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RESEARCH ARTICLE

Ecologically-related variation of digit morphology in *Cyrtodactylus* (Gekkota, Squamata) reveals repeated origins of incipient adhesive toepads

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Abstract

1. Exploitation of different locomotor substrates in different ecological niches has driven the evolution of specialized morphological structures, and similar ecological demands, such as the structure of the microhabitat, often lead to convergent or parallel evolution.
2. The evolution of adhesive toepads in geckos remains understudied because of the paucity of phylogenetically-informed investigations of candidate clades exhibiting purported incipient expression of these (i.e. species having evolved some, but not all, parts of the complex adhesive system of pad-bearing geckos).
3. Using *Cyrtodactylus*, a speciose genus with well-established ecotypes, we tested the hypothesis that microhabitats that require more climbing will lead to the acquisition of incipient adhesive morphology.
4. We measured subdigital scale area, a proxy for adhesive toepad evolution, and quantified subdigital scale shape for 77 of the 354 described species, including at least one representative of each ecotype.
5. Subdigital scale area increased from terrestrial through generalist and saxicoline (rock-dwelling) to arboreal ecotypes, with subdigital scale shape evolving from ancestral conditions for padless lizards to lateromedially expanded lamella-like scales only in the arboreal ecotypes.

6. This significant link between phenotype and environment supports the contention that scansorial, and particularly arboreal, *Cyrtodactylus* ecotypes have evolved incipiently expressed adhesive toepads. This highlights the suitability of this genus as a model system for studying the ecology and evolution of adhesive toepads as well as being a promising candidate for research on adaptive radiations.

KEYWORDS
2D geometric morphometrics, adaptative radiation, adhesive system, bent-toed geckos, ecomorphology, ecotypes, toepad

1 | INTRODUCTION

Effective locomotion is challenging and critical for the survival of motile animals. Consequently, exploitation of different locomotor substrates in different ecological niches (e.g. burrowing, climbing, level-running) has driven the evolution of specialized morphological structures (Higham, 2015; Polet & Bertram, 2021). Similar ecological demands and functional or physical constraints often lead to convergent or parallel evolution when different clades evolve phenotypically similar morphological structures in association with their adaptation to similar structural microhabitats. For example, chameleons and some birds have zygodactylous feet that aid in grasping narrow perches (Bock, 1999; Molnar et al., 2017; Peterson, 1984), whereas arboreal mammals have an opposable pollex/hallux for the same function (Toussaint et al., 2020). Similarly, prehensile tails, which are beneficial for grasping perches, have evolved independently in association with climbing in mammals, salamanders, and squamate reptiles (Baken & Adams, 2019; Meldrum, 1998; Zippel et al., 1999).

Adhesive pads on the distal segments of limbs have evolved in insects, spiders, mammals, frogs, and lizards (Arzt et al., 2003; Büscher & Gorb, 2021; Labonte & Federle, 2015; Langowski et al., 2018; Riskin & Fenton, 2001). These provide compelling examples of specialized morphological adaptations associated with challenging locomotor environments, resulting in astonishing climbing abilities on vertical or inverted surfaces and, at least in lizards, the ability to arrest falls from the canopy (Higham, Russell, & Niklas, 2017). Alternatively for spiders, it is hypothesized that adhesive pads evolved as an adaptation for prey capture rather than climbing (Wolff et al., 2013). Among lizards, adhesive toepads have evolved independently in anoles, some skinks, and on multiple occasions in geckos (Gamble et al., 2012; Irschick et al., 2006; Russell, 2002; Russell et al., 2019; Russell & Garner, 2023; Williams & Peterson, 1982). Of these, gekkotans (many of which possess adhesive toepads) are the most diverse clade, comprising more than 2250 species distributed among seven families, and exhibiting substantial ecological and morphological diversity (Bauer, 2019; Meiri, 2020; Riedel et al., 2020; Uetz et al., 2020, 2022).

Gecko toepads comprise occasionally single, but most often multiple, laterally expanded subdigital scales, called scansors or lamellae depending on their internal anatomy (Russell, 1986, 2002; Russell et al., 2019). These scales are underpinned by modified muscles, tendons, bones, and other tissues which function to fine-tune the control of the scansors during locomotion, allowing for their correct placement onto—and removal from—the substratum (Russell, 1975, 2002; Russell & Gamble, 2019). The ultimate agents of adhesion are microfibrillar stalks (setae) arising from the "Oberhäutchen"—the outermost layer of the epidermis (Autumn, 2007; Hiller, 1968; Maderson, 1970), which generate adhesion via van der Waals forces (Autumn, 2006; Autumn & Peattie, 2002), probably acting in concert with electrostatic interactions (Izadi et al., 2014; Song et al., 2022) and surface chemistry (Rasmussen et al., 2022; Singla et al., 2021).

As the physical and functional principles of adhesive toepads are reasonably well understood, the scope of research has expanded to examine the substantial range of variation in toepad morphology (Russell, 1976), aiming to more fully comprehend the evolution of adhesive toepads in geckos (Collins et al., 2015; Gamble et al., 2012; Higham et al., 2019; Riedel et al., 2021; Russell & Gamble, 2019). Critical open questions related to toepad evolution are how, and under which ecological circumstances, adhesive toepads arose (Hagey et al., 2014; Russell et al., 2019).

Adhesive toepads have evolved multiple times independently in geckos (Gamble et al., 2012; Russell & Gamble, 2019), along with multiple independent reductions (Higham et al., 2015). Although there are detailed studies of the morphological variation of gecko toepads, evolutionary extrapolations based on these studies may be regarded as essentially speculative because extant forms investigated are either entirely lacking adhesive toepads or have fully expressed toepads (Peattie, 2008). Intermediates between those of padless terrestrial and pad-bearing climbing forms, would prove highly informative for improving our understanding of the evolution of adhesive toepads (Higham, Gamble, et al., 2017), especially if the phylogenetic context of such morphologies is known and the ancestral trait values of intermediate forms can be estimated (Russell & Gamble, 2019).

To date, two taxa exemplifying two independently evolved (Gamble et al., 2012; Russell & Gamble, 2019) intermediate morphologies have been studied in detail. The sphaerodactylid *Gonatodes humeralis* (Guichenot, 1855) has evolved simple adhesive structures

on enlarged subdigital scales and is able to climb smooth vertical substrates (Higham, Gamble, et al., 2017). This species seemingly exhibits no modifications of internal digital morphology typical of pad-bearing forms (Higham, Gamble, et al., 2017; Russell et al., 2015) and shares an overall digit morphology with its ancestrally terrestrial congeners. The second example constitutes two saxicoline (rock-dwelling) lineages within the otherwise terrestrial or generalist gekkonid species complex *Heteronotia binoei* (Gray, 1845). These two saxicoline lineages have independently evolved longer, more complex setae and associated enlarged terminal subdigital scales (Riedel et al., 2021). The internal digital morphology of *H. binoei* apparently shows no internal anatomical digital modifications typical of climbing, pad-bearing forms (Russell & Gamble, 2019). Thus, both examples, coming from distantly related ancestrally padless lineages (Russell & Gamble, 2019), indicate that subdigital scale area and microornamentation are among the first morphological traits to change when toepads evolve.

Another clade repeatedly suggested to harbour such intermediate forms is the gekkonid genus *Cyrtodactylus* Gray, 1827 (Gamble et al., 2012; Russell, 1976; Russell & Gamble, 2019), which again is distantly related to both above-mentioned examples (Gamble et al., 2012; Russell & Gamble, 2019). Although *Cyrtodactylus* is traditionally regarded as being padless, some scansorial species (climbing species—a categorisation subsuming arboreal and saxicoline forms), show various degrees of broadening and shortening of subdigital scales located ventrally at the mid-digit inflexion point and proximal thereto (Figure 1a–c; Gamble et al., 2012; Russell, 1976; Russell & Gamble, 2019). Species of *Cyrtodactylus* that have so far been examined anatomically, except for the arboreal *C. brevipalmatus* (Smith, 1923) (Russell, 1972), show no associated internal anatomical structures typical of geckos with fully expressed toepads. Subdigital setae are known in only two arboreal species, *C. novaeguineae* (Schlegel, 1837) and *C. louisiadensis* (De Vis, 1892), both of which possess simple setal morphology—for example, relatively short and not branched very often compared to typical pad-bearing geckos (Russell, 1976). Anecdotal reports indicate that some scansorial species can adhere to and climb on vertical glass surfaces (Figure 1d; Scholdei, 2023).

With 354 described species, *Cyrtodactylus* is the most speciose gecko genus (Grismer et al., 2020; Uetz et al., 2022). This diversity coincides with an extensive variation in microhabitat preferences among species, with most having been assigned to an ecotype characterized by distinct structural microhabitat preferences. *Cyrtodactylus* ecotypes span terrestrial, generalist and various scansorial categories (Figure 2; Grismer et al., 2020, 2021). Some of these ecotypes also show distinct differences in limb and body proportions, providing preliminary evidence that the genus might have radiated adaptively, thereby rendering this clade well-suited for examination of patterns of toepad evolution, and also promising for elucidating under which ecological circumstances toepads evolve (Grismer & Grismer, 2017; Kaatz et al., 2021; Riedel, Grismer, et al., 2024).

Because adhesive performance is positively correlated with toepad area in lizards (Irschick et al., 1996), we quantified subdigital scale area of both autopodia—hand (manus) and foot (pes)—in 25 of the 31 species groups (subclades) of *Cyrtodactylus*, collectively representing all the *Cyrtodactylus* ecotypes suggested by Grismer et al. (2020, 2021). Additionally, we analysed subdigital scale shape, applying 2D geometric morphometrics to the pes to examine finer scale changes in scale proportions (Howell et al., 2022). Both datasets were analysed using phylogenetic comparative methods. We hypothesized that *Cyrtodactylus* species representing distinct microhabitats would vary in relative subdigital scale area and shape. We predicted that terrestrial species would have smaller scale areas than the scansorial species, and that generalist species would be intermediate in area to terrestrial and scansorial forms. We predicted terrestrial species would have relatively large, round to quadratic subdigital scales, typical of padless lizards, whereas scansorial species should exhibit relatively shorter but broader subdigital scales, more comparable to the typical lamellae or scansors of pad-bearing geckos. Again, generalist species were predicted to occupy an intermediate position in morphospace between

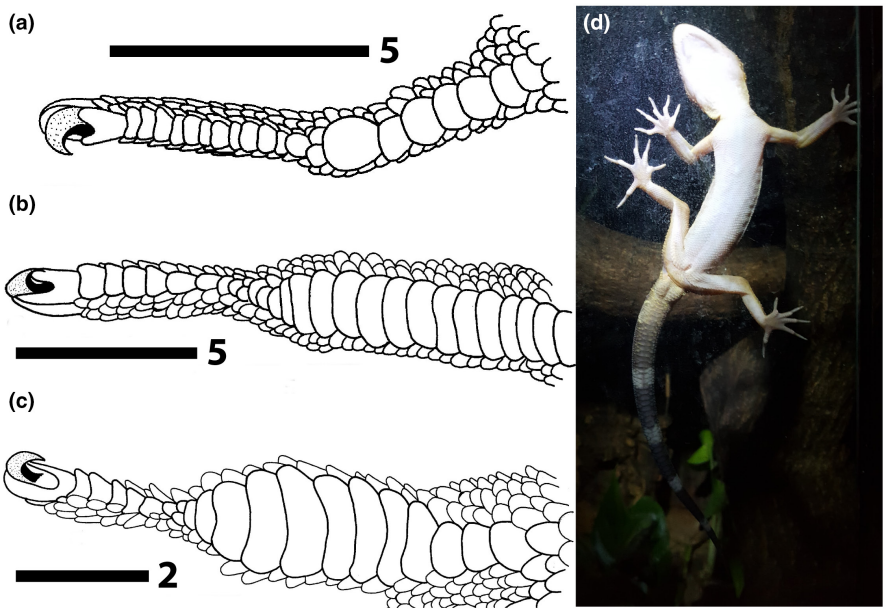

FIGURE 1 Exemplar *Cyrtodactylus* species representing putative intermediate forms in toepad evolution. Ventral aspect of digit IV left pes of (a) *C. khasiensis*, (b) *C. novaeguineae*, and (c) *C. brevipalmatus*. Scale bars in mm. (d) *C. consobrinus* clinging to a vertical glass surface in a terrarium; Photo: Jochen Scholdei. For an image of digit IV left pes of *C. consobrinus* Appendix S1—Figure SF1 in Supporting Information.

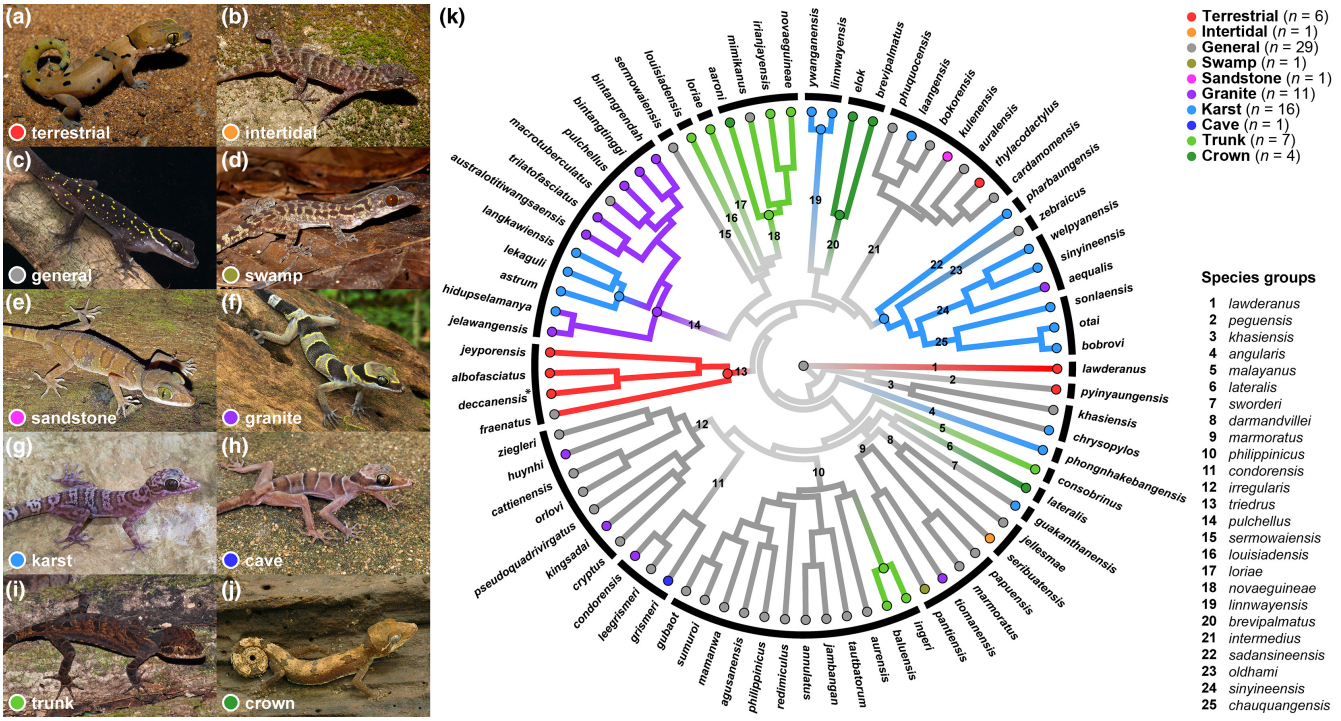

FIGURE 2 Representatives of the 10 ecotypes of the genus *Cyrtodactylus* (a–j) modified from fig. 4 in Grismer et al. (2021) and (k) the phylogenetic relationships of *Cyrtodactylus* species included in this study, based on the phylogeny of Grismer, Poyarkov, et al. (2022). (a) *Cyrtodactylus yakhuna*, Sri Lanka; (b) *C. seribuatensis*, Malaysia; (c) *C. oldhami*, Thailand; (d) *C. payacola*, Malaysia; (e) *C. kulenensis*, Cambodia; (f) *C. trilatofasciatus*, Malaysia; (g) *C. sanpelensis*, Myanmar; (h) *C. honteensis*, Vietnam; (i) *C. serratus*, Papua New Guinea; (j) *C. elok*, Malaysia. Photographs by (a) Suranjan Karunaratha, (b–d, f–h, j) L. Lee Grismer, (e) Peter Geissler, (g) Evan S. H. Quah, (i) Steve J. Richards. (*) C. deccanensis is included only in the manus dataset.

scansorial and terrestrial ecotypes. Because adhesive toepads are suggested to be most strongly associated with locomotion on smooth surfaces (Higham et al., 2019; Higham, Gamble, et al., 2017; Naylor & Higham, 2019), which appear to be more prevalent in arboreal microhabitats (Pillai et al., 2020a, 2020b), we predicted that arboreal ecotypes might have evolved features more similar to those of toepad morphologies expressed by pad-bearing geckos (e.g. larger relative subdigital scale area and/or more lamella-like subdigital scales (defined here as scales that visually appear to be wider than long)) compared to saxicoline ecotypes. However, quantitative measurements of roughness of the *Cyrtodactylus* microhabitat categories are currently unavailable, so our detailed comparisons necessarily remain exploratory, as do potential differences within both arboreal and saxicoline ecotypes, due to the high variability of roughness among rock and plant surfaces, respectively (Higham et al., 2019; Johnson et al., 2009; Pillai et al., 2020b).

2 | MATERIALS AND METHODS

2.1 | Study system

The geographic range of *Cyrtodactylus* spans from India and Nepal across Southeast Asia to the Solomon Islands and northern Australia, with peak diversity in Indochina and Sundaland (Grismer, Poyarkov, et al., 2022). Currently recognized ecotypes (Figure 2a–j) are summarized in Table 1. The generalist ecotype is most likely ancestral, and it has been hypothesized that multiple independent transitions among ecotypes have occurred (Grismer et al., 2020, 2021).

Because we could not formulate a priori predictions regarding differences between arboreal and saxicoline ecotypes, we ran each analysis twice: first, with broad microhabitat categories (terrestrial, broad general, saxicoline and arboreal) to increase sample size per category, and secondly employing individual ecotypes, to explore differences among more specific substrate use categories (Table 1). Ecotypes for which we had only one representative species (cave, intertidal, sandstone and swamp) were excluded from our ecotype analyses. For broad microhabitat analyses we lumped intertidal and swamp classes with generalists as broad generalists. Swamp species were lumped this way because these are typically encountered lower than 1 m from ground, use all available structural microhabitats within their swampy habitats, and group with generalists in multivariate plotting analyses (Kaatz et al., 2021). The intertidal species was so lumped because this species uses both rocky boulders and the ground (Grismer et al., 2020, 2021)—similar to generalist species.

2.2 | Dataset and image generation

In total, our ethanol-preserved museum voucher dataset consisted of 77 species (with 3–10 specimens per species), representing all

TABLE 1 Summary of ecotypes and broad microhabitat categories employed in this study.

Ecotype	Broad microhabitat	Number of species	Description of microhabitat preference
Terrestrial	Terrestrial	6/5[a] (29)	On the ground
Generalist	(Broad) Generalist	28 (134)	All available structural microhabitats
Swamp		1 (5)	Low vegetation in swampy habitats
Intertidal		1 (1)	Rocky intertidal zones of small islands
Sandstone	Saxicoline	1 (1)	A sandstone massif
Granite		11 (32)	Large granite boulders
Karst		16 (86)	Limestone rock (karst) formations
Cave		1 (7)	Cave-like environments formed by granite boulders
Trunk	Arboreal	7 (39)	Trunks and large branches of large trees
Crown		4 (13)	Small tree branches, leaves, trunks of varying sizes, and shrubs

Note: The number of species per ecotype represents the sample size for this study, with the total number of species currently assigned to each ecotype category given in parentheses. For more detailed descriptions of the ecotypes see Grismer et al. (2020, 2021).

[a]Six species included for manual data, and five for pedal data.

ecotypes (Figure 2k, Appendix S1—Table ST1). To minimize allometric effects, only adult specimens were included. A detailed list of the voucher numbers and sources of all measured specimens together with the raw measurements is available from the Dryad Digital Repository https://doi.org/doi:10.5061/dryad.f4qrfj73j (Riedel, Eisele, et al., 2024). The fourth digits of both manus and pes were photographed in ventral view with a scale bar included, using a light microscope at magnifications between 5× and 20×. Digits were flattened using either forceps or a glass slide if necessary (Donihue et al., 2018). We used the left extremity unless it was damaged, with images of the right extremities being mirrored for the scale shape analysis. For *Cyrtodactylus deccanensis* (Günther, 1864) we were only able to acquire images for the manus for the minimum of three specimens, so this species was excluded from the analysis of the pes data.

2.3 | Analysis

All analyses were conducted in R (version 4.3.1) and R studio (version 223.6.2+561) (R Core Team, 2023). We used the phylogeny of Grismer, Poyarkov, et al. (2022), pruned to contain only species included in our dataset (Felsenstein, 1985). Species for which we collected data, but which are absent from Grismer, Poyarkov, et al.'s (2022) phylogeny, were placed at the position of their putative closest relative, as described by Riedel, Grismer, et al. (2024): *Cyrtodactylus aaroni* (Günther & Rösler, 2003) was inserted at the position of *C. rex* (Oliver et al., 2016) and *C. irianjayaensis* (Rösler, 2001) at the position of *C. zugi* (Oliver et al., 2008).

2.4 | Subdigital scale area

Subdigital scale area (SSA) was measured in imageJ (Version 1.53t, Schindelin et al., 2015). Each measurement was repeated thrice and average values used for further statistical analysis. Body size, measured as snout-to-vent-length (SVL), was taken from Riedel, Grismer, et al. (2024), which sampled the same specimens. To improve normality and reduce heteroscedasticity, all measurements were log-transformed prior to analysis.

First, we reconstructed the evolution of size-corrected SSA measurements separately for our manual and pedal data, using a maximum likelihood ancestral state estimation based on Felsenstein (1985), as implemented in the 'contMap' function in phytools (Revell, 2012). Because gekkotan adhesive pad area has been shown to be correlated with body size (Bauer & Good, 1986; Irschick et al., 1996; Webster et al., 2009), we extracted residuals from phylogenetic generalized least square regression (PGLS) models (Martins & Hansen, 1997; Revell & Collar, 2009), regressing scale area against SVL. Models were implemented using the 'gls' function of the nlme package (Pinheiro et al., 2018), and the 'corPagel' function of the ape package (Paradis

et al., 2018), including a maximum likelihood (ML) estimation of the scaling parameter λ, ranging from 0 (indicating no phylogenetic signal) to 1, convergent upon a Brownian Motion model of trait evolution (Freckleton et al., 2002). For models with ML estimated λ-values >1 or <0, λ was manually set to 1 or 0 respectively. We accounted for within-species variation by adding standard errors as fixed weights.

Second, we tested whether SSA differed among broad microhabitat preferences or ecotypes respectively. We constructed one PGLS model for each categorisation for the manual and pedal data respectively, resulting in four models. Each model used the (log-transformed) area measurements as the response variable and (log-transformed) SVL and broad microhabitat or ecotype as the explanatory variables. Models were otherwise implemented as described above. Models were then analysed with a Type II ANOVA (Langsrud, 2003) and an estimated marginal means (EMM) post hoc comparison implemented with a *Tukeys* adjustment for multiple comparisons in the emmeans package (Russell, 2019).

2.5 | Subdigital scale shape

Two-dimensional geometric morphometrics has recently been applied to the analysis of toepad shape differences in anoles and a broad range of geckos (Howell et al., 2022; McCann & Hagey, 2024). Because there may be different numbers of toepad scales among and within species (which is typically the case in *Cyrtodactylus*, e.g. Grismer, Aowphol, et al., 2022; Murdoch et al., 2019), care must be taken to compare functionally homologous points (Zelditch et al., 2012). Nevertheless, 2D geometric morphometrics can be informative for examining finer scale differences of scale shape. Therefore, we defined eight landmarks and 10 curves of eight sliding semilandmarks each using tpsUtil (v. 1.81) and tpsDig2 (v.2.32, Rohlf, 2004), focusing on the scale under the inflexion point at the joint between the second and third phalanges (Russell, 1976) and the two scales proximal thereto. Eight landmarks were defined as points where the scales in question meet with the adjacent subdigital scale and the scales lateral or medial thereto, respectively (Figure 3). These landmarks were connected through eight sliding semi-landmarks each, following the border of the three subdigital scales (Figure 3).

First, we ran a Procrustes analysis with the 'gpagen' function of the geomorph package (Adams & Otárola-Castillo, 2013) for each species individually, with semi-landmarks slid based on minimizing bending energy (Bookstein, 1997). We calculated a mean scale shape for each species using the 'mshape' function (geomorph), which was then again aligned with our Procrustes analysis, as described above. Our aligned dataset of species mean shapes was used for downstream analysis. We then ran a principal component analysis (PCA) using the 'gm.prcomp' function in geomorph, and plotted the morphospace of axes that explained more than 5% of the total variance. We then plotted the phylomorphospace using the 'phylomorphospace' function of the package phytools (Revell, 2012), including an ancestral state reconstruction of the structural microhabitat preferences employing the 'ace' function of the ape package (Paradis et al., 2018).

For both microhabitat categorizations (broad and individual ecotypes), we first conducted a phylogenetic ANOVA on the PC axes that explained more than 5% of total variance using the 'phylANOVA' function from the Geiger package (Harmon et al., 2008) run for 10,000 simulations. For the post hoc test, *p*-values were adjusted using the Benjamini-Hochberg (BH) function (Benjamini & Hochberg, 1995). Additionally, we used the 'mvgls' function of the mvMORPH package (Clavel et al., 2019; Clavel & Morlon, 2020) to construct a PGLS model directly using the 2D geometric morphometric data. For each model, we ran a phylogenetic MANOVA with the 'manova.gls' function running for 1000 simulations, including a maximum likelihood estimation of λ and using Pillai's test statistic (Pillai, 1955) to assess model fit. Post hoc comparison was calculated using the 'pairwise.glh' function (mvMORPH), run for 1000 simulations, assessed employing Pillai's test statistics (Pillai, 1955), and *p*-value adjustments using the BH function (Benjamini & Hochberg, 1995).

3 | RESULTS

3.1 | Subdigital scale area

The log-transformed manual and pedal data for SSA, plotted against SVL, are shown in Figure 4. Snout-to-vent length was significantly and positively correlated with SSA of both autopodia, necessitating the extraction of residuals for ancestral state reconstructions (Appendix S1—Table ST2). Both crown and trunk ecotypes have larger SSA's relative to body size, whereas terrestrial species possess smaller relative SSA's (Figure 4). The remaining groups scatter without any obvious pattern.

3.2 | Ancestral state reconstruction

Overall, evolutionary trends elucidated here are comparable for the manus and pes (Figure 5). For both autopodia SSA increases in the

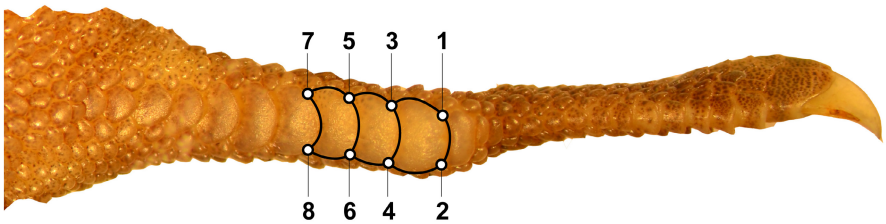

FIGURE 3 Example digit IV of the pes of *C. bintangtinggi*, showing 8 landmarks as white dots and 10 curves of 8 sliding semilandmarks each as black lines.

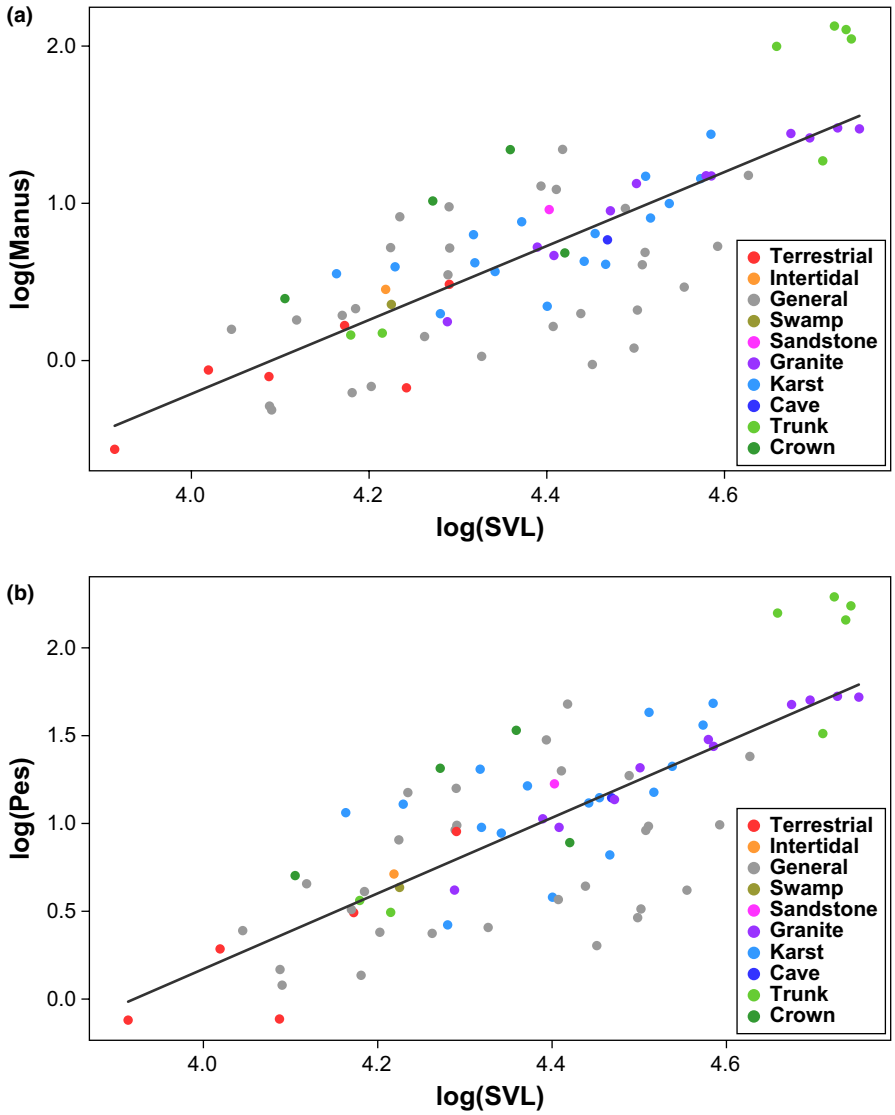

FIGURE 4 Log-transformed measurements for subdigital scale area, plotted against log-transformed SVL. Plotted points are species means for (a) manus and (b) pes; black line = regression line (not accounting for phylogeny).

lineage leading to several large-bodied trunk species from Papua New Guinea (*louisiadensis*, *loriae*, and *novaeguineae* groups), in the *brevipalmatus* group (crown ecotypes) and, to a lesser degree, in the saxicoline *pulchellus* and *linnwayensis* groups (Figure 5). In some terrestrial species and in the generalists of the *phillipinicus* group SSA decreases. A moderate SSA increase was also observed in the *sadansiensis* and *sinyiensis* groups (karst ecotypes with some granite species in the latter clade) as well as for the *intermedius* group, which is mostly and ancestrally generalist but also contains terrestrial and saxicoline species. The two generalist species *C. fraenatus* (Günther 1864) and *C. khasiensis* (Jerdon 1870) also show a noticeable increase in SSA.

3.3 | PGLS analyses

The SSA's of both autopodia were significantly positively correlated with SVL and significantly correlated with the respective habitat category (broad microhabitat or individual ecotype, Table 2). The phylogenetic signal was strong, with maximum likelihood λ values ranging from 0.863 to >1.000 (manually set to 1). For the broad microhabitat categories, our post hoc tests for the manus model revealed significant differences among all four categories, with SSA increasing from terrestrial, through broad generalist, saxicoline, and finally arboreal species (Figure 6a). The respective pes model showed similar results, but terrestrial and broad generalist species did not differ significantly (Figure 6c). For the individual ecotypes, our post hoc comparison of our manus model showed significantly higher values for crown species compared to all other ecotypes except for trunk species, which also overlapped with all other ecotypes (Figure 6b). We noted a non-significant trend in which generalist and particularly terrestrial species possessed lower values when compared to granite, karst, and trunk species. Our pes model showed comparable results to the manus model, except that karst-dwelling species had significantly larger SSA values than generalists, with granite and terrestrial dwelling species overlapping both (Figure 6d).

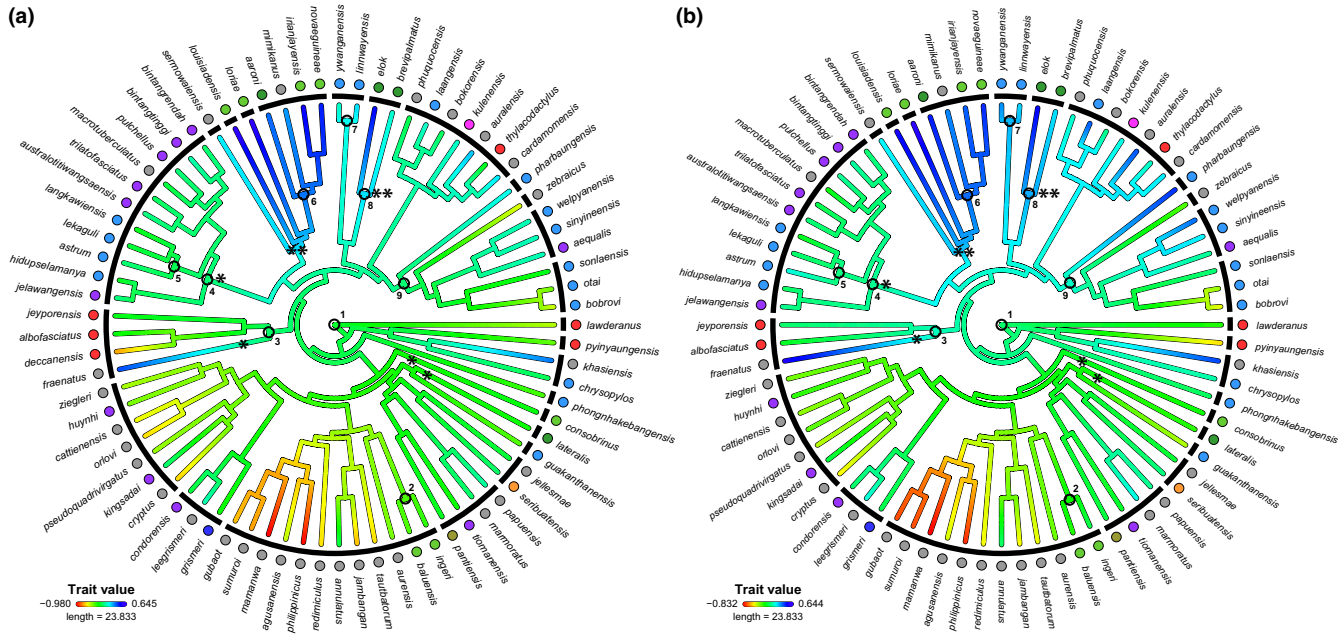

FIGURE 5 Maximum likelihood ancestral state reconstructions for size corrected (a) manual and (b) pedal subdigital scale area. Phylogeny based on Grismer, Poyarkov, et al. (2022). The reconstruction was conducted applying the 'fastanc' algorithm in the R package phytools (Revell, 2012). Black circumferential lines indicate phylogenetic groups. Coloured circles before the species names indicate ecotype (colour code as in Figure 2k). Black open circles at basal nodes indicate shifts in habitat use at that node analogously to Figure 2k. 1: generalist ancestor of the genus, 2 and 6: shift from generalist to trunk habit, 3: shift from generalist to terrestrial habit, 4: shift from generalist to karst habit, 5, 7 and 9: shift from generalist to karst habit, 8: shift from generalist to crown habit. Asterisks indicate likely origins of incipiently expressed toepads based on this ancestral state reconstruction and the phylomorphospace for the shape data (Figure 8), with double asterisks indicating greater likelihood.

TABLE 2 Results of the PGLS models for the influence of SVL and habitat categories on subdigital scale area of the manus and pes.

	Broad microhabitat				Ecotype			
Variable	λ	df	χ^2	*p*-value	λ	df	χ^2	*p*-value
Manus								
SVL	1 [1.010]	1	100.772	**<0.001**	1 [1.060]	1	88.555	**<0.001**
Habitat		3	58.648	**<0.001**		5	61.554	**<0.001**
Pes								
SVL	0.863	1	112.729	**<0.001**	0.915	1	129.594	**<0.001**
Habitat		3	43.724	**<0.001**		5	55.073	**<0.001**

Note: Significant *p*-values are highlighted in bold. Maximum likelihood λ-values >1 (which were manually set to 1) are shown in brackets.

3.4 | Geometric morphometric data

For the PCA analysis, 75.5% of the total interspecific variance in pedal subdigital scale shape was explained by the first PC axis, whereas the second axis explained 5.9%; the remaining axes explained less than 5% each. The degree to which ecotypes overlapped along the first axis was non-uniform. (Figure 7), with species clustering relatively independently of phylogeny (Figure 8). The generalist ecotype showed the largest variation in scale shape, overlapping in morphospace with all other ecotypes (Figure 7a), although most generalist species have scales that are more circular in outline (indicative of positive values on PC 1—Figure 7b, Appendix S1—Figure SF1B,D) and of roughly equal size (indicative of positive values on PC2—Figure 7c). The terrestrial ecotype is also characterized by scales with quasi-circular outlines, which are of roughly equal size in some species, while the distal-most scale is somewhat enlarged relative to the other two in others (indicative of variation along PC 2—Figure 7b, Appendix S1—Figure SF1F). In karst and granite species these scales are also overall quasi-circular in outline. Both of these ecotypes have scales that are more variable in shape than those of terrestrial species, but less so than generalists. The two arboreal ecotypes, trunk, and crown are the most distinctive, with scales that are much broader than long, resembling typical lamellae, with the distalmost lamella being somewhat smaller than the others (indicative of negative values on PC1—Figure 7a,c, Appendix S1—SF1A,C,E).

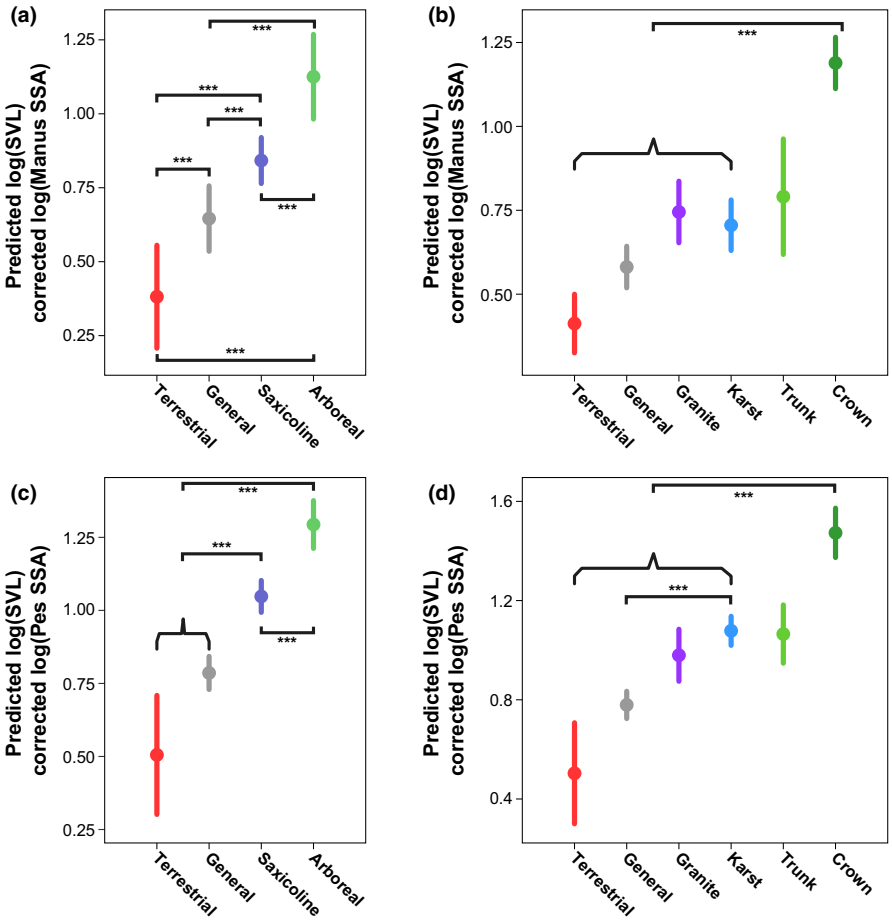

FIGURE 6 *Post Hoc* comparisons for subdigital scale area of manus (a, b) and pes (c, d) for broad habitat categories (lumped ecotypes) (a, c) and individual ecotypes (b, d) respectively. Dots represent predicted means (bars = standard error). Bars with three asterisks indicate significant differences among ecotypes ($p \geq 0.05$ in a *tukeys EMM* post hoc test) or groups of ecotypes encompassed by brackets.

The phylogenetic ANOVA of PC 1 and 2 revealed significant differences on the first axis for both the broad microhabitat categories ($F_{1,3}$: 18.114, $p < 0.001$) and the individual ecotypes ($F_{1,5}$: 10.270, $p < 0.001$). Ordination along Axis 2 was non-significant for both categorisations (broad microhabitats: $F_{1,3}$: 3.347, $p = 0.232$; individual ecotypes: $F_{1,5}$: 2.509, $p < 0.294$). Post hoc comparison for PC1 showed that the arboreal ecotypes (crown and trunk) differed from all other groups independent of the categorisation (Tables 3 and 4).

Our MANOVA of landmark data revealed significant differences among broad microhabitat categories (Pillai's test statistic = 2.319, $p = 0.017$). The λ for the model was 0.315; the regularization parameter gamma was 0.006. Further post hoc comparison demonstrated that arboreal species differ significantly from generalists and saxicoline species and that differences between arboreal and terrestrial species approach statistical significance (Table 5). For the individual ecotype categories, our model had a λ of 0.291 and a gamma parameter of 0.007. Overall differences among ecotypes were marginally non-significant (Pillai's test statistic <0.001, $p = 0.053$).

Collectively our ancestral state reconstruction of scale area data (Figure 5) and the phylomorphospace of scale shapes (Figure 8), indicate that incipiently expressed adhesive toepads appear to have originated at least once in the *brevipalmatus* group and once at the base of the Melanesian trunk species (clade A15 in Grismer, Poyarkov, et al., 2022). Potential additional independent cases of the evolution of incipient toepads are evident in the *lateralis*, *malayanus* and *pulchellus* groups, in *C. frenatus* of the *triedrus* group, and *C. cardamomensis* and *C. laangensis* of the *intermedius* group, although these are more weakly expressed compared to those of the *brevipalmatus* group and the Melanesian trunk species (Figures 5 and 8). If incipient toepads have also evolved in the *pulchellus* group, it would be more parsimonious to assume a single origin in the ancestor of this group and the clade A15, because they are sister clades (Figures 5 and 8). Trends towards the expression of incipient toepads thus appear to have occurred on multiple occasions within *Cyrtodactylus*.

4 | DISCUSSION

4.1 | General pattern of microhabitat-associated digit morphology

Our study supports the longstanding suggestion (e.g. Russell, 1976) that scansorial species of the genus *Cyrtodactylus* exhibit trends towards the acquisition of macroscopically recognizable toepads, having evolved enlarged subdigital scale areas and, in the case of the arboreal ecotypes, modified lamella-like subdigital scale shapes. We set these findings in the context of the recently established ecotypes of the genus (Grismer et al., 2020, 2021). Our first prediction, that subdigital scale area should be relatively larger in scansorial versus terrestrial species (with generalists occupying intermediate values

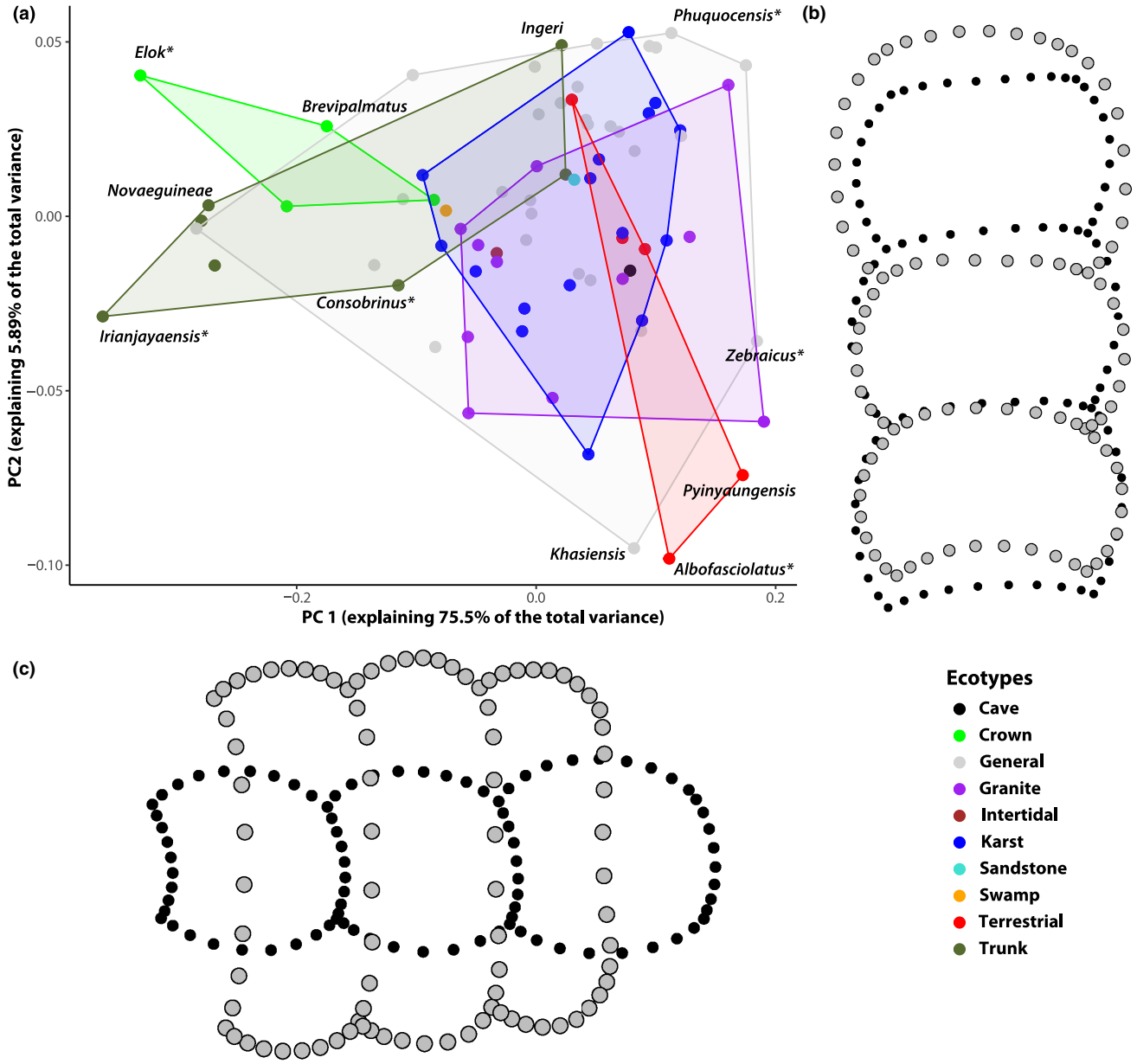

FIGURE 7 Morphospace (a) of the first two PC axes, explaining 75.50% (PC 1) and 5.89% (PC 2) of the variance, respectively. Extreme shapes for each axis are shown to the right of (b), and below (c) for their respective axes. Minimum shapes are illustrated with grey dots, and maximum shapes with black dots. Species names of selected species at the extreme values of both axes are included for illustration. Photographs of digit 4 left pes of species marked with an asterisk are provided in Appendix S1—Figure S1.

between these groups), is supported (Figure 6). However, in the individual ecotype analysis only crown species have a significantly higher SSA than terrestrial and generalist ecotypes, with karst species having a higher pedal SSA than generalists. Non-significant trends among the other ecotypes aligned with the results when comparing broad habitat groups. Our second prediction, that scansorial species should evolve relatively shorter but broader lamella-like subdigital scales was supported for the arboreal ecotypes (crown and trunk; Figure 7, Appendix S1—Figure SF1). The greater relative scale area and more lamella-like scale shape of arboreal ecotypes (compared to saxicoline ecotypes), accords with previous suggestions that lizard toepads might be more strongly associated with smoother arboreal structural microhabitats (Higham, Gamble, et al., 2017; Naylor & Higham, 2019; Russell et al., 2019).

The result of the shape analysis highlights the applicability of 2-D geometric morphometric (GM) approaches to research on the shape of adhesive toepads (Howell et al., 2022). However, care must be taken to compare functionally homologous points (Zelditch et al., 2001, 2012). Recently, McCann and Hagey (2024) applied 2-D GM in a study examining the evolution of toepads across Gekkota. Although they made a commendable effort to investigate toe pad evolution in geckos, the broad phylogenetic scope of their study putatively resulted in a comparison of non-homologous points as landmarks (McCann & Hagey, 2024).

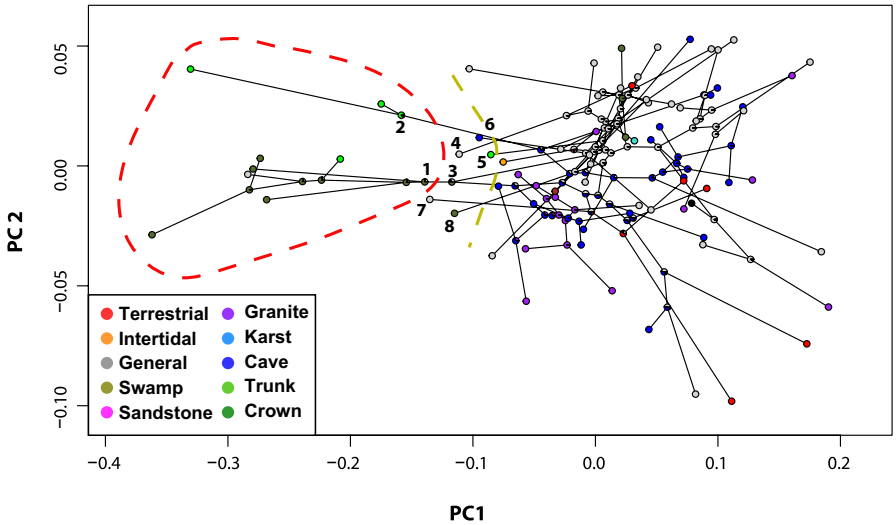

FIGURE 8 Phylomorphospace characterized by bivariate ordination of PC 1 versus PC 2. Terminal nodes are colour-coded by ecotype, with internal nodes colour-coded by probabilities of ancestral states. The closed dashed red line circumscribes lineages with robustly expressed incipient toepads, and the open dashed yellow line segregates taxa with more weakly expressed incipient toepads (based on shape and area data—compare to Figure 5) from the remainder of the species examined. Some clades and species are highlighted for comparison with Figures 2 and 5: (1) Common ancestor (CA) of the Melanesian trunk species (clade A15 in Grismer, Poyarkov, et al., 2022). (2) *brevipalmatus* group. (3) CA of 1 and the *pulchellus* group. (4) *C. cardamomensis*. (5) *C. lateralis*. (6) *C. laangensis*. (7) *C. fraenatus*. (8) *C. consobrinus*.

TABLE 3 *Tukey's EMM* post hoc comparison for the phylogenetic ANOVA on PC 1 for broad microhabitat categories.

Broad microhabitats	Terrestrial	Generalist	Saxicoline	Arboreal
Terrestrial		1.708	1.344	5.598
Broad generalists	0.314		−0.667	6.259
Saxicoline	0.368	0.729		6.689
Arboreal	**<0.001***	**<0.001***	**<0.001***	

Note: *T*-values are shown in the upper right half of the table (above the empty cells), and *p*-values in the lower left. Significant values are highlighted in bold and marked with an asterisk.

Application of 2-D GM to the form of digital scalation within a monophyletic cluster with a well-resolved phylogeny and plentiful ecological information about the taxa examined, as performed by Howell et al. (2022) and in this study, provides for a much more controlled application of GM to the investigation of evolution of form (Zelditch et al., 2012).

4.2 | *Cyrtodactylus* as an exemplar clade for toepad evolution

Exemplar species of the genus *Cyrtodactylus* have previously been assembled into a morphotypic series suggestive of a transition from padless to pad-bearing geckos (Gamble et al., 2012; Russell, 1976, 1977; Russell & Gamble, 2019). Since this was first mentioned (Russell, 1976), the number of described *Cyrtodactylus* species has increased from around 60 to over 350 (Grismer et al., 2021; Uetz et al., 2022), and recent research has revealed that this speciose clade is divisible into distinct ecotypes (Grismer et al., 2020, 2021). Some ecotypes differ with regard to external morphology (Grismer & Grismer, 2017; Kaatz et al., 2021; Riedel, Grismer, et al., 2024), providing an excellent opportunity for a detailed examination of the evolution of incipient toepads in different ecological circumstances (structural microhabitats). Indeed, our findings indicate that several lineages within *Cyrtodactylus* independently exhibit trends towards the expression of toepads (Figures 5 and 8), some more extensively than others. Species included in Russell's (1976) morphotypic series are now mostly assigned to the crown ecotype, such as *C. brevipalmatus*, or to the trunk ecotype, for example *C. novaeguineae* and *C. louisiadensis* (Gamble et al., 2012; Russell, 1976; Russell & Gamble, 2019). Thus, the morphotypic series trending towards toepads as presented by Russell (1976), in the absence of species-level phylogenetic data, included examples from different lineages within the genus.

Our study statistically confirms, for the first time, that trunk and crown ecotypes have evolved enlarged subdigital scale areas and modified scale shapes that resemble the lamellae/scansors of pad-bearing geckos—confirming their status as examples of species with incipiently expressed toepads. *Cyrtodactylus novaeguineae* and *C. louisiadensis* are the only *Cyrtodactylus* species for which microornamentation in the form of adhesive microstructures (setae) has been documented (Peattie, 2008; Russell, 1976), and *C. brevipalmatus* is the only species so far documented to

TABLE 4 *Tukey's EMM* post hoc comparison of ecotype categories for phylogenetic ANOVA on PC 1.

Ecotypes	Terrestrial	General	Granite	Karst	Trunk	Crown
Terrestrial		1.342	0.024	0.807	3.546	0.742
Generalist	0.430		−1.798	−1.759	3.388	−0.285
Granite	0.503	0.937		1.022	4.268	0.830
Karst	0.503	0.929	0.929		3.670	0.151
Trunk	**0.002***	**0.002***	**0.003***	**0.003***		−2.519
Crown	**0.003***	**0.003***	**0.005***	**0.003***	0.929	

Note: *T*-values are shown in upper right half of the table (above the empty cells), and *p*-values in the lower left. Significant values are highlighted in bold and marked with an asterisk.

TABLE 5 *Pillai's* post hoc comparison for broad (ecotypes lumped) microhabitat categories for a MANOVA model comparing broad habitat categories.

Broad microhabitats	Terrestrial	Generalist	Saxicoline	Arboreal
Terrestrial		0.766	0.730	0.813
Broad Generalists	0.400		0.748	0.835
Saxicoline	0.495	0.426		0.873
Arboreal	0.059	**0.042**	**0.012**	

Note: Pillai's test statistics values are shown in the upper right half of the table (above the empty cells) and *p*-values in the lower left. Significant values are highlighted in bold.

exhibit modifications of the internal muscular anatomy in line with what would be expected for pad-bearing species (Russell, 1972). Additionally, anecdotal reports suggest that besides the trunk species *C. consobrinus* (Peters, 1871), the saxicoline *C.* cf. *pulchellus* (Gray, 1827) can adhere to vertical glass surfaces (Scholdei, 2023). This observation confirms adhesive competency (Garner & Russell, 2021) which may also be present in other saxicoline species. Because adhesive competency is only confirmed for gecko species with setae (Russell & Garner, 2023), we therefore predict that minimally the above-mentioned trunk, crown and saxicoline species possess adhesive setae, although a thorough investigation of the subdigital microornamentation of the genus is needed to corroborate this prediction.

Furthermore, adhesive performance is positively correlated with toepad area in pad-bearing lizards (Irschick et al., 1996; Pillai et al., 2020b). Additionally in chameleons, which exhibit non-setal filamentous outgrowths, frictional forces are positively correlated with contact area (Herrel et al., 2012; Khannoon et al., 2014; Spinner et al., 2014). Because almost all geckos examined so far at least possess small filamentous integumentary outgrowths (Riedel et al., 2019; Ruibal, 1968; Ruibal & Ernst, 1965), increased SSA should be beneficial for climbing and clinging in all *Cyrtodactylus* species, either by increasing fiction or friction and adhesion. Thus, arboreal ecotypes can be expected to outperform saxicoline ecotypes in regard to clinging and climbing. A formal analysis of the locomotor performance of species representing different ecotypes is, however, highly warranted. Locomotor performance data would be greatly informative about the functional consequences of the differentially evolving incipient toepad morphologies when placed into an ecological framework (Bock, 1994; Garland Jr & Losos, 1994), particularly if microornamentation should turn out to differ among species or ecotypes. Ecologically associated differences have been found in *Anolis* lizards (Garner et al., 2022) and phasmatodean insects (Büscher et al., 2018). Such variation could lead to complex interactions between the influence of variation in microornamentation and the effect of increased SSA on locomotor performance. The results of such endeavours could, in turn, enlighten us about the evolution of adhesive pads in other pad-bearing taxa such as treefrogs, insects and spiders (Büscher et al., 2018; Büscher & Gorb, 2021; Langowski et al., 2019; Moen et al., 2013; Russell & Garner, 2023).

Another promising endeavour would be the examination of the internal digit morphology of *Cyrtodactylus*. The hypothetical endpoint of the proposed morphological series of *Cyrtodactylus* is the morphology displayed by the pad-bearing genus *Hemidactylus* (Gamble et al., 2012; Russell, 1976), which, together with *Dravidogecko* forms the sister taxon to *Cyrtodactylus* (Chaitanya et al., 2019; Russell & Gamble, 2019). *Hemidactylus* is characterized by a strongly reduced and vertically oriented antepenultimate phalanx, which is the product of paedomorphic developmental patterns (Griffing, Gamble, Cohn, et al., 2022), and paraphalanges (cartilaginous structures) supporting the toepads (Griffing, Gamble, Bauer, et al., 2022; Russell & Bauer, 1988). A shortening and reorientation of the antepenultimate phalanx is also assumed for *Cyrtodactylus* while paraphalanges are unknown in the genus (Gamble et al., 2012; Russell & Gamble, 2019). Thus, a detailed examination of relative phalanx dimensions, ideally accompanied by a 3D geometric morphometrics approach, as well as an examination of the underlying developmental patterns across *Cyrtodactylus* ecotypes could further highlight our understanding of the evolution of adhesive toepads in geckos.

4.3 | Toepad types

Toepad morphology is highly diverse among geckos (Gekkota). Although occasionally questioned (Hagey et al., 2017; Harrington & Reeder, 2017), there is ample evidence for multiple independent

origins of toepads across the evolutionary history of the Gekkota (Gamble et al., 2012, 2017; McCann & Hagey, 2024; Russell & Gamble, 2019). Gekkotan toepads have been broadly qualitatively recognized as being basal, multiscansorial terminal or leaf-toed terminal, each pattern having arisen independently on numerous occasions. The basal configuration is the most widespread (Russell & Bauer, 1990; Russell & Gamble, 2019). McCann and Hagey (2024) added incipient toepads as an additional category but subsumed the anatomically distinct (Russell, 1976; Russell & Gamble, 2019) multiscansorial leaf-toed species into their basal category, thereby potentially confounding the underlying morphological signal.

Independent of these different classification schemes, *Cyrtodactylus* can be regarded as exhibiting intermediate stages in the evolution of basal toepads (Gamble et al., 2012; McCann & Hagey, 2024; Russell & Gamble, 2019). Of the previously established examples of incipiently expressed adhesive toepads, *Gonatodes humeralis* provides another example of incipient basal toepads (Higham, Gamble, et al., 2017; Russell et al., 2015), whereas the saxicoline *Heteronotia binoei* lineages represent precursors of leaf-toed terminal toepads (Riedel et al., 2021). The latter toepad type has been suggested to be more generally associated with saxicoline microhabitats (Riedel et al., 2021; Russell & Bauer, 1989). Furthermore, pad-bearing geckos with distally-situated toepads have been shown to be able to outcompete geckos with basal toepads on some naturally dusty and friable rock surfaces, possibly associated with their ability to independently control the scansors of the toepads and the claws (Cole et al., 2005; Russell & Delaugerre, 2017). Basal toepads, conversely, are hypothesized to be more generally associated with arboreal microhabitats (Higham et al., 2019; Higham, Gamble, et al., 2017), which, although roughness data on natural surfaces is still sparse, have been found to be tentatively smoother than saxicoline microhabitats (Higham et al., 2019; Pillai et al., 2020a). This supposed distinction is reinforced by observations pertaining to previous examples of taxa exhibiting incipiently expressed toepad morphologies. The incipiently basally-padded *Gonatodes humeralis* is arboreal and the incipiently leaf-toed terminally-padded *Heteronotia binoei* lineages are saxicoline (Higham, Gamble, et al., 2017; Riedel et al., 2021). The dimensional differences (between saxicoline and arboreal ecotypes) of incipient toepads revealed in this study further reinforce these natural history and functional microhabitat specialization associations. Detailed data on the surface roughness of locomotor surfaces used by the different *Cyrtodactylus* ecotypes would be useful for further evaluating predictions derived from this apparent phenotype–environment correlation, and for testing the hypothesis of adaptive radiation in this species-rich clade (Higham et al., 2019).

For most pad-bearing taxa, including most geckos, toepads work in concert with claws during locomotion on naturally rough vertical or inverted surfaces (Büscher et al., 2018; Büscher & Gorb, 2021; Naylor & Higham, 2019; Zani, 2000). In insects, there is accumulating evidence that adhesive pads are optimized for very smooth surfaces while claws are most efficient on rough surfaces, often resulting in a performance minimum on intermediately or fine grained rough surfaces (e.g. Burack et al., 2022; Büscher & Gorb, 2019; Scholz et al., 2010; Song et al., 2016; Winand et al., 2023). Although studied in less detail, research on substrate dependent interaction of claws and adhesive pads in lizards so far confirm this pattern (Naylor & Higham, 2019; Pillai et al., 2020b). However, Garner et al. (2021) examined maximum shear force in Tokay geckos before and after claw ablation on surfaces of varying roughness and found that claw removal did not have an impact. They did not test natural surfaces on which these geckos would move in nature, so it is possible that claws are important on arboreal surfaces. Additionally, claw morphology in *Anolis* lizards can be used to predict adhesive force, suggesting that slight differences in claw tip diameter, curvature, length, and depth can have strong influences on clinging (Pamfilie et al., 2023). Since claws also exhibit morphological patterns of differentiation in relation to scansorial locomotion in many animal groups, including lizards (e.g. Baeckens et al., 2019; Birn-Jeffery et al., 2012; D'Amore et al., 2018; Pfingstl et al., 2020), and have been demonstrated to have co-evolved with adhesive toepads in *Anolis* lizards (Crandell et al., 2014; Yuan et al., 2019), it is likely that claws might also be differentially configured among *Cyrtodactylus* ecotypes (Riedel et al., 2023). Thus, future studies should examine their claw morphology, for which it is predicted that there will be strong associations of claw morphology with habitat and substrate type, with saxicoline ecotypes exhibiting stronger associations relative to arboreal ecotypes.

4.4 | Biogeographic patterns and phylogenetic signal

Despite the ecologically-associated signal recovered in this study, our ancestral state reconstruction revealed some patterns of phylogenetic clustering that contribute to trait variation within ecotypes, in accord with the high λ value for subdigital scale area (SSA; Table 2, Figure 5). The relative increase in SSA in trunk species is more prominent in the Melanesian clade (clade A15 in Grismer, Poyarkov, et al., 2022) than in *C. consobrinus* (*malayanus* group) or the trunk species of the *philippinicus* group. Partially consistent with these results, Riedel, Grismer, et al. (2024) found a similar pattern of evolution of large body size in the trunk ecotype, which is most strongly expressed in the Melanesian clade and least expressed in the trunk species of the *philippinicus* group. Increased body size, and thus body mass, might facilitate a more dramatic increase in SSA, and thus climbing performance, to ensure high enough safety factors (Higham, Russell, et al., 2017; Irschick et al., 2006; Russell et al., 2019).

The relatively reduced SSA of the generalist species of the *philippinicus* clade, compared to other generalists, further indicates that the Philippine generalist species might deviate from the general morphology of the generalist ecotype, which has already been shown for their relative limb proportions and body size (Riedel, Grismer, et al., 2024). Some other generalist species, however, also show a moderate relative decrease in SSA (Figure 5); thus, additional data are needed to confirm or refute this deviation. Unlike these exceptions, *C. frenatus* and *C. khasiensis* deviate from the typical pattern of a generalist ecotype by their increased relative SSA (Figure 5).

Although described in the literature as a generalist (Batuwita & Bahir, 2005), *C. frenatus* has evolved longer hindlimbs typical of the trunk and saxicoline ecotypes (Riedel, Grismer, et al., 2024). *Cyrtodactylus khasiensis* is the only generalist to have been included in the morphotypic series depicting trends towards expression of adhesive toepads (fig. 1 in Russell & Gamble, 2019) although, in contrast to *C. frenatus*, this species does not show noticeable deviations from the generalist ecomorphology in limb proportions or body size (Riedel, Grismer, et al., 2024). In terms of incipient toepad shape, *C. fraenatus* has evolved somewhat towards lamella-like scales, whereas *C. khasiensis* has not (Figures 7 and 8). In the absence of detailed ecological or life history data that might explain such patterns, we can only emphasize the necessity for fine-scale, quantitative ecological data for more lizard species (Riedel et al., 2020; Riedel, Grismer, et al., 2024). The only non-arboreal species that expresses lamella-like scales is *C. mimikanus* (Boulenger, 1914), a secondarily generalist species belonging to the Melanesian clade (Figure 8; Grismer et al., 2020). Thus, increased adhesive competency might not be reduced so readily in generalist species.

4.5 | Ecotypes and adaptive radiation

Adhesive toepads have been advocated to represent a putative key innovation for accessing arboreal habitats (Miller et al., 2022; Miller & Stroud, 2021), although more likely the functional adhesive competency facilitated by sufficiently elaborated microornamentation constitute the actual key innovation rather than the macroscopically recognizable toepads (Garner & Russell, 2021; Higham, Gamble, et al., 2017). Key innovations, in turn, have been posited to be one potential trigger of ecological opportunity leading to adaptive radiations (Miller et al., 2022; Rabosky, 2017; Schluter, 2000; Stroud & Losos, 2016; Yoder et al., 2010). With the increasing accrual of evidence that suggests that particular portions (clades) of *Cyrtodactylus* possesses, at least in part, some of the attributes traditionally employed to diagnose and recognize adaptive radiations (Grismer & Grismer, 2017; Kaatz et al., 2021; Riedel, Grismer, et al., 2024), and the confirmation herein that several of its lineages have independently differentiated their digital form sufficiently to bear incipiently expressed adhesive toepads (although adhesive competency [sensu Garner and Russell (2021)] has yet to be confirmed experimentally), we advocate that *Cyrtodactylus* is a promising clade for the investigation of the association of a putative key innovation as an initiator, or trigger, of processes resulting in adaptive radiation, such as increased adaptive speciation (Glor, 2010) or increased utilization of larger portions of the available structural niche space of particular clades (Rabosky, 2017).

Furthermore, our findings add to the evidence that many of the *Cyrtodactylus* ecotypes may actually be ecomorphs. In a recent examination of limb proportions and body size, morphological differences were elucidated among terrestrial, generalist and crown ecotypes on one hand and the trunk, granite and karst ecotypes on the other. Although trunk, granite and karst ecotypes could tentatively be discriminated on morphological grounds, generalist and crown ecotypes were indistinguishable (Riedel, Grismer, et al., 2024). Here we expand the definition of the crown and trunk ecotypes by their possession of lamella-like subdigital scales that are much wider than long and located under the basal part of the digits as far distally as the mid-digit inflexion point. Also, the crown ecotype has a larger relative subdigital scale area on both autopodia than all other ecotypes except the trunk ecotype. Thus, crown and generalist ecotypes can be distinguished morphologically, and the trunk ecotype can be further discriminated morphologically from the granite and karst ecotypes.

5 | CONCLUSIONS

Overall, our study shows that although subdigital scale area is relatively enlarged in all scansorial ecotypes compared to their generalist ancestors and to terrestrial species (Figure 5), this increase is most pronounced in arboreal species, and particularly so in the crown ecotype. Additionally, only the arboreal ecotypes exhibit changes in subdigital scale shape towards a toepad-like configuration (i.e. with lamella-like, broadened subdigital scales), with this transition occurring in several lineages (Figure 8). Arboreal ecotypes may be further along the transitional pathway to the expression of what are generally regarded as basal adhesive toepads than is the case for the saxicoline ecotypes, in accord with the suggested stronger association of basal adhesive toepads with the smoother substrata encountered in arboreal microhabitats (Pillai et al., 2020a; Russell et al., 2019). The limited data available indicate that arboreal ecotypes may possess adhesive microstructures (setae) that increase adhesive competency (Garner & Russell, 2021; Russell, 1976). A more focused examination of subdigital microornamentation and experiments examining potential adhesive performance is needed to corroborate these hypotheses.

AUTHOR CONTRIBUTIONS

JR, LLG, TEH, TZ, APR, KE and DR conceived the ideas and designed the methodology. JR, KE, JW, QHD, CGM, TEH, TQN and RMB collected the data, and JR curated the data. JR analysed the area data while JR, KE and MG analysed the geometric morphometric data. JR acquired project funding and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Timothy Higham is an Associate Editor of *Functional Ecology* but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

All measurements used in this study are included in the Supplementary Material. Data available from the Dryad Digital Repository: https://doi.org/doi:10.5061/dryad.f4qrfj73j (Riedel, Eisele, et al., 2024).

STATEMENT ON INCLUSION

This study is conducted using museum specimens with most specimens sampled in collections in Europe and the United States, although the distribution of the species sampled is centred in South-East Asia. We reached out to researcher from the countries of origin of some of these species and could secure collaborations namely in Vietnam and with a researcher form the Philippines (although currently based in the United States).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table ST1. Species included in this study.

Table ST2. Results from model used to extract residuals for Ancestral State Reconstruction.

Figure SF1. Photographs of selected specimens for illustration of subdigital scale shapes.

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