

Environmental correlates of morphological diversity in Australian geckos

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Abstract

Aim: Climatic variation has long been regarded as a primary source of morphological variation. However, there is mixed support for the adherence of reptiles to ecogeographical hypotheses, such as Bergmann's rule (body size decreases with temperature) and Allen's rule (limb length increases with temperature). We quantified body and limb morphology among the diverse Australian gecko fauna (4 families, 30 genera, 226 of the 231 described species) to investigate environmental correlates of morphological variation in this radiation.

Location: Australia.

Major taxa studied: Geckos (Squamata: Gekkota; the families Gekkonidae, Carphodactylidae, Diplodactylidae and Pygopodidae).

Methods: We measured 20 external features of ethanol-preserved museum specimens. We investigated whether principal component axes of morphology were correlated with three key environmental variables, and the microhabitat occupied by each species.

Results: Morphology varied greatly among Australian gecko families and genera, although there was a strong phylogenetic signal in morphology. After accounting for phylogeny, morphology was correlated with a species' microhabitat use. Saxicolous species and species with variable microhabitat requirements (i.e., generalists) had larger body dimensions than terrestrial species. Saxicolous species also had longer proportional forelimbs and hindlimbs than terrestrial species.

Main conclusions: Our results highlight the importance of phylogeny and microhabitat use in shaping the morphology of Australian geckos. We find little evidence that Australian geckos adhere to Bergmann's rule or Allen's rule, suggesting that these ecogeographical hypotheses provide limited insight into the adaptive potential of lizard species to altered environmental conditions.

KEYWORDS

Allen's rule, Bergmann's rule, body size, climate, ecogeographical rules, environmental variation, limb length, morphology

1 | INTRODUCTION

Understanding the complex processes that contribute to the evolution and diversification of species has long been of interest to evolutionary ecologists (Collar et al., 2010). The remarkably high diversity of some lineages has led to numerous studies investigating relationships between environmental variables and different aspects of biodiversity (e.g., phylogenetic, morphological and ecological diversity). Many classic cases of clade diversification have been in response to a morphological innovation or ecological opportunity (Benton & Emerson, 2007; Gavrillets & Losos, 2009; Losos & Mahler, 2010; Mahler et al., 2010; Yoder et al., 2010). On the one hand, the emergence of phenotypic similarities between species can point to predictable responses to ecological challenges and selection pressures (Marques et al., 2017). On the other hand, morphological differences among lineages, and individual species can occur for a variety of reasons, including adaptive responses to the physiological demands of an environment or local habitat conditions (Vidal-García et al., 2014), and neutral processes (e.g., genetic drift). This in turn leads us to the question: what conditions and environmental challenges are critical in driving this morphological divergence?

Many studies have attributed variation in morphological traits among species to differences in ecological and environmental parameters. Climate can influence the morphology of animals directly via its impact on ecophysiology (e.g., the size and shape of animals influence rates of heat loss and retention), or indirectly by shaping vegetation, geological characteristics (e.g., soil properties) and available microhabitats (Gardner et al., 2011; Kearney & Porter, 2004). At a broad scale, climatic conditions can include factors such as temperature and aridity (Jaffe et al., 2016). In addition, fine-scale correlations between an animal's morphology, habitat characteristics and microhabitat use can highlight intricate links between phenotype and environment (Vanhooydonck et al., 2005). Thus, looking for patterns in morphology within species-rich taxa, in relation to environmental conditions, could provide key information regarding the mechanisms involved in promoting and shaping morphological diversity.

Environmental variation can impact selection on organismal morphology, which can in turn lead to covariation between traits and geographical gradients (Pincheira-Donoso et al., 2008). For example, it has long been postulated that animal body sizes adhere to an ecogeographical principle known as Bergmann's rule, which proposes that body size increases with increasing latitude and elevation, and thus, decreasing environmental temperatures (Blackburn et al., 1999; Pincheira-Donoso et al., 2008). This hypothesis posits that larger endotherms have an increased ability to conserve heat compared to smaller individuals due to a reduced surface area to volume ratio (Feldman & Meiri, 2014). Whilst birds and mammals seem to conform to Bergmann's rule (Meiri & Dayan, 2003), the extent to which this rule applies to ectotherms – and the mechanisms that either drive Bergmann's rule or the reverse pattern in them – are still debated (Ashton & Feldman, 2003; Feldman & Meiri, 2014; Olalla-Tárraga & Rodríguez, 2007; Olalla-Tárraga, 2011; Pincheira-Donoso

& Meiri, 2013; Rivas et al., 2018; Slavenko et al., 2019; Wishingrad & Thomson, 2020; Zamora-Camacho et al., 2014). Indeed, there has been a recurrent lack of support for Bergmann's rule in ectotherms; for example, *Liolaemus* lizards failed to support Bergmann's rule, with none of the studied clades displaying increased body size with increasing latitude or elevation (Cruz et al., 2005; Moreno Azocar et al., 2015; Pincheira-Donoso et al., 2008; Pincheira-Donoso & Meiri, 2013). In contrast, some lizard species have been found to reverse this rule, with larger body sizes occurring in warmer environments (Ashton & Feldman, 2003). Thus, the adherence of lizard species to Bergmann's rule requires further investigation.

Another ecogeographical principle that has received much less attention is Allen's rule, which predicts that endotherms inhabiting colder climates will have shorter limbs and appendages (bills, ears, tails), compared to warm adapted individuals (Alho et al., 2011; Campbell-Tennant et al., 2015; Nudds & Oswald, 2007; Symonds & Tattersall, 2010). Longer appendages facilitate heat exchange with the environment. Volynchik (2014) investigated the body shape of lacertid lizard species in relation to environmental conditions and found that relative hind limb lengths increased with increasing temperature (Volynchik, 2014, see also Liang & Shi, 2017; Ray, 1960). However, the applicability of Allen's rule to ectotherms at a large spatial and phylogenetic scale has been little explored and empirical data are largely lacking. Furthermore, it has been suggested that climatic variables other than temperature, such as aridity, may also influence body size and shape; such that a larger individual, for example, would have a reduced surface area to volume ratio, and hence would be less susceptible to desiccation (Hipsley & Müller, 2017; Malhotra & Thorpe, 1997).

Morphology is not only influenced by broad-scale climatic variation, but also by fine-scale microhabitat use. The relationship between morphology and habitat use has been particularly well studied in several lizard groups, including *Anolis* lizards (Hagey et al., 2017; Losos, 1990b, 2011; Williams, 1972), agamids (Collar et al., 2010), varanids (Thompson et al., 2009), skinks (Foster et al., 2018; Goodman et al., 2008), and geckos (Riedel et al., 2020). Lizard species exhibit a diverse suite of lifestyles, and their ability to exploit a wide variety of habitats, varying from wet rain forest environments to dry, arid regions, makes them ideal study species (Greer, 1989; Kohlsdorf et al., 2001; Wilson & Swan, 2017). The ecological diversity exhibited by lizards directly correlates with variation in traits such as body size, limb proportions, tail length and head dimensions, all of which likely represent adaptations to different aspects of their specific microhabitat.

Several studies have provided evidence for how selection for microhabitat specialization may drive interspecific differences in lizard morphology (Foster et al., 2018; Goodman et al., 2008; Hagey et al., 2017; Losos, 2011; Riedel et al., 2020). Among the most studied examples of adaptive links between morphology and microhabitat use are the Caribbean *Anolis* lizard 'ecomorphs' (Losos, 2011). Anole ecomorphs are morphologically adapted to occupy different parts of their environment, with differences in limb lengths pertaining to perch diameter (Losos, 1990a, 1990b, 2011; Losos & Irschick, 1996).

The ability to effectively move within the environment has led to several generalizations regarding limb lengths and microhabitat use. It is thought that ground-dwelling terrestrial species may encounter more obstacles with the potential to impede locomotion, and therefore, benefit from having shorter limbs (Foster et al., 2018; Melville & Swain, 2000). In contrast, climbing species occupying arboreal and saxicolous microhabitats would require greater stability and encounter fewer obstacles, allowing for faster rates of movement, and thus, evolve longer limbs (Foster et al., 2018; Goodman et al., 2008; Tan et al., 2020, but see Hagey et al., 2017 who showed that arboreal species had shorter femora, and Kaliontzopoulou et al., 2010 who showed terrestrial species had longer femora than scansorial species). Whilst these patterns have been observed within skinks (Foster et al., 2018; Goodman et al., 2008; Melville & Swain, 2000), attempts to link limb morphology and microhabitat use in non-anoline lizards have often failed (e.g., Foster et al., 2018; Kulyomina et al., 2019; Olberding et al., 2016). The ecological and morphological similarities between many lizard groups, however, make further investigation into microhabitat-morphology relationships in lizard species potentially illuminating.

Australia is rich in lizard diversity compared to other vertebrate groups (Powney et al., 2010; Roll et al., 2017). Many lizard lineages have undergone elaborate radiations, and Australia's gecko fauna is no exception. Four distinct families of gekkotan lizards are present in Australia, comprising c. 230 species (Meiri, 2020; Uetz et al., 2020). These four families include the Carphodactylidae, Diplodactylidae, Gekkonidae and the unique Pygopodidae, comprising the limbless geckos endemic to the continent (Brennan et al., 2016; Greer, 1989; Wilson & Swan, 2017). Australian geckos inhabit a wide range of habitats, from the rain forests of the north-east to the arid plains of the centre, and may be terrestrial, arboreal, saxicolous or occupy a mix of these microhabitats, with some pygopodid species known to occupy a fossorial microhabitat (Cogger, 2014; Greer, 1989; Pianka, 1981; Wilson & Swan, 2017). Gecko hotspots of species richness have been noted in central Australia, particularly in the highlands of Western Australia (Figure 1). Due to the vast spread of gecko species and clades across the continent (Figure 1), and their diverse morphology, ecology, and habitat use, they make excellent candidates for studying morphological variation in association with microhabitat use and climatic gradients. Furthermore, gecko species are mostly nocturnal, which means they use residual heat gained during the day when foraging at night (Penniket & Cree, 2015). This may impact whether gecko species adhere to Bergmann's and Allen's rules, and provide novel insight into the degree to which activity patterns impact temperature-morphology relationships.

Here, we provide a new, detailed approach to quantifying morphology using 20 external measurements to analyse gecko body shape and size in relation to climate and habitat use. We examined museum specimens of 98% of Australian gecko species (recognized as of early 2019). We aim to: (a) quantify the degree of morphological variation across Australian gecko species, (b) investigate the environmental correlates of this variation, and (c) test the applicability of Bergmann's and Allen's rules to Australian gecko species.

2 | MATERIALS AND METHODS

2.1 | Specimens

We examined specimens from almost all described species (226 of 231 described species; as of early 2019) of Australian geckos. This included species from all 30 genera of Australian geckos from the four families that occur in Australia (see Supporting Information Table S1.1, Appendix S1): Carphodactylidae ($n = 30$), Diplodactylidae ($n = 92$), Gekkonidae ($n = 61$) and Pygopodidae ($n = 43$). We excluded the following species because no specimens were available: *Cyrtodactylus kimberleyensis* and *Diplodactylus kenneallyi* (known only from their holotypes), *Strophurus rankini*, *Gehyra pulingka* and *Aprasia picturata*. To account for potential taxonomic issues, all museum specimen records acquired from the Online Zoological Collections of Australian Museums (<https://www.ozcam.org.au/>) were georeferenced in qGIS v3.6.2 (<https://qgis.org/en/site/>) against expert verified distributional data collated as part of the 2017 International Union for Conservation of Nature (IUCN) Red List assessment of all Australian squamates (Chapple et al., 2019; IUCN, 2019; Tingley et al., 2019). Specimens within the distributional polygons were preferentially chosen to minimize potential taxonomic issues.

2.2 | External morphological measurements

We measured five specimens (where possible) of the 226 species of Australian geckos to quantify and contrast the morphological diversity present in each family (Supporting Information Table S1.1, Appendix S1). We did not use tail length because many of the specimens we measured had broken, or fully or partially regenerated, tails. We consider five specimens appropriate, as we focus on interspecific, rather than intraspecific variation (Vidal-García et al., 2014). Within-species variation in the traits we measured is much lower than differences between species and genera: variance partitioning revealed that intraspecific variation amounts, on average, to 12% of the total variance (maximum 23% for pelvic height [PH]). In contrast, taxonomic family explains 46%, and genus explains 42%, on average (Supporting Information Appendix S2). Only adult specimens were selected for measurement, as juvenile specimens would not provide an accurate representation of body size and potentially shape. We did not record sex because it is difficult to accurately sex geckos based on external morphology alone, and small gecko species are generally not sexually dimorphic (e.g., Zuffi et al., 2011). The specimens we examined were fixed in formalin, and stored in ethanol. We measured 20 head, body and limb dimensions, using digital callipers (Mitutoyo 500-763-20 8"/200 mm Coolant Proof Digimatic Calipers with data output; Supporting Information Table S1.2, Figure S1.1). Specimens were examined from museum collections (see Acknowledgments) between May and August 2019. To ensure consistency, all measurements were conducted by the senior author (JN). Specimens that had been preserved in a flat, straight posture were preferentially selected, to improve measurement accuracy and

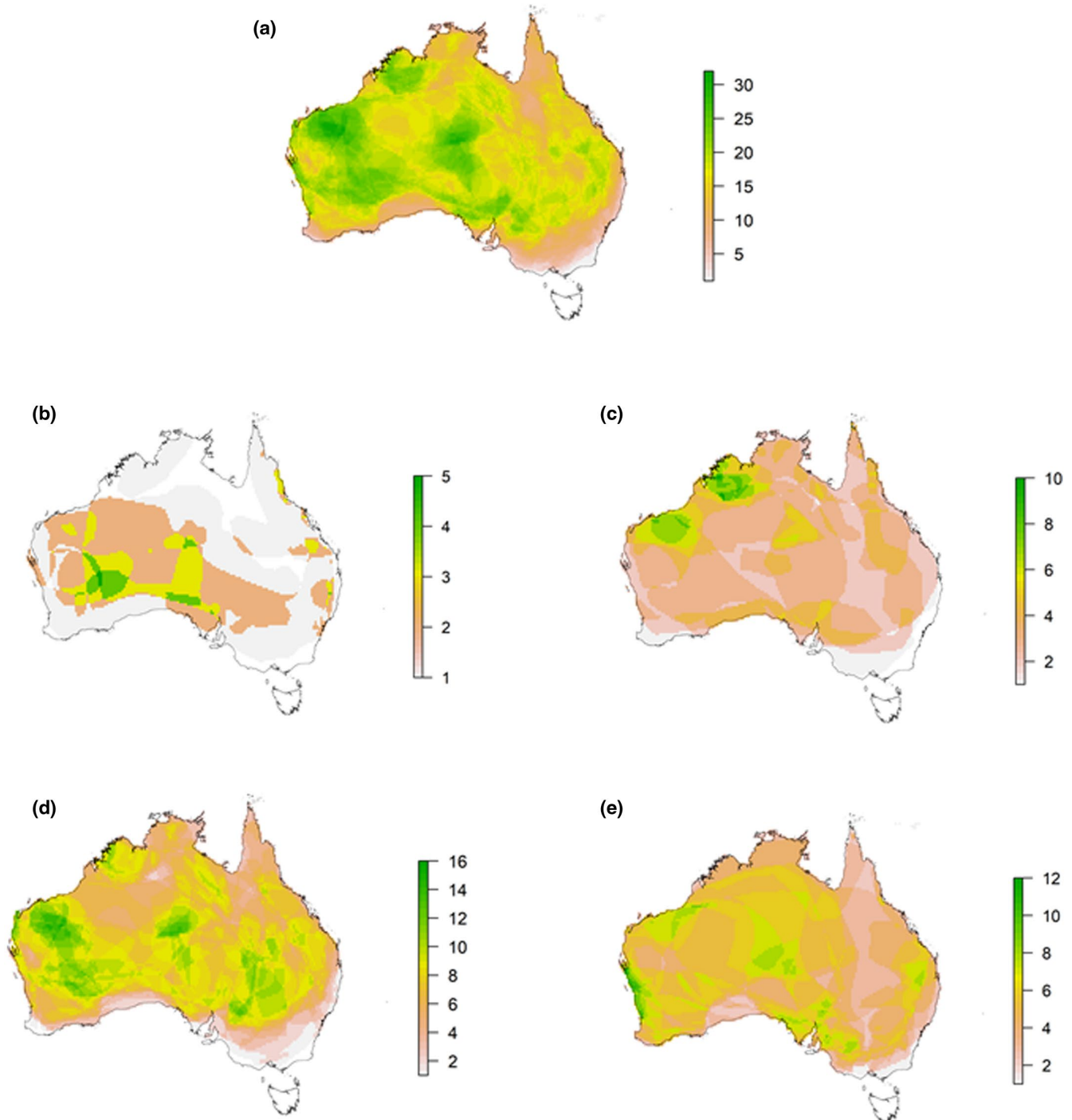


FIGURE 1 Distributional species richness maps for Australian geckos, and each of the four gecko families. Colour map on the right represents amount of species richness in each grid cell. Order as follows (a) geckos overall, (b) Carphodactylidae, (c) Gekkonidae, (d) Diplodactylidae, (e) Pygopodidae. Data from IUCN (2019) [Colour figure can be viewed at wileyonlinelibrary.com]

comparability across measurements. All morphological data can be found in Supporting Information Appendix S3.

2.3 | Micro-CT analyses

Pygopodid species lack visible forelimbs, and their hindlimbs are greatly reduced. Several morphological measurements were

thus difficult to take based on external features (e.g., snout–axilla length, inter-limb length). In order to obtain limb measurements for limb-reduced pygopodid species, we used micro-CT (Computed Tomography) scanning and VG STUDIO MAX software v3.3 (<https://www.volumegraphics.com/en/products/vgstudio-max.html>) to visualize the internal morphology of these species and infer fore and hind limb positioning. The locations of the pectoral and pelvic girdles were identified and used to locate the vertebrae associated with the

fore limb and hind limb (Camaiti et al., 2019; Stanley et al., 2016). Snout-axilla length (SAL) and inter-limb length (ILL) were measured using the polyline digital measuring tool. This method was carried out for one specimen per species for each of the seven pygopodid genera (i.e., a total of seven species/specimens). These measurements were then used to calculate where the limbs would have been located in all pygopodid species. Specimens for which all other external measurements were collected were chosen for micro-CT scanning. In the case of one species, *Pletholax gracilis*, we acquired a micro-CT image from MorphoSource (Boyer et al., 2016) and applied the same method.

2.4 | Environmental data

Data on microhabitat use (arboreal; fossorial; saxicolous; terrestrial; or variable, for species that occupied more than one microhabitat type) were sourced from a comprehensive global database (Meiri, 2018). For newly described species (e.g., *Gehyra*), the relevant information was sourced from published literature and the Western Australia Museum records, where possible (Doughty et al., 2018). Distributional data were collated as part of the 2017 IUCN Red List assessment of all Australian squamates (Chapple et al., 2019; Tingley et al., 2019) and used to estimate median values of three climate variables across each species' geographical range: aridity (CGIAR-CSI Global-Aridity Database v2; Zomer et al., 2007, 2008), and mean annual temperature and temperature seasonality (standard deviation) from the WorldClim Database v2 (Fick & Hijmans, 2017). All variables were downloaded at 30 arc-second resolution (c. 1 km at the equator) and covered the period 1970–2000.

2.5 | Statistical analysis

All analyses were conducted using R (version 3.4.3) and R Studio (version 1.1.447) (R Development Core Team, 2018). In the rare instances in which we were unable to obtain a measurement due to imperfectly preserved specimens, missing trait values were imputed by taking the mean value of other specimens in the species. In addition, where we were unable to fully extend limbs for measurement, individual limb segment lengths (i.e., upper fore limb, lower fore limb, fore-foot) were combined to calculate forelimb length (FLL) and hindlimb length (HLL). Morphological variables were log-transformed before being analysed using principal component analyses (PCAs; *prcomp* function) to generate orthogonal axes that captured morphological variation among species. Two PCAs were run, one using a data set that included pygopodid species and excluded all limb data, and a second that excluded pygopodid species and included all 20 morphometric variables. The PC scores were used as response variables in subsequent regression analyses.

Due to the importance of phylogenetic history on morphology, we used phylogenetic generalized least squares (PGLS) via the *caper*

package in R. Using the R package *ape* and a near-fully sampled phylogenetic tree of global squamate species (Tonini et al., 2016), we produced a tree containing all gecko species for which we had morphological, environmental and phylogenetic data ($n = 144$ species, excluding pygopodids). The PGLS approach allows for the estimation (via maximum likelihood) of a phylogenetic scaling parameter (λ). Values of $\lambda = 1$ indicate complete phylogenetic dependence whilst values of $\lambda = 0$ indicate phylogenetic independence (Dale et al., 2015; Freckleton et al., 2002). Separate PGLS analyses were conducted in which PC1 scores, PC2 scores, proportional fore limb lengths (fore limb length/snout-vent length), and proportional hind limb lengths (hind limb length/snout-vent length) were response variables, and microhabitat and the three climate variables were fixed effects. We also ran 20 separate PGLS models, in which each individual morphological measurement was used as a response variable, and snout-vent length was used as a covariate. Terrestrial microhabitat use was used as the reference category in all PGLS models. Climate variables were centred and scaled prior to analysis. All analyses were run excluding pygopodids, due to their unique ecology, morphology (see PCA results) and distribution (Figure 1).

To account for spatial autocorrelation in morphology, we used Moran's eigenvector maps: orthogonal vectors that minimize the spatial autocorrelation (as measured by Moran's I) present in model residuals (Dray et al., 2006). This approach requires the definition of a spatial weighting matrix that defines the spatial relationships between sites (in this case, the centroids of each species' geographical range). We used a K -nearest neighbour approach, in which the five nearest range centroids were considered neighbours. Links between neighbours were then weighted by $f(D_{ij}) = 1 - (D_{ij}/\max(D_{ij}))$, where D_{ij} is the Euclidean distance between centroids i and j , and $\max(D_{ij})$ is maximum distance between any two centroids i and j (Bauman et al., 2018). For each response variable, we extracted the residuals from the PGLS model, and selected the subset of eigenvectors that minimized the autocorrelation in the PGLS residuals (function *mem.select* in the *adespatial* package in R; Bauman et al., 2018; Dray et al., 2020).

Using taxonomic random effects (family, and genus nested within family) in the aforementioned analyses in lieu of a phylogeny using the R package *lme4* led to broadly similar results. We therefore present the results of PGLS models here, which were more conservative.

3 | RESULTS

3.1 | Morphological variation

The first two principal components on the morphological data set, including pygopodid species and excluding limb data, accounted for 94% of the total morphometric variation in the data (Table 1). PC1 was highly correlated with size measurements. All morphological measurements loaded positively on PC1. PC2 had strong positive loadings for head width (HW), body width (BW) and eye distance (ED) but strong negative loadings for inter-limb length

TABLE 1 Principal component analysis (PCA) loadings for the morphological data set, both including pygopodid species (with no forelimb and hindlimb measurements) and excluding pygopodid species

| PC axis | 1 | 2 |
|-------------------------------------|-----------|-----------|
| Total variance explained (%) | 76 | 18 |
| Including pygopodids | | |
| Snout-vent length | 0.14 | -0.61 |
| Snout-axilla length | 0.32 | 0.07 |
| Inter-limb length | 0.06 | -0.67 |
| Body width | 0.31 | 0.13 |
| Pelvic width | 0.31 | -0.16 |
| Pelvic height | 0.30 | -0.15 |
| Tail width | 0.28 | -0.11 |
| Head width | 0.32 | 0.13 |
| Head length | 0.32 | 0.10 |
| Snout-naris | 0.32 | 0.11 |
| Eye distance | 0.30 | 0.24 |
| Head depth | 0.32 | 0.02 |
| PC axis | 1 | 2 |
| Total variance explained (%) | 91 | 3 |
| Excluding pygopodids | | |
| Snout-vent length | 0.23 | -0.05 |
| Snout-axilla length | 0.23 | -0.03 |
| Inter-limb length | 0.23 | -0.04 |
| Body width | 0.21 | -0.46 |
| Pelvic width | 0.22 | -0.39 |
| Pelvic height | 0.21 | -0.12 |
| Tail width | 0.19 | -0.46 |
| Head width | 0.23 | -0.13 |
| Head length | 0.23 | 0.0028 |
| Snout-naris | 0.23 | 0.018 |
| Eye distance | 0.23 | 0.12 |
| Head depth | 0.22 | -0.0060 |
| Forelimb length | 0.23 | 0.21 |
| Upper fore limb | 0.22 | 0.34 |
| Lower fore limb | 0.23 | 0.22 |
| Fore-foot | 0.23 | -0.049 |
| Hindlimb length | 0.23 | 0.23 |
| Upper hind limb | 0.23 | 0.19 |
| Lower hind limb | 0.23 | 0.28 |
| Hind-foot | 0.23 | -0.017 |

(ILL) and snout-vent length (SVL). Consequently, we interpreted PC2 to largely represent body width versus elongation (i.e., long and thin versus short and wide). Morphological interpretations of the two PC axes were broadly similar when excluding pygopodids, although PC1 explained a much greater proportion of the variation in the morphological data, and PC2 a much lower proportion (91

and 76 for PC1 versus 18 and 3% for PC2) when pygopodids were excluded (Table 1).

Body size (PC1) and body shape (PC2) varied among families. Pygopodids, in particular, occupied a different area of the morphospace than the other three lineages (Figure 2). Body size (PC1) varied substantially across the 30 gecko genera, with the pygopodid genus *Aprasia* displaying the most negative loadings and the carphodactylid *Saltuarius* displaying the most positive loadings (Figures 3 and 4). Body shape (PC2) also differed noticeably between genera, with the pygopodids (*Pygopus*) displaying the most negative loadings and the diplo-dactylid *Crenadactylus* displaying the most positive loadings (Figure 4).

3.2 | Correlates of morphological variation

Given the very distinct morphology of pygopodids revealed by our PCAs, we excluded pygopodid species from all analyses. PGLS analyses excluding pygopodids revealed strong phylogenetic signals in body size (PC1 $\lambda = .94$) and shape (PC2 $\lambda = .82$). Body size varied among microhabitat types – saxicolous species and species with variable microhabitat requirements (i.e., generalists) had higher PC1 scores than terrestrial species (Table 2). Climatic variables were weak predictors of PC1. There were no significant correlates of PC2, although mean annual temperature had a weak, positive effect (Table 2).

3.3 | Correlates of limb length

We found strong phylogenetic signal in proportional fore limb length ($\lambda = .95$) and proportional hindlimb length across species ($\lambda = .93$). There was weak evidence that saxicolous species had longer proportional fore limb and hind limb lengths than terrestrial species, and that microhabitat generalists had longer proportional forelimb lengths than terrestrial species (Figure 5). Climatic variables were not significantly correlated with either proportional hind- or forelimb length (Table 3).

3.4 | Correlates of morphological measurements

Using individual morphological measurements as response variables in PGLS led to similar qualitative conclusions regarding impacts of covariates (Supporting Information Appendix S4). For example, saxicolous species and species with variable microhabitat requirements had longer snout-vent lengths than terrestrial species. In addition, saxicolous species had longer raw forelimb and hindlimb length measurements than terrestrial species when snout-vent length was used as a covariate (although effects were weaker than when proportional limb lengths were used as response variables). Climate variables were significantly correlated with some individual measurements but the exact correlates, and the direction and magnitude of their effects, were variable among measurements.

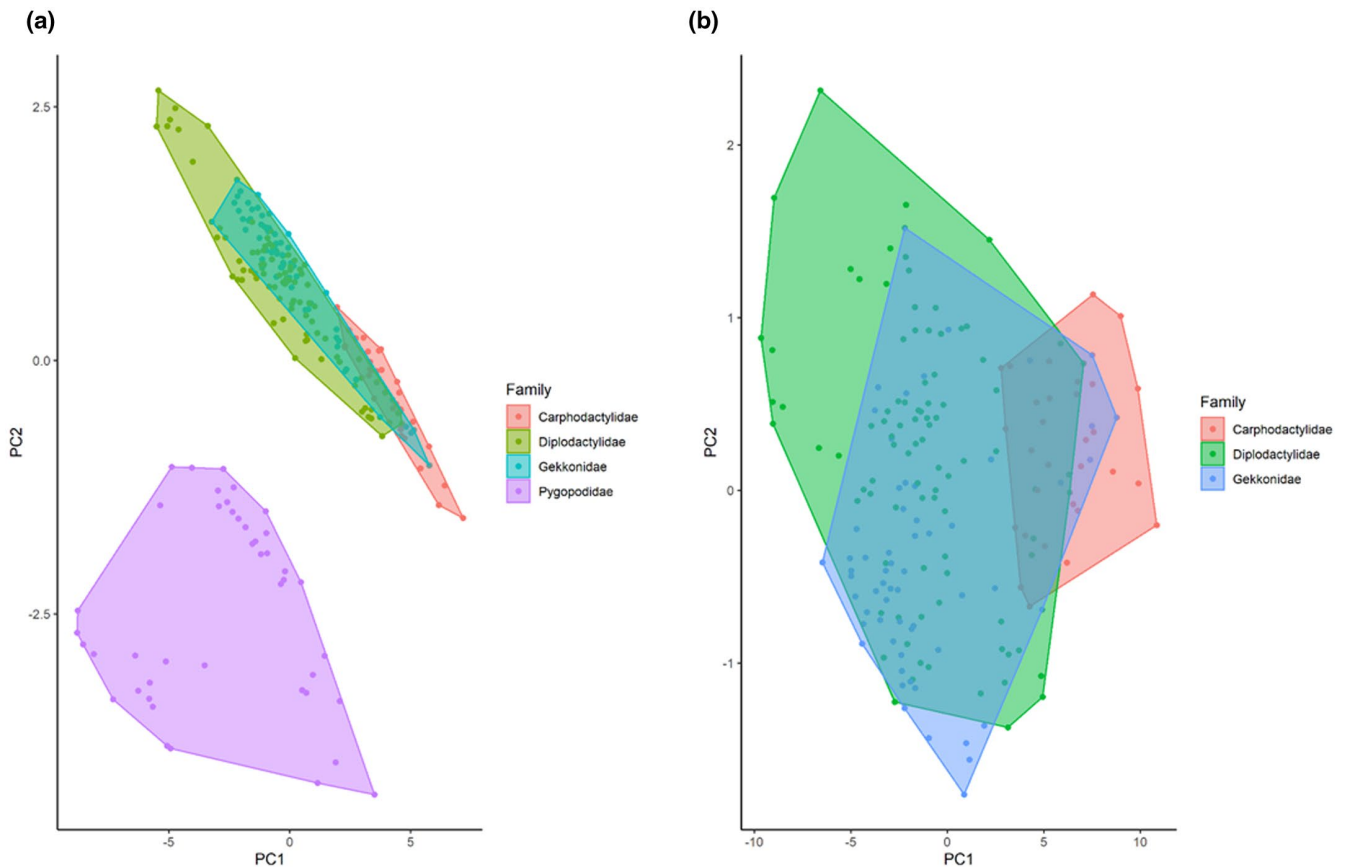


FIGURE 2 Morphology principal component analysis (PCA) ordination plot for Australian gecko species, (a) including pygopodid species, and (b) excluding pygopodid species. Morphological measurements displayed are those listed in Supporting Information Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Unlike most previous studies investigating environmental correlates of morphological variation in reptiles, which have focused on single morphological variables such as snout–vent length, we have comprehensively quantified the degree of morphological variation in Australian geckos (4 families, 30 genera, 226 species) using 20 external measurements. Our results revealed that three of the four Australian gecko families (Carphodactylidae, Diplodactylidae, Gekkonidae) shared similar body shapes and sizes. The considerable overlap between the three families (despite their considerable phylogenetic distance; Gamble et al., 2015; Melville et al., 2006) indicates retention of the standard gecko body plan. Our results are consistent with previous studies, which indicate that, despite being a species-rich radiation, geckos share broad similarities in some aspects of their appearance and behaviour (Wilson & Swan, 2017). Morphological variation observed in the Pygopodidae, however, varied considerably from the gekkotan gecko norm, with pygopodids occupying a distinct part of the gekkotan morphospace.

4.1 | No evidence for Bergmann's rule in Australian geckos

Body size in Australian geckos was not correlated with mean annual temperature, providing no evidence of Bergmann's rule in this group.

This finding is consistent with those of many studies that have failed to find evidence of Bergmann's rule in squamates (e.g., Pincheira-Donoso et al., 2008; Pincheira-Donoso & Meiri, 2013; Slavenko et al., 2019). Other studies identified either positive (e.g., Ashton & Feldman, 2003; Oufiero et al., 2011), negative (e.g., Aragon & Fitze, 2014; Volynchik, 2014) or mixed (e.g., Sears & Angilletta, 2004) size–temperature associations.

Why do reptiles not strongly and consistently conform to Bergmann's rule? Many potential explanations revolve around the potential disadvantages of large body size in lizards occupying cold climates. Ectotherms have a reduced capacity to both produce and conserve heat when compared to endotherms, and their heating and cooling capacity is critically determined by body mass (Pincheira-Donoso et al., 2008; Seebacher & Shine, 2004). An increased body size in lizards inhabiting cold climates could prevent them from gaining heat quickly enough to start their activity (Angilletta et al., 2004, but see Zamora-Camacho et al., 2014, who found that large size was associated with lower cooling rates but that size did not affect heating rates). From this we can assume that Bergmann's rule, and the heat conservation hypothesis of increasing body size in low-temperature environments, may not be applicable to ectotherms, as heating and cooling rates may offset each other's influence. Some studies have suggested that lizards evolve smaller body sizes in cold climates so that a higher surface area to volume ratio can assist with more rapid heat gain when basking (Ashton & Feldman, 2003; Bogert, 1949; Stevenson, 1985; cf.

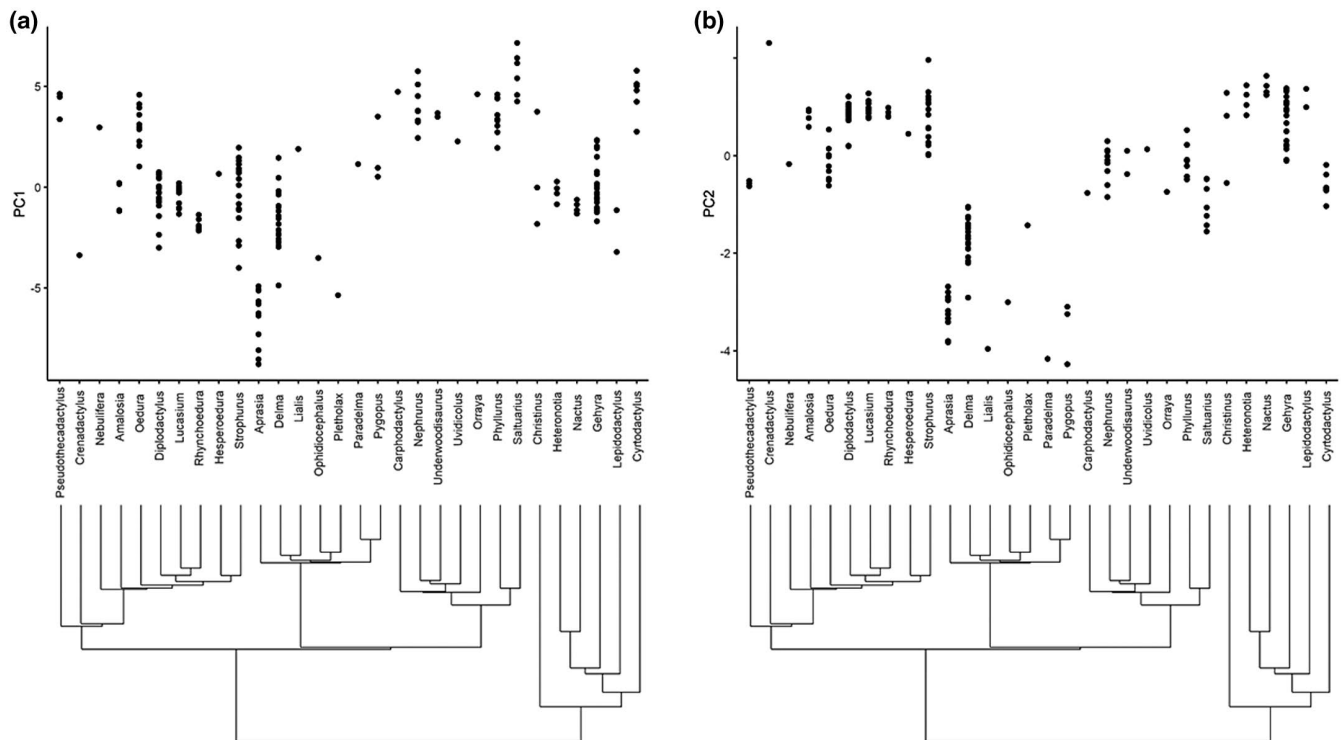


FIGURE 3 Summary of (a) principal component 1 (PC1) values and (b) PC2 values of the morphological data set for every species showing the morphological breadth in body shape and size displayed in each genus, including all 30 genera

Zamora-Camacho et al., 2014). This converse trend, however, was not evident in Australian geckos. We note that in nocturnal species – including all but two non-pygopodid Australian geckos (Meiri, 2018) – heat gain rates are nearly irrelevant. Nocturnal geckos emerge at times where heat loss, rather than heat gain, is the limiting factor. Thus, one may assume that large size would be beneficial in colder regions of Australia (Feldman & Meiri, 2014). Geckos, however, are nearly absent from the coldest regions of Australia (Figure 1). Furthermore, some cold-region geckos show remarkable adaptations to activity during cold temperature, which may negate the need to evolve large body size (e.g., Cree & Hare, 2010; Hare & Cree, 2016).

We also did not find any evidence that temperature seasonality impacted gecko morphology. Ashton and Feldman (2003) found that seasonality was a strong predictor of body size variation in ectotherms, potentially because environmental seasonality alters food availability (Griffiths & Christian, 1996). This ‘fasting-endurance hypothesis’ posits that larger individuals are better equipped to survive scarcities in food supply due to having a greater ability to store fat (Horváthová et al., 2013; Lindstedt & Boyce, 1985). This may be a less important mechanism for ectotherms, which can withstand long periods without food, than for endotherms.

4.2 | No evidence for Allen’s rule in Australian geckos

Our analyses did not reveal a correlation between proportional fore limb length or proportional hind limb length and mean annual

temperature in Australian gecko species, as predicted by Allen’s rule. Allen’s rule states that the size of an appendage, relative to body size, should be smaller in colder climates compared to warmer climates to reduce heat loss (Jaffe et al., 2016; Nudds & Oswald, 2007). The mechanistic explanation behind this hypothesis is similar to that of Bergmann’s rule in endotherms; shorter appendages in colder climates help to minimize heat loss by reducing surface area to volume ratios, while longer appendages aid heat dissipation in warm climates. However, ectotherms rely on external heat sources to increase their body temperature; therefore, we might expect to observe traits that increase heat uptake in colder climates, such as a high surface area to volume ratio in smaller animals. Jaffe et al. (2016) found that limb lengths of the lizard *Anolis carolinensis* were longer in cold regions than in hot ones. In contrast, we found no evidence for Allen’s rule, either the traditional or reverse relationship, for proportional limb lengths in Australian geckos. Although we also failed to detect relationships between proportional limb lengths and temperature seasonality or aridity, it is plausible that additional environmental correlates influence limb morphology in Australian gecko species (Riedel et al., 2020). Direct comparisons of surface to volume ratios may prove more direct tests of Allen’s and Bergmann’s rules.

4.3 | Relationship between morphology and microhabitat in Australian geckos

Microhabitat is an important determinant of lizard morphology (Foster et al., 2018). We found weak evidence for different body

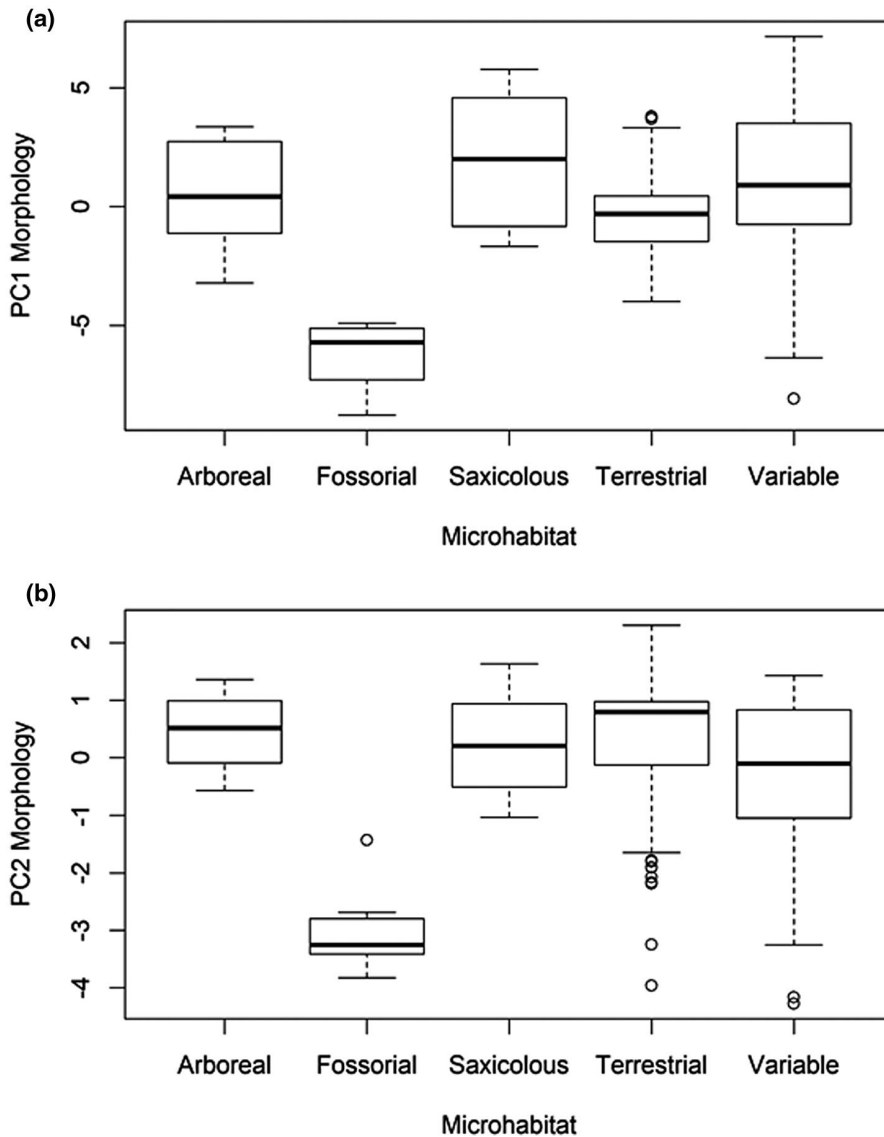


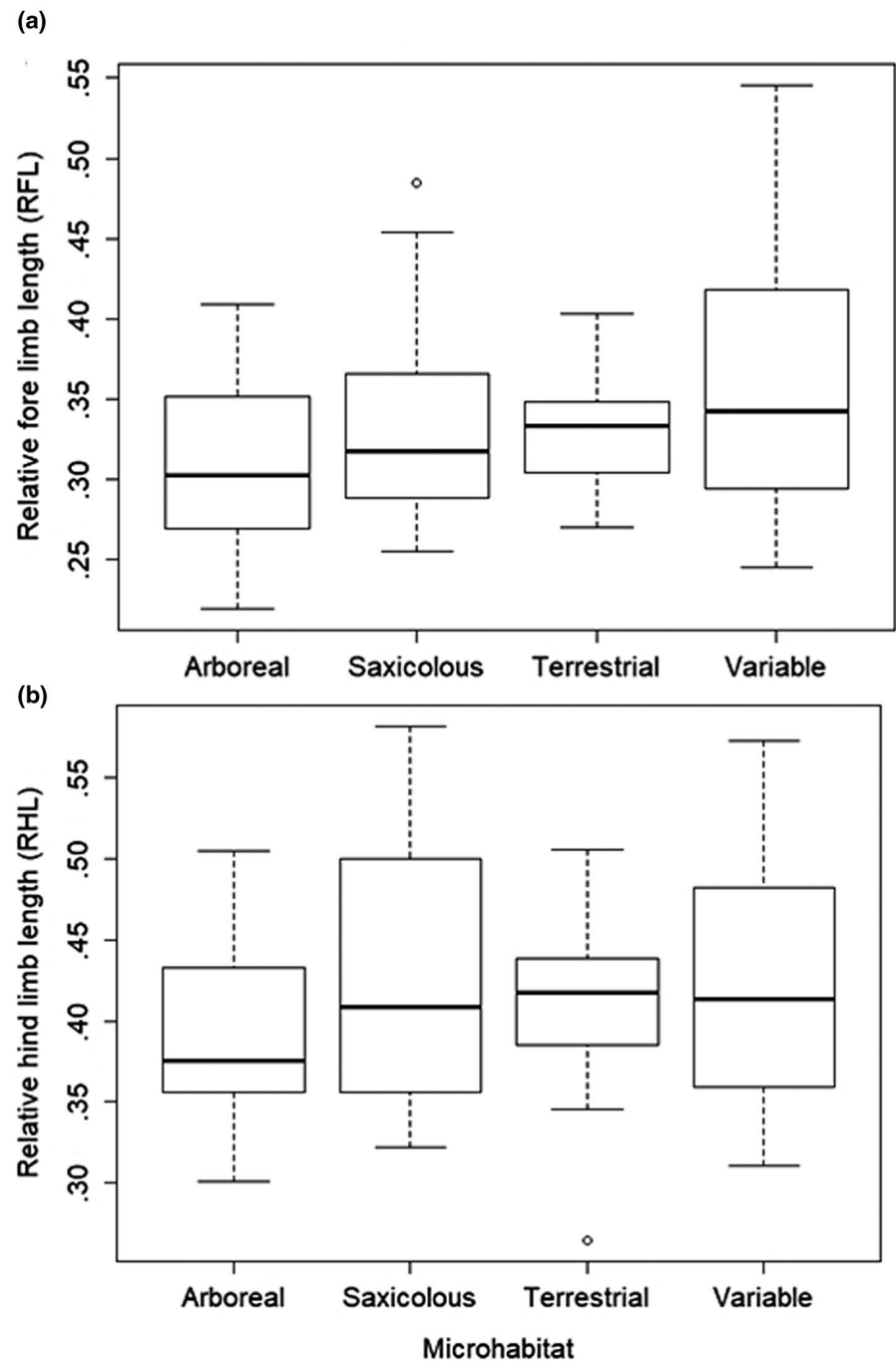
FIGURE 4 Boxplots displaying the relationship between (a) principal component 1 (PC1; body size) and microhabitats occupied by Australian gecko species including pygopodid species and (b) PC2 (body elongation) and microhabitat occupied. Boxplots show the median, first and third quartiles and the lower and upper limits for the data in both principal component axes

| Predictors | PC1 | | | PC2 | | |
|------------------------------|----------|------|------------|----------|------|----------|
| | Estimate | SE | <i>p</i> | Estimate | SE | <i>p</i> |
| (Intercept) | -0.04 | 1.63 | .98 | 0.04 | 0.37 | .91 |
| Terrestrial [Arboreal] | 0.33 | 0.75 | .66 | 0.005 | 0.21 | .98 |
| Terrestrial [Saxicolous] | 1.77 | 0.66 | .01 | 0.20 | 0.19 | .28 |
| Terrestrial [Variable] | 1.11 | 0.55 | .04 | -0.10 | 0.15 | .52 |
| Mean annual temperature | 0.07 | 0.27 | .79 | 0.12 | 0.06 | .07 |
| Aridity index | 0.45 | 0.38 | .24 | -0.07 | 0.11 | .53 |
| Temperature seasonality (SD) | 0.07 | 0.37 | .85 | -0.06 | 0.11 | .59 |
| MEM2 | -0.27 | 0.24 | .25 | | | |
| MEM5 | 0.14 | 0.23 | .54 | | | |
| Observations | 144 | | | 144 | | |
| Adjusted R^2 | .053 | | | .057 | | |

Note.: MEM = Moran's eigenvector map axes. Bold *p* values are statistically significant at $\alpha = .05$.

TABLE 2 Results of phylogenetic generalized least squares (PGLS) models investigating correlates of morphological variation in Australian geckos (excluding pygopodids), in which principal component 1 (PC1) or PC2 was used as a response variable. Note that high values of the aridity index are associated with less arid regions.

FIGURE 5 Boxplots displaying the relationship between (a) raw measurements of proportional forelimb length (forelimb length/snout-vent length) and (b) proportional hindlimb length (hindlimb length/snout-vent length) and microhabitat occupied by Australian gecko species (excluding pygopodids). Boxplots show the median, first and third quartiles and the lower and upper limits for relative forelimb (RFL) and relative hindlimb (RHL) data



sizes (but not shapes) among microhabitats; saxicolous species and species that occupy multiple microhabitats had larger body size measurements (higher PC1 scores) than terrestrial species. The most clear-cut difference in morphology among microhabitats was between pygopodids (all of which are fossorial) and the other gecko families. Pygopodid bodies are elongated and their limbs practically absent. In contrast, all other geckos in Australia (and elsewhere) have four fully developed limbs (Kluge, 1974; Shea, 1993). The unique pygopodid morphology has enabled them to successfully exploit a specific microhabitat. No other body form has permitted geckos to occupy the fossorial niche. This further emphasizes the important role of phylogeny in affecting traits relating to body shape and size in Australian gecko fauna. We opine, however, that phylogenetic

analyses are highly misleading in this case; because the shift to the pygopodid, limbless and elongated morphology has happened only once, phylogenetic comparative methods are unable to reject the null hypothesis (Uyeda et al., 2018; Westoby et al., 1995). A broader phylogenetic perspective, however, would have likely revealed that the evolution of pygopodid-like morphology is associated with fossorial habits in many squamate lineages, including multiple skink radiations, gymnophthalmids, dibamids, amphisbaenids, annelids and snakes (e.g., Morinaga & Bergmann, 2020; Wiens et al., 2006).

Similar to our results for body size, we found that saxicolous species had longer proportional forelimb and proportional hindlimb lengths than terrestrial species. In other lizard groups, terrestrial species have also been found to have shorter limbs than climbing species

| Predictors | RFL | | | RHL | | |
|--------------------------------|----------|-------|-------------|----------|-------|------------|
| | Estimate | SE | <i>p</i> | Estimate | SE | <i>p</i> |
| (Intercept) | 0.32 | 0.02 | 0 | 0.41 | 0.03 | 0 |
| Terrestrial [Arboreal] | 0.01 | 0.01 | .56 | -0.002 | 0.01 | .89 |
| Terrestrial [Saxicolous] | 0.02 | 0.01 | .05 | 0.03 | 0.01 | .04 |
| Terrestrial [Variable] | 0.02 | 0.01 | .06 | 0.004 | 0.01 | .68 |
| Mean annual temperature | 0.001 | 0.004 | .84 | -0.004 | 0.01 | .41 |
| Aridity index | 0.01 | 0.01 | .31 | 0.01 | 0.01 | .32 |
| Temperature seasonality (SD) | 0.004 | 0.01 | .53 | 0.002 | 0.01 | .82 |
| MEM1 (MEM2) | 0.002 | 0.003 | .53 | 0.01 | 0.004 | .04 |
| MEM2 (MEM5) | 0.01 | 0.003 | .01 | 0.002 | 0.004 | .63 |
| MEM15 (MEM15) | 0.0004 | 0.002 | .87 | 0.003 | 0.003 | .39 |
| MEM24 | -0.01 | 0.002 | .002 | | | |
| Observations | 144 | | | 144 | | |
| Adjusted <i>R</i> ² | .15 | | | .068 | | |

Bold *p* values are statistically significant at $\alpha = .05$.

(e.g., Tan et al., 2020), and sometimes no important differences were found (e.g., Kohlsdorf et al., 2001; Olberding et al., 2016). It is possible that the relevance of limb proportions to microhabitat use is small when compared to other key adaptations. In geckos, such a key adaptation may be the evolution of adhesive toepads (Gamble et al., 2012; Hagey et al., 2017). Many geckos (especially arboreal and saxicolous ones) possess complex digital morphologies, with adhesive toepads that allow them to exploit vertically structured habitats and interact with their environment quite differently to that of most other lizards (Gamble et al., 2012). The limb lengths of species possessing such adhesive mechanisms may therefore be under weaker selection than would have otherwise been the case. Indeed, Kulyomina et al. (2019) found that pad-less gecko species have longer limbs than pad-bearing ones (a result also borne out by our own data, especially for large-bodied species; results not shown) – and found little shape differences between arboreal, saxicolous and terrestrial pad-bearing geckos. Zaaf and Van Damme (2001) examined the limb proportions of 29 gecko species in an attempt to identify differences between climbing and ground-dwelling species. They suggested that relative limb lengths did not evolve in response to the physical demands of their respective environment. Alternatively, short limbs may be adaptive for species living in narrow rock crevices, and climbing thin branches, as has been shown in the ‘twig’ *Anolis* ecomorph (e.g., Williams, 1983, but see Hagey et al., 2017). The overarching microhabitat definitions may further hide considerable variability – for example, between species adapted to narrower and broader perches, active foragers, and sit-and-wait species.

4.4 | Conclusion

We present the first quantitative study of Australian gecko morphology comprising almost all described species from across all 30 genera

TABLE 3 Results of phylogenetic generalized least squares (PGLS) models investigating correlates of limb length in Australian geckos (excluding pygopodids), in which proportional forelimb length (RFL) or relative proportional length (RHL) was used as a response variable. Moran's eigenvector map axis (MEM) predictors in parentheses () refer to those selected for RHL

and all 4 families. We show that, as predicted, pygopodids are extremely morphologically divergent, whilst the other three gecko families exhibit conserved morphology. Relating the observed variation in body and limb morphology to environmental correlates revealed little support for our hypothesis that environmental conditions influence body size, shape, and limb morphology in Australian gecko species. We found no evidence for either Bergmann's rule, or for Allen's rule. Instead, our results highlight the importance of phylogeny and microhabitat use on morphological traits in Australian gecko species.

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AUTHOR CONTRIBUTIONS

All authors were involved in the development of the project; JN conducted the morphological analyses; JN, RT and SM completed the analyses; JN and DGC wrote the initial draft of the MS, with support from RT and SM.

DATA AVAILABILITY STATEMENT

All data are available in Supporting Information Appendix S3.

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BIOSKETCH

The authors have interests in the macroecology, biogeography and conservation of squamate reptiles.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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