to a degree with arboreal species. Rock-climbing  
237 species occupy the smallest region of the morphospace of our investigated substrates,  
238 occupying a range of both PC1 and PC2 but in a very narrow band.

239

240 On the PC3 and PC4 axes (~~Figure~~Figure 8) terrestrial substrate use again occupies the largest area  
241 of the morphospace. No particular substrate use distinctly separates from any other, with  
242 significant overlap between all substrates and a varied PC distribution, scoring both  
243 positively and negatively on PC3 and PC4.

244

## 245 **Discussion**

246

247 The value of phylogenetic correction in datasets like the one used here is contentious. For  
248 studies examining the relationships between groups and evolutionary trends, the use of a  
249 phylogenetic correction is undeniably valuable. However, when the study examines  
250 functional traits over a relatively short ecological timescale, a phylogenetic correction can  
251 affect the perception of results ([de Bello \*et al.\*, 2015](#)); this latter describes the study  
252 presented here. Regardless, ~~to inform ourselves whether or not the data we used would~~  
253 ~~benefit from a phylogenetic correction~~, we tested for a signal using ~~five commonly used~~  
254 ~~signal indicators~~Page's  $\lambda$ . This test was chosen as it is frequently the most robust with  
255 ~~suboptimal branch length information (Molina-Venegas & Rodríguez, 2017), as may be the~~  
256 ~~case where we have substituted closest relatives for species in our dataset~~. Due to the  
257 absence of a signal for a facultatively bipedal locomotor mode, which was the trait we were  
258 primarily investigating, we concluded that a phylogenetic signal correction was unnecessary  
259 and risked obscuring of any results regarding this locomotor mode. The presence of a signal  
260 in ~~two~~~~one~~ of the four substrate traits alludes to a scope for application of phylogenetic  
261 correction in some of this study, but to allow comparisons between substrates and  
262 locomotor mode, ~~(an uncorrected trait)~~, we opted to continue the study without  
263 correction. ~~Additionally, since GPA outputs are not a form of raw anatomical data, they are~~

264 [not subject to the same concerns regarding phylogenetic non-independence as other types](#)  
265 [of data](#) (Felsenstein, 1985). ~~Additionally, the use of phylogenetic correction can lead to~~  
266 ~~complications identifying positive results, particularly when examining functional traits as in~~  
267 ~~this study (de Bello et al., 2015).~~

268

269 The shape of the pelvis in facultatively bipedal extant lepidosaurs falls within the overall  
270 morphospace of lepidosaurs generally. However, it is generally found in a very concentrated  
271 area of that morphospace (Figure 3). This suggests that the changes in shape, while not  
272 necessarily indicative of bipedal capacity in their entirety, are very much enabling factors.  
273 Based on the results presented here, facultative bipeds generally possess: iliac blades that  
274 are straight-to-concave, generally robust pelvises, large and pronounced preacetabular  
275 processes, anteriorly extended pubic tubercles, and a long ischial base. [In some texts,](#)  
276 [particularly regarding fossil lepidosaur species, the preacetabular process is called the](#)  
277 [anterior iliac tubercle or the preacetabular spine.](#) These morphologies, along with other key  
278 anatomies discussed later, are visible in the pelvic profile of the green iguana (*Iguana*  
279 *iguana*, [FigureFigure 3](#)), a facultatively bipedal species. This is the observed case across the  
280 majority of the facultatively bipedal taxa in this study.

281

282 The sexes of the majority of specimens used in this study have not been identified, and thus  
283 we cannot comment on sexual distribution within a dataset where species are represented  
284 by a single specimen. However, previous works have not identified sexual dimorphism in the  
285 pelvis of the green iguana, and thus we infer there to not be a sexually dimorphic effect in  
286 our dataset (Prieto-Marquez, Gignac, & Joshi, 2007).

287

288 Conclusions can be drawn regarding pelvic morphology and substrate use, though not with  
289 the same clarity as locomotor mode. Preferential terrestrial substrate use is both the most  
290 widely distributed in the morphospace and most numerous in our dataset. It occupies a  
291 range of PC1 and PC2 values, having several tighter clusters of points as well as several  
292 isolated ones. This indicates a variety of different terrestrial morphs (e.g. the thorny devil  
293 (*Moloch horridus*) at maximum negative PC2, skinks at maximum positive PC1, lacertid  
294 species at  $\approx 0.1$  PC1 values; [FigureFigure 7](#)). This is apparent in the lifestyles of these animals:  
295 the thorny devil is regarded as a particularly slow moving lizard (Clemente *et al.*, 2004),  
296 skinks commonly burrow and have relatively short limbs, and lacertids tend to express  
297 similar ecologies to one-another, hence their grouping. It is difficult to make particularly  
298 detailed inferences regarding the effect of different niches on these morphs due to the  
299 umbrella term “terrestrial” encompassing a range of more specific substrates, such as sand,  
300 leaf-litter, burrowing, urban, grassland etc (Meiri, 2018).

301

302 The arboreal subset of the dataset is far more concentrated with regards to PC distribution,  
303 occupying primarily negative PC1 and positive PC2 values ([FigureFigure 7](#)). There is a  
304 significant overlap between the arboreal morphospace and that of the facultatively bipedal  
305 species, despite only [threefour](#) of the eight facultative bipeds [usinging](#) a primarily arboreal  
306 substrate, implying shared functionality of the pelvis between these two groups. Many of  
307 the species defined as “semi-aquatic” by Meiri (2018) can also be considered semi-arboreal  
308 or rock-climbing (e.g. the marine iguana (*Amblyrhynchus cristatus*) is considered semi-  
309 aquatic, but spends a significant portion of its life living and climbing on rocky shores). To  
310 remain objective and reproducible, this research has retained the classifications from the  
311 study above. When considering rock-climbing species (saxicolous in Meiri (2018)), the

312 overall morphospace for these species forms an almost linear “y=x” distribution across PC1  
313 and PC2, heavily overlapping with semi-aquatic species. At a species level comparison, there  
314 appear to be a subset of these arboreal species sharing the specific morphologies seen in  
315 our facultatively bipedal species, forming what we will refer to as the “common morph” for  
316 the remainder of this study.

317

318 PC3 and PC4 provide little-to-no useful information for identifying differences between our  
319 substrate choices due to significant overlap of all species, and thus are not discussed in  
320 further detail here ([FigureFigures 6 and 8](#)).

321

322 These osteological morphologies in the common morph likely have a significant functional  
323 impact on the environmental demands of these animals ([FigureFigure 7](#)). In particular,  
324 negative PC1 values are dominantly for non-terrestrial species, such as those that swim and  
325 climb, as well as facultative bipeds. Based on works on the musculoskeletal anatomy of the  
326 lepidosaur pelvis (Lunn, 1948; Snyder, 1954; Russell & Bauer, 2008; Fischer *et al.*, 2010;  
327 Bergmann & Hare-Drubka, 2015; Dick & Clemente, 2016; Diogo *et al.*, 2018), the functional  
328 implications of the osteology defining this morph and its differences relative to other pelvic  
329 morphologies are discussed herein. It is noted that, at least in varanid lizards, the range of  
330 femoral abduction, rotation and ankle extension are all restricted in climbing species, such  
331 as those that use primarily arboreal or rocky substrates (Clemente *et al.*, 2013). Additionally,  
332 we expect that rapid limb recovery during stride (swing phase musculature) is especially  
333 important in bipedal species, but also that this is less important in climbing species that  
334 spend more time maintaining a braced position on surfaces. For reasons of succinctness, we

335 address a selection of these morphologies we infer to be impactful, rather than an  
336 exhaustive list of all morphological elements observed.

337

338 Firstly, the functional implications of an altered ilium must be considered. In the common  
339 morph, the iliac blade tends to be relatively shallow in angle and is straight-to-concave. The  
340 iliac blade is the origin site for multiple important muscles used during locomotion,  
341 including the *M. iliofemoralis* (ILFEM), *M. iliotibialis* (ILTIB) and *M. iliofibularis* (ILFIB). These  
342 muscles serve as swing phase femoral abductor, stance phase knee extensor and swing  
343 phase knee flexor, respectively (Dick & Clemente, 2016). Additionally, there is the  
344 ilioischiadic ligament (IILIG) connecting the tip of the iliac blade to the ischiadic tuberosity,  
345 which serves as the muscle origin *M. flexor tibialis internus* (FTI), a knee flexor during the  
346 stance phase (Dick & Clemente, 2016). A shallower angle on the iliac blade has a significant  
347 effect on the moment arms of these muscles. In particular, as a relatively distal muscle, the  
348 ILFIB should be subject to a marked change in muscle moment arm significantly altering the  
349 effective mechanical advantage of this muscle (Biewener, 1989). This is of note for bipedal  
350 species, who rely on powerful limb musculature to support their body weight on just one  
351 limb at a time – should that limb not be ready to support the animal, the stride would fail.  
352 Incidentally, this is often observed in facultatively bipedal lizards that are unable to maintain  
353 bipedal locomotion for extended periods of time – a matter of fatigue linked to their ability  
354 to meet metabolic demand. Regarding stance phase musculature, the ILTIB is responsible,  
355 alongside the *M. femorotibialis* (FTIB), for extending the knee and driving forward  
356 locomotion of the animal, both on two- and four-legged terrestrial locomotion as well as  
357 during climbing. This muscle extends along the majority the length of the iliac blade,  
358 attaching dorsally to the ILFEM and ILFIB. The patella is imbedded in the distal tendon of

359 this sheet-like muscle (Dick & Clemente, 2016). Modification of the iliac blade results in a  
360 significantly different moment arm angle for this structure which, along with increased FTIB  
361 muscle mass, may increase the efficacy of knee flexion (Snyder, 1954).

362

363 Additionally, the ilium has a preacetabular process ([Figure 3](#), PAP), a structure on which  
364 two important soft tissue elements originate. The first of these is the *M. quadratus*  
365 *lumborum* (QL), equivalent to the psoas muscle in mammals (Diogo *et al.*, 2018). This muscle  
366 originates on the medial aspect of the preacetabular process and inserts on the posterior  
367 dorsal ribs, connecting the pelvis to the axial skeleton, forming a more anterior soft tissue  
368 attachment between the pelvis and the axial skeleton. This muscle appears to serve little  
369 function during quadrupedal locomotion in varanid lizards (Ritter, 1995, 1996), certainly not  
370 contributing to the lateral trunk bending utilised to augment stride length in many  
371 lepidosaurs. Instead, this muscle serves as an axial skeletal dorsoventral flexor, particularly  
372 involved in antigravitational dorsal flexion (Russell & Bauer, 2008). This elevation of the  
373 anterior body is essential to both branch-to-branch arboreal locomotion and bipedal  
374 locomotion, perhaps making the enlarged preacetabular process the most functionally  
375 significant aspect of the common morph. The second soft tissue structure of importance  
376 here is the iliopubic ligament (IILIG), connecting the preacetabular process to the pubic  
377 tubercle. This ligament performs a restrictive function, encapsulating a variety of nerves and  
378 vessels, as well as the *M. puboischiofemoralis internus* (PIFI), in a vacuity formed between  
379 the two osteological processes it connects. The PIFI is a  
380 muscle originating on the pubis and ischium, inserting into both sides of the femoral  
381 trochanter (Clemente *et al.*, 2011). The increase in the size of the preacetabular process and  
382 the anteriorly projecting pubic tubercle creates a larger vacuity beneath this ligament



383 enabling a larger PIFI (an important femoral protractor), greater innervation and vascular  
384 flow to the area, all of which may contribute to hindlimb intensive activities including  
385 bipedal locomotion and hindlimb-driven vertical climbing. ~~These features~~[Presence of a large](#)  
386 [preacetabular process has been](#) ~~were~~ noted in bipeds (Snyder, 1962; Russell & Bauer, 1992)  
387 ~~by Russell & Bauer (1992)~~, but ~~has~~[ve](#) previously not been correlated with arboreality  
388 [independent of facultative bipedality](#). Additionally, the extended ischial base provides a  
389 larger attachment site for the PIFI in species presenting the common morph, thus making up  
390 a larger portion of the pelvic girdle musculature. This further highlights the important role of  
391 this muscle as a femoral protractor during the swing phase (Dick & Clemente, 2016). Many  
392 of the anatomies highlighted here relate in particular to movement of the femur and  
393 flexion-extension of the knee joint, which are deemed important in lepidosaur locomotion  
394 (Snyder, 1952; Bergmann & Hare-Drubka, 2015). Naturally, the pelvis is involved in these  
395 functions regardless of the morphology presented, but the functional significance of  
396 modifications to these specific osteologies allows us to infer similarities between the  
397 hindlimb functions of facultatively bipedal and arboreal species.

398

399 Some studies in recent years have investigated the differences between terrestrial,  
400 quadrupedal running and branch climbing *Anolis* species (Anzai *et al.*, 2014; Anzai, Cádiz, &  
401 Endo, 2015). These studies found that running species exhibited greater muscle masses in  
402 the hindlimb extensors (*M. ambiens*, FTIB and ILTIB), and that climbing species tended to  
403 have greater muscle mass in their hindlimb retractors (*M. caudofemoralis longus* (CFL), *M.*  
404 *caudofemoralis brevis* (CFB)). Many studies on the evolution of bipedal locomotion have  
405 noted the significance of the CFL in enabling this mode (Gatesy *et al.*, 1990; Hutchinson,  
406 2004a, 2004b; Persons & Currie, 2017). Combining these findings with our own, enables us

407 to identify an association between the use of arboreal substrates and a facultative bipedal  
408 locomotor mode in extant lepidosaurs that is observable in the osteology of the pelvis. Our  
409 findings demonstrate that the same pelvic morphologies are present in facultative bipeds as  
410 are found in arboreal species (enlarged preacetabular process, iliac blade morphology, large  
411 ischial base). Based on findings from modern literature (Russell & Bauer, 2008; Anzai *et al.*,  
412 2014, 2015) and historical (Snyder, 1952) we expect that the muscle architecture of these  
413 animals would follow similar trends, and that these may be distinct from those animals that  
414 tend to run quadrupedally. Further analysis of muscle mass variation in a wide range of  
415 facultative bipeds would enable more thorough testing of this hypothesis.

416  
417 There are several different whole-body morphs present in the lepidosaur group that prefer  
418 an arboreal substrate and climbing locomotion: the chamaeleonid morph (highly specialised  
419 girdle, autopodial and tail morphologies), the gekkonid morph (specialised toe pads in many  
420 species) and the less specialised morph common to most other arboreal dwellers (iguanids,  
421 corytophanids, anolids, lacertids, etc.). These less specialised forms tend to rely on limb  
422 proportions, gripping claws, balancing tails and often less-than-graceful movement through  
423 branches. These less specialised forms are those expressing the common pelvic morph that  
424 we have highlighted in this study. We propose that these groups may be predisposed  
425 towards the acquisition of a facultatively bipedal locomotor mode when moving out of their  
426 usual arboreal environment, aided by commonalities in the musculoskeletal adaptations for  
427 an arboreal, climbing lifestyle and a facultatively bipedal locomotor mode. This general  
428 pattern echoes the most widely supported model of hominin bipedality locomotion,  
429 whereby a facultatively bipedal locomotor mode was adopted in response to a shift from  
430 arboreal to terrestrial habitats.

431  
432 [Due to the nature the taphonomic process, and the complicated 3D structure of the pelvis,](#)  
433 [it is not uncommon for pelvises to be poorly or unpreserved in lizard fossils. We have](#)  
434 [included an assessment of an exemplar fossil specimen from Lepidosauria and provided our](#)  
435 [inference regarding their locomotor ecology, demonstrating the potential value of this work](#)  
436 [in the fossil record.](#)

437  
438 [The Maastrichtian \*Polyglyphodon\* \(Gilmore, 1942\) has been hypothesized to lie nested](#)  
439 [within Macroteiida, a clade within Teiidae. Some species of teiid, such as \*Ameiva ameiva\*,](#)  
440 [are known to exhibit facultative bipedality \(Urban, 1965\). The pelvis of \*Polyglyphodon\*](#)  
441 [sternbergi bears a striking resemblance to that of northern caiman lizard \(\*Dracaena\*](#)  
442 [guianensis\), a semi-aquatic and semi-arboreal species featured in this study \(supplementary](#)  
443 [file\), and thus would likely score similarly in a principal components analysis. Shared](#)  
444 [anatomies are a stout iliac blade with a midshaft swelling, a small but distinct preacetabular](#)  
445 [process, a rounded iliac tip, reasonably short ischium with a distinct ischial tuberosity. The](#)  
446 [pubis as similar across the two species as other parts of the pelvis. The northern caiman](#)  
447 [lizard does not place \*\*itself\*\* within the range of facultative bipeds on any principal](#)  
448 [component, thus we predict that \*P. sternbergi\* was likely an obligate quadruped; ~~it~~ most](#)  
449 [likely used a terrestrial substrate, potentially climbing low level rockery or shrubbery. We](#)  
450 [do not predict a semi-aquatic lifestyle, as is observed in the northern caiman lizard based,](#)  
451 [on shared pelvic morphology due to there being many other whole-body osteological](#)  
452 [features that are more informative for such a behaviour, such as bone density and limb](#)  
453 [morphology.](#)

454

455 **Conclusion**

456

457 In conclusion, we have used 3D landmark-based geometric morphometrics to demonstrate  
458 that the overall morphospace for the lepidosaur pelvis is broad and wide-ranging. Within  
459 this overall morphospace, a small region is occupied by facultative bipeds. The vast majority  
460 of this smaller morphospace overlaps that occupied by species that show a preference for  
461 arboreal habitats. Pelvic morphological adaptations relevant for living in an arboreal  
462 environment are similar to those necessary to facilitate facultative bipedality. We highlight  
463 some of the anatomical and functional variations seen in these groups and propose a  
464 hypothesis that a particular morphotype of arboreal species is naturally predisposed for  
465 facultative bipedality. [We also demonstrate how our findings may be of use in identifying](#)  
466 [locomotor mode in ~~exemplar \[?\]~~ well-preserved fossil specimens.](#)

467

468 **Acknowledgements**

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473 [overall quality and clarity of this manuscript.](#)

474

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604

605

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**Commented [LG3R2]:** Mendeley issue – fixed now

606 **Figure Captions**

607

608 Figure 1: The phylogenetic relationships of the species in the sample, along with locomotor  
609 mode and substrates used. Black dot represents the preferred substrate. Colour  
610 correspondence maintained ~~for INin~~ all ~~further~~ SUBSEQUENT subsequent figures.

611

612 Figure 2: Representative morphology, in side profile, for a range of species in the study.  
613 Species as follows: A – *Varanus exanthematicus*, B – *Tiliqua rugosa*, C – *Cachryx defensor*, D  
614 – *Iguana iguana*, E – *Amblyrhynchus cristatus*, F – *Ctenosaura similis*, G – *Lacerta trilineata*,  
615 H – *Chlamydosaurus kingii*, I – *Basiliscus basiliscus*, J – *Sphenodon punctatus*, K –  
616 *Acanthodactylus schreiberi*.

617

618 Figure 3: Green iguana pelvis in left lateral and medial view. Key hard and soft tissue  
619 osteologies are highlighted. Modified from Snyder (1954) and Russel & Bauer (2008). Ace. –  
620 acetabulum; cfb – M. caudofemoralis brevis; IB – iliac blade; ilig – ilioischadic ligament;  
621 ilfem – M. ilifemoralis; ilfib – M. iliofibularis; iltib – M. iliotibialis; iplig – iliopubic ligament; IT  
622 – ischidiac tuberosity; OF – obturator foramen; PAP – preacetabular process; pife – M.  
623 puboischiofemoralis externus; pifi – M. puboischiofemoralis internus; PT – pubic tuberosity;  
624 ql – M. quadratus lumborum.

625

626 Figure 4: LaSEC output indicating the percentage shape variation captured by different  
627 numbers of landmarks, based on iterative models.

628

629 Figure 5: Distribution of locomotor mode across Principal Components 1 and 2. Colours  
630 follow those in Figure 1. Warped meshes of the green forest lizard indicate the range of  
631 morphologies present on each principal component.

632

633 Figure 6: Distribution of locomotor mode across Principal Components 3 and 4. Colours  
634 follow those in Figure 1.

635

636 Figure 7: Distribution of preferred substrate use across Principal Components 1 and 2.

637 Colours follow those in Figure 1.

638

639 Figure 8: Distribution of preferred substrate use across Principal Components 3 and 4.

640 Colours follow those in Figure 1.

641

642 **Tables**

643

644 [Table 1: Sources for specimens and scans used in this study.](#)

	Lambda	p-value	Lambda
Bipedal	0		±
Arboreal	0.669		0.011
Saxicolous	0		±
Semi-Aquatic	0		±
Terrestrial	0.421		0.239

645

Table 12: Results from the five tests for phylogenetic signal Sources for specimens and scans used in this study.

Species	Museum code (if applicable)	Museum	Source
<i>Ablepharus pannonicus</i>	fmnh-amphibians and reptiles-83533	Field Museum of Natural History	Morphosource.org
<i>Acanthocercus cyanogaster</i>	fmnh-amphibians and reptiles-12522	Field Museum of Natural History	Morphosource.org
<i>Acanthodactylus boskianus</i>	fmnh-amphibians and reptiles-68769	Field Museum of Natural History	Morphosource.org
<i>Acanthodactylus schreiberi</i>	BMNH 1888.11.3.7	Natural History Museum, London	Primary
<i>Adolfus africanus</i>	fmnh-amphibians and reptiles-154745	Field Museum of Natural History	Morphosource.org
<i>Agama agama</i>	fmnh-amphibians and reptiles-188910	Field Museum of Natural History	Morphosource.org
<i>Amblyrhynchus cristatus</i>	uf-herp-41558	Florida Museum of Natural History	Morphosource.org
<i>Ameiva ameiva</i>	ummz-herps-245032	University of Michigan Museum of Zoology	Morphosource.org
<i>Anolis carolinensis</i>	ummz-herps-245698	University of Michigan Museum of Zoology	Morphosource.org
<i>Basiliscus basiliscus</i>	BMNH 1914.5.21 16	Natural History Museum, London	Primary
<i>Basiliscus vittatus</i>	R.19025	University Museum of Zoology, Cambridge	Primary
<i>Bronchocela cristatella</i>	uf-herp-112989	Florida Museum of Natural History	Morphosource.org
<i>Cachryx defensor</i>	uf-herp-41534	Florida Museum of Natural History	Morphosource.org

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<i>Chlamydosaurus kingii</i>	R.8429 1	University Museum of Zoology, Cambridge	Primary
<i>Cophotis ceylanica</i>	uf-herp-86474	Florida Museum of Natural History	Morphosource.org
<i>Cordylus cordylus</i>	uf-herp-63302	Florida Museum of Natural History	Morphosource.org
<i>Crotaphytus collaris</i>	BMNH 1889.7.3.14	Natural History Museum, London	Primary
<i>Ctenosaura similis</i>	uf-herp-181929	Florida Museum of Natural History	Morphosource.org
<i>Cyclura carinata</i>	uf-herp-32820	Florida Museum of Natural History	Morphosource.org
<i>Dracaena guianensis</i>	uf-herp-129938	Florida Museum of Natural History	Morphosource.org
<i>Draco dussumieri</i>	uf-herp-19920	Florida Museum of Natural History	Morphosource.org
<i>Egernia whitii</i>	uf-herp-133957	Florida Museum of Natural History	Morphosource.org
<i>Heloderma suspectum</i>	uf-herp-167975	Florida Museum of Natural History	Morphosource.org
<i>Iguana iguana</i>	uf-herp-181922	Florida Museum of Natural History	Morphosource.org
<i>Lacerta trilineata</i>	uf-herp-65017	Florida Museum of Natural History	Morphosource.org
<i>Lophognathus temporalis</i>	ummz-herps-245428	University of Michigan Museum of Zoology	Morphosource.org
<i>Lyriocephalus scutatus</i>	uf-herp-126295	Florida Museum of Natural History	Morphosource.org
<i>Moloch horridus</i>	uf-herp-126296	Florida Museum of Natural History	Morphosource.org

<i>Shinisaurus crocodilurus</i>	UF-H-60925	Florida Museum of Natural History	Morphosource.org
<i>Sphenodon punctatus</i>	QMBC 0614	Queen Mary University London	<a href="https://osf.io/bds35/">https://osf.io/bds35/</a>
<i>Tiliqua rugosa</i>	uf-herp-87304	Florida Museum of Natural History	Morphosource.org
<a href="#"><u><i>Tropicagama temporalis</i></u></a>	<a href="#"><u>ummz-herps-245428</u></a>	<a href="#"><u>University of Michigan Museum of Zoology</u></a>	<a href="#"><u>Morphosource.org</u></a>
<i>Tropicolotes tripolitanus</i>	cas-herp-123433	California Academy of Sciences	Morphosource.org
<i>Varanus exanthematicus</i>	V3 (live scan)		<a href="https://datadryad.org/resource/doi:10.5061/dryad.v1d30">https://datadryad.org/resource/doi:10.5061/dryad.v1d30</a>
<i>Zonosaurus haraldmeieri</i>	uf-herp-72878	Florida Museum of Natural History	Morphosource.org

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648 [Table 2: Pagel's  \$\lambda\$  test for phylogenetic signal. Bold field indicates signal presence \( \$p\$ -value<0.05\).](#)

<a href="#">Trait</a>	<a href="#"><math>\lambda</math> value</a>	<a href="#">p-value</a>
<a href="#">Bipedal</a>	<a href="#">0.0000717</a>	<a href="#">1</a>
<a href="#">Arboreal</a>	<a href="#">0.683</a>	<a href="#"><b>0.00982</b></a>
<a href="#">Rock-dwelling</a>	<a href="#">0.0000411</a>	<a href="#">1</a>
<a href="#">Semi-aquatic</a>	<a href="#">0.0000582</a>	<a href="#">1</a>
<a href="#">Terrestrial</a>	<a href="#">0.437</a>	<a href="#">0.227</a>

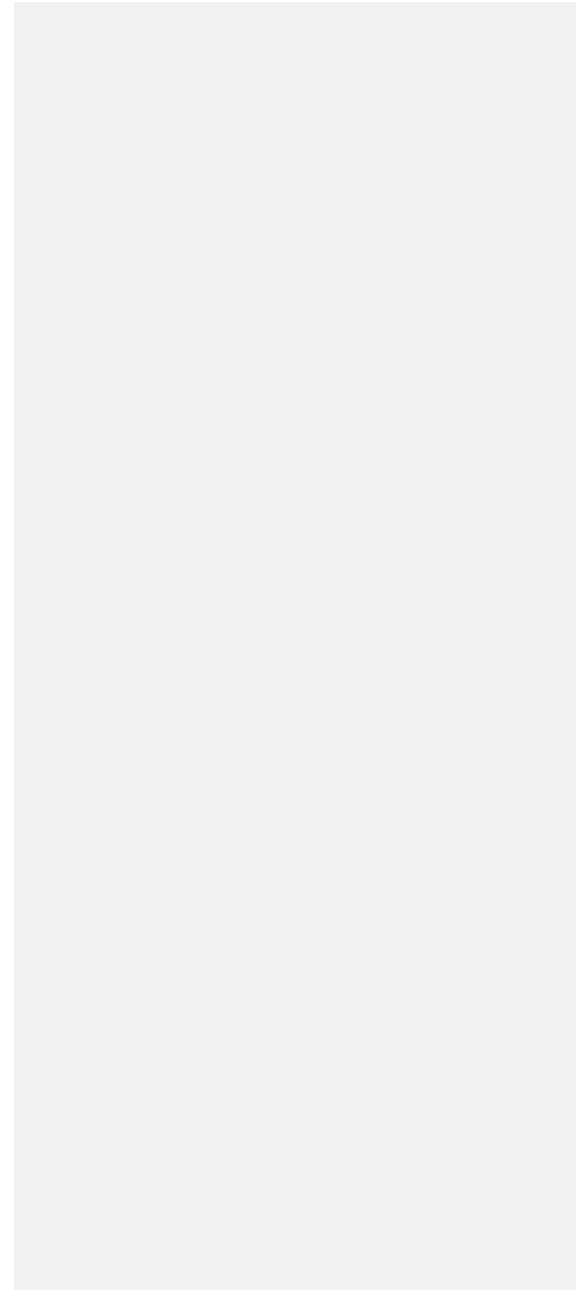
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650

651 Table 3: Landmark locations and definitions.

Landmark	Type	Location
1	II	Distal tip of iliac blade
2	III	Apex of iliac blade dorsal surface curve
3	III	Dorsal aspect prior to preacetabular process
4	II	Tip of preacetabular process
5	III	Ventral aspect prior to preacetabular process
6	II	Pectineal process, near acetabulum
7	II	External edge of pubis perpendicular to obturator foramen
8	II	Processus lateralis pubis
9	II	Inward apex between landmarks 9 and 10
10	II	Pubic tubercle
11	II	Anterior-most point of obturator foramen
12	II	Posterior-most point of obturator foramen
13	II	Puboischiadic symphysis, most ventral point
14	II	Articulation between ischium and proischiadic cartilage
15	II	Articulation between ischium and hypoischium
16	II	Most posterior point of ischidiac tuberosity
17	II	Most posterior point of the second portion of the ischidiac tuberosity
18	II	Articulation between ischium and ilium, on acetabular rim
19	II	Lateral entre acetabulum
20	III	Opposite preacetabular process, on ventral aspect of iliac blade
21	III	Opposite landmark 2, on ventral aspect of iliac blade
22	III	Inner ischium, perpendicular to the narrowest portion of the ischium
23	III	Top external rim of acetabulum, just below supracetabular process
24	III	Bottom of external rim of acetabulum
25	II	Medial centre acetabulum, approximately opposite 19



653 Table 4: Principal components analysis scores for each species.

Species	PC1	PC2	PC3	PC4	PC5	PC6
<i>A. africanus</i>	0.129	0.054	-0.041	0.014	0.002	0.033
<i>A. agama</i>	-0.051	0.001	0.082	0.083	-0.026	-0.023
<i>A. ameiva</i>	-0.033	0.028	0.052	-0.024	0.067	-0.046
<i>A. boskianus</i>	0.051	0.033	0.064	-0.003	0.037	-0.001
<i>A. carolinensis</i>	-0.005	0.086	-0.047	-0.006	-0.038	-0.060
<i>A. cristatus</i>	-0.071	-0.037	-0.019	0.074	0.027	0.038
<i>A. cyanogaster</i>	-0.064	-0.019	0.046	0.037	0.019	-0.018
<i>A. pannonicus</i>	0.252	-0.005	0.020	-0.021	-0.040	-0.030
<i>A. schreiberi</i>	0.065	0.036	0.070	0.003	0.023	-0.003
<i>B. basiliscus</i>	-0.089	0.023	0.025	-0.004	-0.041	-0.020
<i>B. cristatella</i>	0.002	-0.005	0.025	0.053	-0.046	-0.028
<i>B. vittatus</i>	-0.091	0.066	0.051	-0.045	-0.056	-0.020
<i>C. carinata</i>	-0.058	-0.011	-0.020	0.020	0.039	-0.021
<i>C. ceylanica</i>	-0.074	0.015	-0.076	-0.025	-0.039	0.003
<i>C. collaris</i>	-0.053	-0.003	0.022	0.023	0.087	0.060
<i>C. cordylus</i>	0.094	-0.069	-0.016	0.071	-0.018	0.030
<i>C. defensor</i>	-0.018	-0.036	-0.052	-0.044	0.027	-0.003
<i>C. kingii</i>	-0.127	0.033	0.033	-0.010	0.017	0.019
<i>C. similis</i>	-0.078	0.037	0.010	0.017	0.081	0.016
<i>D. dussumieri</i>	-0.060	0.080	-0.002	0.097	-0.125	0.026
<i>D. guianensis</i>	0.000	-0.064	-0.018	-0.061	0.033	-0.032
<i>E. whitii</i>	0.199	0.036	0.013	-0.020	-0.020	-0.021
<i>H. suspectum</i>	-0.034	0.060	-0.192	-0.033	0.007	0.051
<i>I. iguana</i>	-0.066	0.011	0.028	0.025	0.021	0.019
<i>L. scutatus</i>	-0.023	-0.023	-0.032	-0.053	0.011	-0.065

<i>L. trilineata</i>	0.109	0.051	0.031	-0.016	-0.013	0.027
<i>M. horridus</i>	-0.041	-0.195	-0.001	-0.003	-0.018	-0.037
<i>S. crocodilurus</i>	0.012	-0.039	-0.103	-0.012	-0.033	0.040
<i>S. punctatus</i>	-0.106	-0.102	0.096	-0.109	-0.079	0.064
<i>T. rugosa</i>	0.139	-0.101	-0.035	0.079	0.052	-0.001
<i>T. temporalis</i>	<u>-0.015</u>	<u>0.038</u>	<u>0.042</u>	<u>0.005</u>	<u>0.025</u>	<u>-0.026</u>
<i>T. tripolitanus</i>	0.058	-0.080	-0.016	-0.022	-0.043	0.020
<i>V. exanthematicus</i>	-0.050	0.039	-0.111	-0.011	0.022	-0.057
<i>Z. haraldmeieri</i>	0.100	0.060	0.071	-0.078	0.040	0.065

655 Table 5: Cumulative variance represented by each principal component.

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalues	0.0081	0.0037	0.0036	0.0022	0.0021	0.0013
Proportion of variance	0.3080	0.1388	0.1379	0.0827	0.0802	0.0492
Cumulative Proportion	0.3080	0.4468	0.5847	0.6675	0.7477	0.7970

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