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Evolution of the Gekkotan Adhesive System: Does Digit Anatomy Point to One or More Origins?

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Abstract

Recently-developed, molecularly-based phylogenies of geckos have provided the basis for reassessing the number of times adhesive toe-pads have arisen within the Gekkota. At present both a single origin and multiple origin hypotheses prevail, each of which has consequences that relate to explanations about digit form and evolutionary transitions underlying the enormous variation in adhesive toe pad structure among extant, limbed geckos (pygopods lack pertinent features). These competing hypotheses result from mapping the distribution of toe pads onto a phylogenetic framework employing the simple binary expedient of whether such toe pads are present or absent. It is evident, however, that adhesive toe pads are functional complexes that consist of a suite

of integrated structural components that interact to bring about adhesive contact with the substratum and release from it. We evaluated the competing hypotheses about toe pad origins using 34 features associated with digit structure (drawn from the overall form of the digits; the presence and form of adhesive scancers; the proportions and structure of the phalanges; aspects of digital muscular and tendon morphology; presence and form of paraphalangeal elements; and the presence and form of substrate compliance-enhancing structures). We mapped these onto a well-supported phylogeny to reconstruct their evolution. Nineteen of these characters proved to be informative for all extant, limbed geckos, allowing us to assess which of them exhibit co-occurrence and/or clade-specificity. We found the absence of adhesive toe pads to be the ancestral state for the extant Gekkota as a whole, and our data to be consistent with independent origins of adhesive toe pads in the Diplodactylidae, Sphaerodactylidae, Phyllodactylidae, and Gekkonidae, with a strong likelihood of multiple origins in the latter three families. These findings are consistent with recently-published evidence of the presence of adhesively-competent digits in geckos generally regarded as lacking toe pads. Based upon morphology we identify other taxa at various locations within the gekkotan tree that are promising candidates for the expression of the early phases of adhesively-assisted locomotion. Investigation of functionally transitional forms will be valuable for enhancing our understanding of what is necessary and sufficient for the transition to adhesively-assisted locomotion, and for those whose objectives are to develop simulacra of the gekkotan adhesive system for biotechnological applications.

Introduction

The diversity of gecko digit form (Autumn et al. 2014; Niewiarowski et al. 2016) has greatly influenced gekkotan taxonomy (Fitzinger 1843; Russell and Bauer 2002), and many generic names describe some aspect of digital morphology. By

1830 *Cyrtodactylus*, *Gymnodactylus*, *Hemidactylus*, *Phyllodactylus*, *Platydactylus*, *Ptyodactylus*, *Sphaerodactylus*, *Stenodactylus*, and *Thecadactylus* were part of the gekkotan taxonomic lexicon (Kluge 1993). Currently 25 recognized gekkotan genera bear *dactylus* or *dactylodes* suffixes (Uetz et al. 2018), and many more are subsumed as junior synonyms of currently recognized genera. Similarity in external appearance of digit form, however, is not congruent with gekkotan phylogeny (Russell and Bauer 2002; Gamble et al. 2008,, 2012); digital evolution has not followed a simple pathway.

Employing recent systematically-based assessments of the pattern and distribution of adhesive toe pads, Gamble et al. (2012) advocated that they were gained and lost, with approximately equal frequency, several times independently, with at least one origin in four (Diplodactylidae, Sphaerodactylidae, Phyllodactylidae, and Gekkonidae) of the six extant limbed gekkotan families. The Carphodactylidae and Eublepharidae were interpreted as never having possessed toe pads. Subsequent studies (Hagey et al. 2017; Harrington and Reeder 2017), however, argued for a single origin of adhesively-competent toe pads within the Gekkota, this occurring at the base of the gekkotan tree, thereby implying that all extant gekkotans (pygopods are also implicated, but are not considered further here) lacking adhesive toe pads do so secondarily. Gamble et al. (2017), responding to such arguments, reaffirmed their previous proposal (Gamble et al. 2012) of multiple origins and suggested that an in-depth assessment of anatomical features of gecko digits might help resolve this question. Herein we undertake this, rooting our approach in the understanding that the fully-expressed gekkotan toe pad is a functional complex (Russell 2002), rather than a single attribute, the form and function of which is highly integrated with its biological role(s) (Bock and von Wahlert 1965) of attachment to various naturally-occurring surfaces (Johnson and Russell 2009; Russell and Johnson 2014). Morphology matters (Bock 1994; Koehl 1996; Nielsen 1998; Smith and Turner 2005), and its examination is essential for inferring the ancestral states, origin, and evolution of complex structural features (Wiens et al. 2007; Assis et al. 2011). In light of the general consensus about how gecko toe pads operate (but see below), we regard this functional complex as residing on digits that essentially operate as two modules, a basal region used to impart

locomotor thrust to the substratum when moving on near-horizontal (terrestrial) surfaces, and a more distal region, carrying the adhesive apparatus, that is unfurled for its adhesive role when ecological and environmental circumstances dictate (Russell and Higham 2009; Collins et al. 2015; Higham et al. 2017). On the basis of this we predict that secondary reduction and loss of the adhesive system will bear the legacy of its prior presence (and its operational demands), thereby rendering such digits morphologically distinguishable from the ancestrally padless condition exemplified by the digits of lizards in general.

The multiple origin hypothesis implies numerous derivations from a conserved ancestral, padless condition, and allows for, but does not require, transitions between pad types. The single origin argument implies, contrastingly, *de facto* transitions between observed pad configurations, because all occurrences must be regarded as variants of a single system, and also incorporates the potential for regaining the ancestral digital attributes of non-gekkotan lizard outgroups upon the loss of toepads, thus seemingly violating Dollo's Law (Gould 1970).

"Discretization" (Desutter-Grandcolas et al. 2005) of structural complexes is necessary for determining whether more than one evolutionary pathway has led to similar, but not identical, outcomes (Gorb and Beutel 2001). Functional complexes can be compartmentalized into structural components (Salton and Szalay 2004), which can be examined through many-to-one mapping, via ancestral state reconstruction, to explore whether or not trait co-occurrences are clade-specific (Kingsolver and Huey 2003; Wainwright et al. 2005; Strobbe et al. 2009; Watanabe 2018). Assessment of correlations between such features, when examined in the context of a phylogeny derived independently of morphological data, can be informative about patterns of character evolution, and whether such patterns repeat in different regions of the tree (Jenner 2004; Desutter-Grandcolas et al. 2007; Revell et al. 2007). Wiens et al. (2006) note that relatively little attention has been paid to explaining the specific number of origins of a trait (or, in this case, structural complex). Before any such explanations can be advanced, however, the likelihood of a multiplicity of origins must be established.

We assess variation in gekkotan digit structure by examining 34 digital attributes relating to aspects of overall digit form (Russell and Bauer 1990a), many of which derive from soft anatomy (Lee 2000; Hertwig 2008): variation in the number and form of the phalanges (Russell and Bauer 1990a, 2008); presence of paraphalangeal elements (Russell and Bauer 1988); musculotendinous patterns (Russell 1976); the presence and form of scansors; and presence of substratum compliance-enhancing mechanisms, such as vascular reticular networks and sinuses (Russell 1981). We undertook a broad-spectrum survey of digital structure to establish whether and, if so, which digital features exhibit sequential and correlated patterns of elaboration, as predicted for emerging functional complexes (Frazzetta 1975, 1982; Lee 1996), and whether or not common attributes are shared by lineages possessing toe pads regardless of how many origins have occurred. We map reconstructed ancestral state occurrence onto a well-resolved phylogeny to explore patterns of covariation. We use the designation of the presence or absence of toe pads employed by Gamble et al. (2012) as our initial basis for categorization, but ultimately temper this with recently-acquired information about the form and function of incipient toe pads in geckos (Russell et al. 2015; Higham et al. 2017).

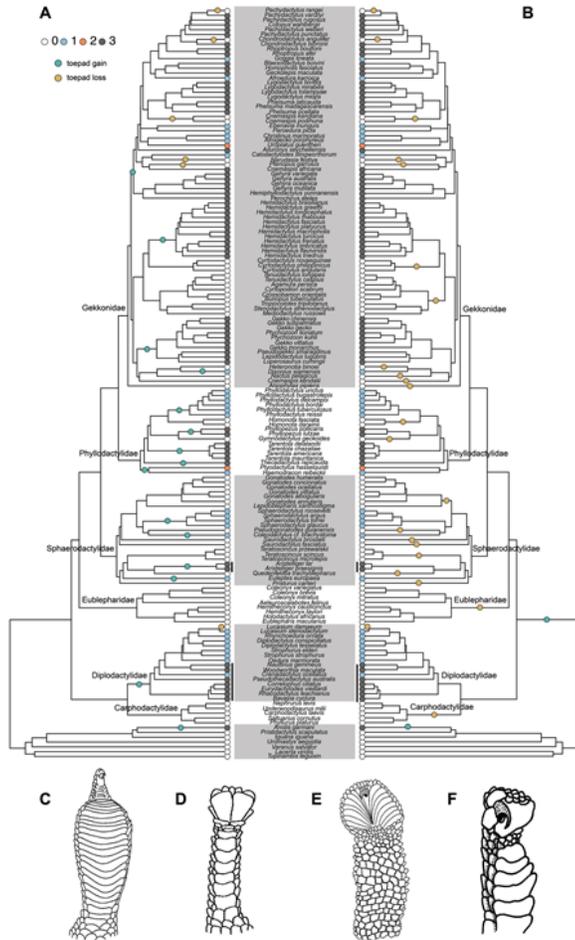
Materials and methods

Sources of anatomical information

Manūs and pedes of 149 species of geckos and seven outgroup taxa (Fig. 1), broadly representative of lizards in general ([Supplementary Table S1](#) lists all species and specimens examined) were investigated through dissection, radiography, clearing and staining, and observation of intact, ethanol-preserved individuals. Individuals of hundreds of additional specimens congeneric with the species included in this study were examined in a similar fashion. In a few instances in which species included in the phylogeny (Fig. 1) were not

available for anatomical investigation, we substituted a closely related congener ([Supplementary Table S1](#)). The 34 digital attributes investigated are provided in [Supplementary Information](#) Document S2 and summarized in Fig. 2.

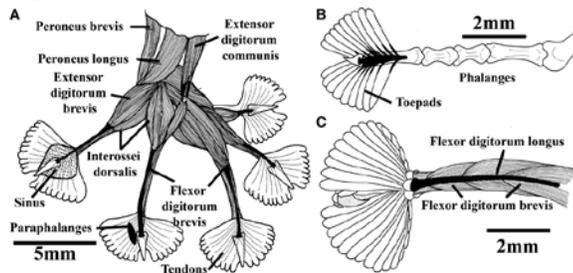
Fig. 1



Phylogenetic relationships of the 149 gekkotan species and 7 outgroup species examined in this study. See the text for the derivation of this phylogeny. The character subjected to ancestral state reconstruction (circles adjacent to the names of the species) is that relating to the presence of scansors on digit IV, manus, and pes (character 0 in the list of characters examined—see [Supplementary Document S2](#)), represented by four states: 0—no expanded scansors present; white circles; 1—scansors in leaf-like pairs associated with the unguis and penultimate phalanges; blue circles; 2—scansors in a terminal fan associated with the unguis and penultimate phalanges; orange circles; 3—transverse, widened scansors involving at least three phalanges; dark gray circles. On the left (A) multiple toe pad gains are depicted, consistent with our ancestral state reconstruction analysis (see the text and [Supplementary Document S2](#)). Toe pad gain is indicated by blue circles superimposed on the stems in the phylogeny, and toe pad loss by gold circles. In total, 14 gains and 6 losses are hypothesized in this scenario, with an independent, extra-gekkotan origin in *Anolis*. On the right (B) a single origin of toe pads, at the base of the gekkotan phylogeny (as hypothesized by Hagey et al. 2017; Harrington and Reeder 2017), is superimposed, resulting in 1 origin and 23 losses, with an independent, extra-gekkotan origin in *Anolis*. The three types of toe pad encountered among geckos are depicted in the lower part of the figure. (C) Ventral aspect of digit IV, right pes of *Gekko smithii* (BMNH 91.8.29.3) representative of the basal pad condition, character state 3, above. (D) Ventral aspect of digit IV, left pes of *Ebenavia inunguis* (BMNH 89.8.1.1) representative of the terminal leaf-like pad condition, character state 1, above. (E) Ventral aspect of digit IV, left pes of *Uroplatus*

ebenau (BMNH 1946.6.1.5) representative of the terminal fan of scansors, character state 2, above. (F) The ventral aspect of digit I, left pes of *Aristelliger lar*, showing the presence of both basal scansors and terminal leaves is depicted, representing state 3 of character S (see [Supplementary Document S2](#)), indicative of the potential for transition between basal and terminal leaf-like toe pads (see the text for details).

Fig. 2



Dissection of the dorsal aspect of the right pes (A) and ventral (B, C) aspects of digit III of the right pes of the phyllodactylid gecko *Ptyodactylus hasselquistii* (BMNH 1954.1.5.40) indicating the various features examined in this study. The 34 features of the digits examined (see [Supplementary Table S2](#)) relate to the overall form and configuration of the digits (five characters); features of the form and proportions of the phalanges (eight characters); presence and form of scansors/toe pads (five characters—*Ptyodactylus* exhibits a terminal fan of scansors, as illustrated in Fig. 1E); the presence of subphalangeal cushioning devices such as vascular sinuses (one character); presence and form of paraphalangeal elements (three characters—*Ptyodactylus* lacks paraphalanges but an indication of their potential location in other taxa is provided); form and pattern of musculotendinous features (12 characters—the digital muscles examined are indicated, and the names of adjacent lower limb muscles are also provided).

Phylogenetic framework

We simultaneously estimated phylogenetic relationships and divergence times in a Bayesian framework using BEAST v1.5.3 (Drummond et al. 2012). We used the data from Gamble et al. (2012), composed of 4100 aligned bases of nucleotide data from five protein coding genes, from 244 gekkotan taxa, and 14 outgroups. Data were analyzed in three partitions, by codon, using a GTR + G model, with an uncorrelated relaxed clock and Yule prior on speciation rates (Drummond et al. 2006). Two replicate analyses were run for 50 million generations. We used fossil calibrations from Gamble et al. (2015) to constrain the minimum ages of nodes in the time tree analyses. Output files were checked for convergence using Tracer (Rambaut and Drummond 2007), and both runs, minus burn-in, were combined to estimate topology and divergence times.

We pruned taxa from the dated phylogeny using Ape 5.2 (Paradis and Schliep 2018), leaving only the 149 gekkotan taxa included in our morphological dataset ([Supplementary Table S1](#)). We employed seven non-gekkotan squamates as outgroups (Grandcolas et al. 2004), incorporating them by grafting the time-calibrated phylogeny from Zheng and Wiens (2016), pruned as above, to include only those taxa with morphological data (Fig. 1A, B). No limbless squamates, including pygopodids, were included in the phylogeny because they lack all relevant characters.

Ancestral state reconstruction

We reconstructed the evolution of digital characters through maximum likelihood using the ace command in the R package Ape 5.2 (Paradis and Schliep 2018) employing the tree with the maximum likelihood from the Bayesian phylogenetic analysis. The transition rate matrix that best fit each character was identified by comparing likelihood scores among alternate transition rate models using the Akaike Information Criterion (AIC).

We considered three transition rate models: A six-parameter model that had different rates for every transition type (ARD); a three-parameter symmetrical rates model that had equal forward and reverse rates between states (SYM); and a single-parameter model with equal rates (ER) among all transitions. To accommodate phylogenetic uncertainty we also conducted stochastic mapping (Nielsen 2002; Huelsenbeck et al. 2003) on a random sample of 50 trees from the posterior distribution using phytools (Revell 2012) in R. We summarized these results on the summary tree from the Bayesian phylogenetic analysis ([Supplementary Document S2](#)).

Results

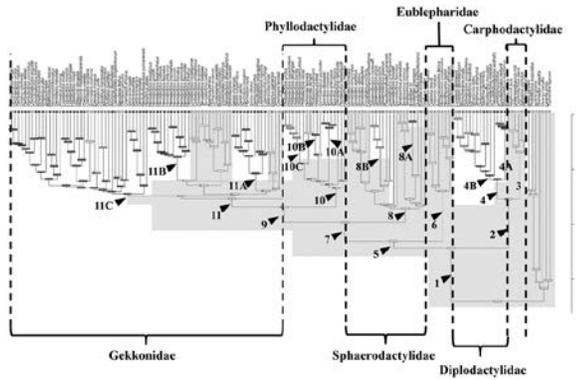
Phylogenetic framework

The time-calibrated phylogeny was concordant with other recent gekkotan phylogenies at well-supported nodes (Gamble et al. 2012,, 2015). Relationships among many genera in the Gekkonidae, Phyllodactylidae, and Sphaerodactylidae exhibit short internal branches with poor support suggesting topological discordance and phylogenetic uncertainty among genera.

Ancestral state reconstruction

Results of the comparative analyses using maximum likelihood and stochastic mapping were largely similar ([Supplementary Document S2](#)). We ground our observations on our understanding of the anatomy of lizard digits in general, as described by Russell and Bauer (2008), and by employing a series of outgroups to establish conditions for lizards beyond the confines of the Gekkota. The 34 digital characters ([Supplementary Document S2](#)) subjected to ancestral state reconstruction (for the data matrix, see Supporting Information [Table S3](#)) resolved into four clusters ([Supplementary Document S2](#)) following initial analysis: (i) those relating to the presence, form, and distribution of toe pads across the Gekkota in general (characters O and S; [Supplementary Document S2](#)); (ii) those able to be scored for all taxa regardless of whether or not toe pads are present (characters B, H, I, J, M, T, U, V, Y, Z, AA, AB, AD, AE, AF, AG, AI) and for which changes in ancestral state are broadly distributed across the Gekkota ([Supplementary Document S2](#)); (iii) those able to be scored for all taxa regardless of whether or not toe pads are present (characters C, D, E, F, G, K, L, N, W, X, AC, AH) and for which changes in ancestral state are of more limited distribution throughout the Gekkota ([Supplementary Document S2](#)); and (iv) those that further characterize toe pad form (characters P, Q, R) for which changes in ancestral state are of limited occurrence within the Gekkota ([Supplementary Document S2](#)). For the purposes of this contribution, only the outcomes of ancestral state reconstruction of the 19 characters included in clusters (i) and (ii) above ([Supplementary Document S2](#)) are considered further, but those for characters included in Clusters (iii) and (iv), above, are also provided in the Supporting Information (Document S2). When reconstructing ancestral states, gradations in the probability of a particular state occurring at a particular node are evident ([Supplementary Document S2](#)). Decisions about the point at which transition from one ancestral state to another occurred along branches were made at nodes at which the occurrence of a new state had a probability of greater than 50%, and where the probability of that state beyond that node showed a further increase. There are many instances of transitions in genera or clusters of genera at more crownward locations in the phylogeny ([Supplementary Document S2](#)), but our focus is confined to trends in major lineages within the Gekkota (Fig. 3).

Fig. 3



The gekkotan phylogeny investigated in this study (see Fig. 1B) depicting the presence of toe pads (character O—see [Supplementary Table S2](#)). Indicated on this are changes in digital characters in category (ii) (see text) at key junctures (see Table 1 for a summary). The gray shading highlights the absence of toe pads, indicating islands of this condition in the Sphaerodactylidae, Phyllodactylidae, and Gekkonidae; its totality in the Carphodactylidae and Eublepharidae; and the ubiquitous presence of toe pads in the Diplodactylidae. Ancestral character state transitions at key points are indicated by numbers on pertinent lineages (see [Supplementary Document S2](#) for a description of the characters, indicated below by letters, and Table 1 for an indication of the anatomical groups to which they belong). Lineage 2: AB 0→1; Lineage 3: AG 0→1; Lineage 4: H 0→2, I 0→1, J 0→1, T 0→4, AA 0→1; Lineage 4A: M 0→1, Y 0→2; Lineage 4B: T 4→1; Lineage 5: J 0→1; Lineage 6: AG 0→1; Lineage 7: H 0→1, I 0→1, AE 0→2; Lineage 8A: H 1→2, M 0→2, T 0→1, Y 0→2, AG 0→1; Lineage 8B: H 1→2, T 0→1, AF 0→1, AI 0→1; Lineage 9: AF 0→2; Lineage 10A: H 1→2, M 0→2, T 0→1, Y 0→2, Z 0→1, AD 0→1; Lineage 10B: H 1→2, M 0→2, T 0→2, U 0→2, V 0→2, Y 0→2, Z 0→1, AD 0→1, AE 2→1; Lineage 10C: H 1→2, T 0→1, AF 2→1, AG 0→3, AI 0→1; Lineage 11A: H 1→2, M 0→2, T 0→1, Y 0→2, Z 0→1, AD 0→1, AE 2→1; Lineage 11B: H 1→2, M 0→2; T 0→2, U 0→1, V 0→2, Y 0→2, z 0→1; AE 2→1, AG 0→1.

(i) Reconstruction of ancestral states pertinent to toe pad distribution

Characters O and S (Fig. 1A; [Supplementary Document S2](#)) provide information about the distribution of toe pads and their form across the Gekkota. Ancestral state reconstruction for whether or not toe pads/scansors are present, and if so what relationship they have with underlying phalanges (character O; Fig. 1A; [Supplementary Document S2](#)), reveals that the most recent common ancestor of the crown group Gekkota lacked toe pads, and that this condition persists along the spine of the phylogeny (Figs. 1A and 3; [Supplementary Document S2](#)). This indicates that toe pads *per se* are non-homologous features among various crown gekkotan clades, the consequences of which are considered further in the “Discussion” section. Our findings imply that the padless ancestral state was inherited unchanged by all carphodactylids and eublepharids as well as by certain lineages of the Sphaerodactylidae, Phyllodactylidae, and Gekkonidae. Thus, two gekkotan families (Carphodactylidae and Eublepharidae) are inferred to have retained the padless ancestral state (Russell and Bauer 2008), three (Sphaerodactylidae, Phyllodactylidae, and Gekkonidae) exhibit at least two origins of toe pads within their ranks, and one (Diplodactylidae) exhibits the pad-bearing condition as its ancestral state (Fig. 1A; [Supplementary Document S2](#)). Furthermore, in two families with pad-bearing members there are inferred instances of secondary loss of toe pads (Fig. 1A). Overall our data indicate 14 gains and 6 losses (Fig. 1A). Among the Iguania there is independent origin of seta-bearing, visibly-identifiable toe pads in the genus *Anolis* (Fig. 1A), which provides us with comparative information for assessing the anatomical attributes associated with toe pad acquisition within the Gekkota. Certain scincid lizards also exhibit analogous structures (Williams and Peterson 1982), although their digital anatomy is not sufficiently understood to permit a detailed structural comparison.

Application of the assumption of a single origin of gekkotan toe pads (Hagey et al. 2017; Harrington and Reeder 2017) requires hypothesizing 23 separate instances of toe pad loss (Fig. 1B).

Subdivision of gecko toe pads into the three major patterns of expression (Fig. 1C–E) (basally-situated pads located beneath the intermediate and, in some cases, the more distal phalanges; leaf-like, paired scansors located distally on the digits; and terminal fans of scansors also located far distally—character O, Fig. 1A, B; [Supplementary Document S2](#)) reveals that the leaf-like and terminal fan configurations are, in the majority of instances, nested within clades exhibiting basally-located toe pads (Fig. 1A and [Supplementary Document S2](#)), although there are some instances of direct origin of the former from a padless ancestral condition (Fig. 1A and [Supplementary Document S2](#)), most notably in the sphaerodactylids *Sphaerodactylus*, *Coleodactylus*, and *Euleptes* and the gekkonid *Dixonius* (Fig. 1A). The presence of both terminal, leaf-like scansors and widened, basally-situated toe pads (character S; Fig. 1F; and [Supplementary Document S2](#)) occurs in some digits of a few taxa and is consistent with the potential (see above) for transformation from basal to terminal, leaf-like toe pads.

(ii) Changeable digital features broadly distributed across the Gekkota

Seventeen of the remaining characters examined exhibit widespread patterns of ancestral state change across the Gekkota, enabling their assessment for potential variation in the structure of toe pads in different regions of the tree (Fig. 3 and Table 1). These characters ([Supplementary Document S2](#)) relate to digit osteology (H, I, J, M), overall digit form (B), musculotendinous attributes (Y, Z, AA, AB, AD, AE, AF, AG, AI), and ancillary soft and hard anatomical attributes that are unique to the Gekkota (T, U, V). Figure 3 and Table 1 summarize the distribution of ancestral state expression for major lineages within the Gekkota, and for localized regions in which toe pads occur within the four families that exhibit them.

Table 1

Ancestral state reconstructions for stems along which toe pad origin in the Gekkota is inferred, with *Anolis* included for comparative purposes

	Charac ters															
Lineage	H	I	J	M	T	U	V	Y	Z	AA	AB	A D	AE	A F	AG	AI
<i>Anolis</i>	H2	I 1	J 1	M 1				Y 2								
1. Gekkota																
2. (Carphodactylidae+Diplodactylidae)											AB 1					
3. Carphodactylidae															AG 1	
4. Diplodactylidae	H2	I 1	J 1		T 4					AA 1						
4A. <i>Bavayia</i> – <i>Correlophus</i> lineage				M 2	T 1			Y 2							AG 3	

4B. <i>Crenadactylus</i> – <i>Lucasium</i> lineage ^a																		
5. Eublepharidae +[<i>Sphaerodactylidae</i> +(<i>Phyllodactylidae</i> + <i>Gekkonidae</i>)]			J 1															
6. Eublepharidae																	AG 1	
7. [<i>Sphaerodactylidae</i> (<i>Phyllodactylidae</i> + <i>Gekkonidae</i>)]	H1		I 1											AE 2				
8. <i>Sphaerodactylidae</i>																		
8A. <i>Aristelliger</i> lineage	H2			M 2	T 1			Y 2									AG 1	
8B. <i>Sphaerodactylus</i> lineage	H2				T 1										A F1		AI 1	
9. (<i>Phyllodactylidae</i> + <i>Gekkonidae</i>)															A F2			
10. <i>Phyllodactylidae</i>																		
10A. <i>Tarentola</i> lineage	H2			M 2	T 1			Y 2	Z 1					A D 1				
10B. <i>Phyllopezus</i> lineage	H2			M 2	T 2	U 2	V 2	Y 2	Z 1					A D 1	AE 1			
10C. <i>Phyllodactylus</i> lineage	H2				T 1										A F1	AG 3	AI 1	
11. <i>Gekkonidae</i>																		
11A. <i>Luperosaurus</i> – <i>Gekko</i> lineage	H2			M 2	T 1			Y 2	Z 1					A D 1	AE 1			
11B. <i>Hemidactylus</i> lineage	H2			M 2	T 2	U 1	V 2	Y 2	Z 1					A D 1	AE 1		AG 1	
11C. <i>Perochirus</i> – <i>Pachydactylus</i> complex ^b																		

Main branches (families and clusters of families numbered with integers 1–11; lineages within families indicated with gray background shading and by suffix letters A–C). ^aMany toepad-related changes occur along various branches within this lineage. ^bAlthough toepads are prevalent in this complex, and their presence is reconstructed basally, the variability of ancestral state combinations at various nodes within this lineage render the determination of a particular suite of states at its base uninformative—see the text and the ancestral state reconstruction maps in the [Supplementary Information \(Supplementary Figure S4\)](#). Skeletal features H, I, J, M; subphalangeal cushioning features T (black background); paraphalangeal features U, V; tendinous features Y (black background); and muscular features Z, AA, AB, AD, AE, AF, AG, AI.

Ancestral state reconstructions of the osteological characters (H, I, J, and M; Fig. 3; Table 1; and [Supplementary Document S2](#)) exhibit correlation and are indicative of changes in phalangeal proportions and structure that precede the inception of toe pads in all lineages in which they occur (Russell et al. 1997). A change in proportions of the phalanges (character J), relative to those of lizards in general (Table 1 and [Supplementary Document S2](#)), characterizes five of the six gekkotan families investigated. The extra-gekkotan ancestral state (Table 1 and [Supplementary Document S2](#)), in which length of the phalanges decreases sequentially along the proximodistal axis of the digit (Russell and Bauer 2008), persists as the ancestral state only in the Carphodactylidae. Secondary reversion to the extra-gekkotan configuration is evident in terminal taxa that exhibit specialized locomotor features compared with their closest relatives (*Aeluroscalabotes* among the eublepharids [Peattie, 2008], *Teratoscincus* among the sphaerodactylids, and *Crossobamon* among the gekkonids). The *Pachydactylus* radiation of gekkonids also exhibits this trend of reversal in some of its members, but in these phalangeal form is highly modified and clearly displays features consistent with secondary toe pad loss (Russell 1976; Lamb and Bauer 2006; Higham et al. 2015).

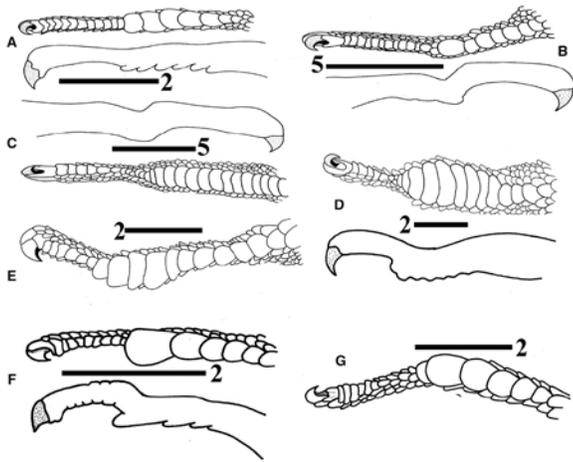
Digital osteology also reveals changes in the form of the joints between adjacent phalanges (character I; Fig. 3; Table 1; and [Supplementary Document S2](#)). The widespread extra-gekkotan ancestral condition of the presence of a ventroposterior process that extends beneath the distal head of the preceding phalanx (Russell and Bauer 2008) limits the degree of flexion of the digits. In the Diplodactylidae and independently in the (Sphaerodactylidae + [Phyllodactylidae + Gekkonidae]) (Fig. 3, branches 4, 7; Table 1) this tongue is greatly reduced, permitting an enhanced range of dorsoventral motion at the interphalangeal joints (Russell and Bauer 2008). Only in the Carphodactylidae and Eublepharidae is the extra-gekkotan ancestral state retained (Fig. 3; Table 1; and [Supplementary Document S2](#)). Putative secondary reversion to more robust interphalangeal joints has occurred in *Ptenopus* (Gekkonidae) ([Supplementary Document S2](#)), possibly in relation to its burrowing habit (Haacke 1974, 1975).

The cross-sectional profile of phalanges 2 and 3 (digit IV) (character H, Table 1; and [Supplementary Document S2](#)) is circular (with the shaft being cylindrical) in lizards in general, but within pad-bearing lineages (Fig. 3, branches 4, 8A, B, 10A–C, 11A, B; Table 1) it becomes depressed (Russell and Bauer 2008) in association with their relative shortening (see above). Intermediate phalanges of robust build and circular cross-section are retained by the Carphodactylidae and Eublepharidae. Lineages within the Sphaerodactylidae, Phyllodactylidae, and Gekkonidae that retain intermediate phalanges of circular cross-section are those that retain the ancestral state of the absence of toe pads ([Supplementary Document S2](#)). Ostensible secondary reversion to a cylindrical cross-section is evident in *Teratoscincus* among the sphaerodactylids, and *Stenodactylus*, *Tropicolotes*, *Ptenopus*, and *Narudasia* among the gekkonids ([Supplementary Document S2](#)).

Change in the form of the penultimate phalanx (character M, [Supplementary Table S2](#)) shows association with the presence of toe pads in some lineages (Fig. 3, branches 4A, 8A, 10A, B, 11A, B; Table 1), indicating variation within families and revealing that not all lineages having toe pads possess an arcuate or erect penultimate phalanx (Fig. 3, branches 4B, 8B, 10C; Table 1). Gekkonid taxa that deviate from this are also encountered in members of the *Pachydactylus* radiation that exhibit toe pad reduction or loss; *Phelsuma* and *Lygodactylus* in which the toe pads are shifted distally and the antepenultimate phalanx is highly modified (in *Phelsuma*, at least—Russell and Bauer 1990b); and in the leaf-toed *Goggia* and *Christinus* + *Afrogecko* ([Supplementary Document S2](#)). Leaf-toed taxa in the Diplodactylidae (variably), Sphaerodactylidae, and Phyllodactylidae also show absence of an arcuate penultimate phalanx ([Supplementary Document S2](#)), but in those taxa exhibiting a terminal fan of scanzors (*Uroplatus* [Gekkonidae] and *Ptyodactylus* [Phyllodactylidae]) (Fig. 1E) it is moderately arcuate ([Supplementary Document S2](#)).

Overall the digits of lizards are elongate and straight (character B) when viewed in lateral profile, although many taxa in various families have digits with inflections, giving them a crooked profile (Fig. 4B, C), this being associated with climbing (Arnold 1998). The apex of the inflection bears integumentary friction plates (Padian and Olsen 1984; Russell et al. 2015). Ancestral character state reconstruction (character B, [Supplementary Document S2](#)) reveals that gekkotan digits are initially not markedly inflected, become inflected in climbing lineages, and assume a secondarily non-inflected arrangement in taxa with toe pads (both basal and terminal leaf-like configurations). Inflected digits are evident in the Carphodactylidae, in *Pristurus*, *Saurodactylus*, and *Gonatodes* of the Sphaerodactylidae, *Homonota* among the phyllodactylids, and are widespread among naked-toed genera of the Gekkonidae, including *Cyrtodactylus*, the sister taxon of *Hemidactylus* (character B, [Supplementary Document S2](#)).

Fig. 4



Digit form in gekkotan taxa belonging to genera generally characterized as lacking toe pads that are advocated as candidates for potential adhesive competency. For those taxa for which a lateral profile is depicted, note the flattened proximal region of the digit, its potential for increased contact with the substratum, and the raised distal portion of the digit that stands proud of substratum contact. (A) Ventral view (BMNH 1947.1047) and lateral profile (BMNH 1971.1049) of digit IV, right pes of *Gonatodes humeralis* (Sphaerodactylidae), a species for which adhesive competency has been demonstrated (Higham et al. 2017). (B) Ventral view and lateral profile of digit IV, right pes of *Cyrtodactylus khasiensis* (Gekkonidae) (BMNH 74.417.134). (C) Ventral view and lateral profile of digit IV, right pes of *Cyrtodactylus novaeguineae* (Gekkonidae) (BMNH 1922.11.24.7). (D) Ventral view and lateral profile of digit IV, left pes of *Cyrtodactylus brevipalmatus* (Gekkonidae) (BMNH 1967.2783). (E) Ventral view digit IV, right pes of *Quedenfeldtia trachyblepharus* (Sphaerodactylidae) (BMNH 1905.11.28.12). (F) Ventral view and lateral profile of digit IV, left pes of *Cnemaspis littoralis* (Gekkonidae) (BMNH 82.5.22.29). (G) Ventral view digit IV, right pes of *Cnemaspis quattuorseriatus* (Gekkonidae) (unregistered specimen). Scale bars in mm.

Modifications of digital musculature are associated with the precise attachment and detachment of the setae in pad-bearing geckos (Russell 2002). The far distal insertion of the extensor digitorum brevis muscle (character Z, [Supplementary Table S2](#)) is evident in phyllodactylid and gekkonid geckos with basally-situated pads (Fig. 3, branches 10A,B, 11A,B; Table 1), in association with the derived state of character AD, in which the dorsal interossei muscles insert on the unguis phalanx (Fig. 3, branches 10A, B; 11A, B; Table 1). These configurations match with the patterns of arrangement of the raphe of the dorsal interossei muscles (character AE), with taxa with basal pads in the Gekkonidae and Phyllodactylidae sharing a similar, but independently derived, configuration (Fig. 3 and Table 1). The aforementioned muscular characteristics contrast with changes in the ancestral state of the number of bellies of the extensor digitorum brevis muscle (character AB) that is unique to

the Carphodactylidae + Diplodactylidae (Fig. 3, branch 2; Table 1), and the fleshy extent of this muscle (character AA) along the digits in the Diplodactylidae (Fig. 3, branch 4; Table 1). These patterns are indicative of different arrangements of the extensor muscles (Landsmeer 1979) at the basalmost dichotomy within the crown Gekkota (Fig. 3, branches 2, 5).

Lizard digits have lateral tendons (character Y—[Supplementary Document S2](#)) that course subcutaneously along their medial and lateral borders and stabilize the interphalangeal joints against medial and lateral deflection (Landsmeer 1981). In geckos with multiscansorial, basally-located toe pads these tendons are reconfigured, losing their close association with the now modified interphalangeal joints (see above) and gaining a secondary association by merging with the stratum compactum of the dermis of the scansors (Russell 1975, 1981). This enables tension to be placed on the scansors, imparting the parallel preload (Autumn et al. 2000; Tian et al. 2006) critical to the attachment phase of adhesion and the employment of shear-based frictional adhesive forces transmitted through the setae (Russell 1975,, 2002). This modification is seen in geckos with basal pads, regardless of their location in the phylogenetic tree (Fig. 3, branches 4A, 8A, 10A, B, 11A, B; Table 1; [Supplementary Document S2](#)). In geckos with terminal, leaf-like pads (Fig. 1A, D), however, whether or not these have been derived from a basally-padded precursor (Fig. 1A), this is not the case. Instead, the flexor digitorum longus muscle (character AI) is involved in placing tension on the distalmost scansors via branches from it to the bases of the leaves (Fig. 3, branch 8B; Table 1; [Supplementary Document S2](#)). These terminal pads are associated with the ungual phalanx, which is served by the flexor digitorum longus muscle (as it is in lizards in general—Russell and Bauer 2008; Russell and Delaugerre 2017). In those lineages where multiple leaf-like plates are present, both lateral digital tendons, attaching to the more proximal scansors (character Y, State 1; [Supplementary Document S2](#)), and branches of the flexor digitorum longus tendon attaching to the terminal leaves (character AI, State 1; [Supplementary Document S2](#)), are present, consistent with the potential for transformation from the basally-padded to the terminal leaf-like padded condition (Fig. 1A).

Scansor release is mediated by tendinous sheets that emanate from the dorsal (extensor) muscles that drive distal to proximal digital hyperextension (Higham et al. 2017). The tendinous sheets involved in the release process (character AF, Fig. 3; Table 1; and [Supplementary Document S2](#)) differ between taxa bearing basally-located and terminal leaf-like pads, in a fashion that compliments that of the distal extent of the dorsal interossei muscles (see above, character AD; Table 1). These attributes are sporadically and differentially (Fig. 3, branches 8A, B; 10C vs. 10A, B; 11A, B; Table 1) distributed across the Gekkota, with lacunae where clusters of padless taxa reside (Fig. 3 and [Supplementary Document S2](#)). Such extensor assembly (Landsmeer 1979) hyperextension mechanisms are not universal for pad-bearing taxa, however, being absent from the diplodactylids that bear basal pads (Fig. 3; Table 1; and [Supplementary Document S2](#)), indicating a possible different means of achieving hyperextension in these taxa.

Other anatomical modifications that supplement the functioning of the toe pads also vary in a mosaic pattern across the gekkotan phylogeny. Compliance mechanisms (character T), either expressed as vascular sinuses and their adnexa (Russell 1981), or adipose tissue, or both, show sporadic distribution across and within various gekkotan lineages in association with the presence of toe pads (Fig. 3, branches 4, 4B, 8A, B, 10A–C, 11A, B; Table 1).

The occurrence of paraphalangeal elements (Russell and Bauer 1988) and their material of composition (character U) also exhibit a mosaic pattern across the phylogeny (Fig. 3, branches 10B, 11B; Table 1; and [Supplementary Document S2](#)). Several lineages with toe pads lack them (all pad-bearing diplodactylids and sphaerodactylids, and the majority of genera of pad-bearing phyllodactylids and gekkonids—Table 1 and [Supplementary Document S2](#)). When present, paraphalanges are sometimes connected directly to the lateral digital tendons (character V, Fig. 3, branches 10B, 11B; Table 1; and [Supplementary Document S2](#)), and sometimes not, showing a further level of lineage-specific differentiation.

Discussion

The overall picture revealed by this analysis

Reconstructing the evolution of phenotypic traits onto a phylogeny is an important tool for testing evolutionary hypotheses (Swofford and Maddison 1987; Harvey and Pagel 1991, Schluter et al. 1997; Pagel 1999; Nunn 2011), but these statistical analyses should be examined critically and serve as a starting point for further investigation of the evolution of traits rather than being ends unto themselves (Strathmann and Eernisse 1994; Schluter et al. 1997; Cunningham et al. 1998; Lee and Shine 1998; Kearney and Rieppel 2006; Assis et al. 2011; Losos 2011; Griffith et al. 2015).

Earlier comparative analyses of gecko adhesive toepads treated digital adhesion as a single, binary trait and uncovered either multiple gains and losses (Gamble et al. 2012) or a single origin with multiple losses (Hagey et al. 2017; Harrington and Reeder 2017). Such treatment, however, belies toe pad complexity and potentially obscures lineage-specific characteristics. By examining structural components that make up the gekkotan digital adhesive apparatus we show that many of its constitutive features are either unique, evolving just once, or evolve in some but not all padded lineages. Collectively the 17 features in category (ii) (above) characterize different clusters of pad-bearing geckos in different combinations (Fig. 3 and Table 1). The distribution pattern of these traits and their absence in lacunae intervening between pad-bearing lineages (Figs. 1A, 3) indicate variation in the structure of the toe pad complex between various clades.

Toe pads are evident in some gekkotans from the Lower Cretaceous to the Lower Eocene (Bauer et al. 2005; Arnold and Poinar 2008; Daza et al. 2016), so the potential for their expression, and its associated skeletal correlates (see above) (Fontanarrosa et al. 2018), is deep-rooted within the Gekkota (Daza et al. 2016), and modifications for scansoriality are evident as far back as the Jurassic (Simões et al. 2017). Currently there is no evidence, however, that toe pads of stem gekkotans (Daza et al. 2016; Gamble et al. 2017) were inherited at the base of the crown group Gekkota. As indicated above, toe pads are variably underpinned by suites of associated anatomical features associated with their functioning. As more becomes known about the finer details of toe pad structure in fossil forms (Fontanarrosa et al. 2018), a more critical appraisal of where in the gekkotan phylogeny adhesively-competent toe pads have arisen. Should some of the pad-bearing taxa currently assigned to the stem Gekkota (Daza et al. 2016; Fontanarrosa et al. 2018) be reassigned to the crown group, then the arguments set forth in this paper will require reconsideration. Indeed, if the interpretation of the ancestral state for the crown Gekkota is inferred to be pad-bearing rather than padless, then wholesale reinterpretation of the evolution of pertinent anatomical features would have to occur, and it would be evident that those extant gekkotans seemingly on the cusp of expressing adhesively-competent toe pads (see below) would have to be interpreted as lineages becoming pad-bearing secondarily. This would imply even more evolutionary plasticity in the expression of the adhesive system. There is still much to learn about the evolution of this fascinating functional complex.

Since the data presented here are gleaned from a global overview of the Gekkota, they must be regarded as representing only a general picture. The specificity of patterns of change within clades must await more locally-focused analyses. On the basis of current evidence, independent origins of toe pads are, however, clearly evident in the Diplodactylidae, Sphaerodactylidae, Phyllodactylidae, and Gekkonidae (Figs. 1A, 3), with the possibility of multiple origins in the latter three families. Lack of clarity with regard to just how many origins is attributable to short internal branches and resultant poor phylogenetic resolution (Rokas and Carroll 2006) associated with the early radiation, especially for the Gekkonidae (Fig. 1A). Although most of the taxa stemming from branch 11C (Fig. 3) exhibit toe pads (Fig. 1B), a broad array of combinations of toe pad-associated features within its ranks makes characterization of such features at its base currently intractable (Fig. 3 and Table 1). Whether the independence of origin of toe pads inferred along branches 11A and C (Fig. 3) survives further

scrutiny, that inferred for branch 11B (Fig. 3) (the *Hemidactylus* radiation) is clearly distinct from the others and is flanked by an extensive cohort of ancestrally padless (contra Machado et al. 2018) taxa (Fig. 1A and [Supplementary Document S2](#)).

Figure 3 and Table 1 summarize the distributions of reconstructed ancestral states of digital features in character categories (i) and (ii) (see above) within the Gekkota. A change in proportions of phalanges (here considered for digit IV) distinguishes the digits of all gekkotan lineages except the Carphodactylidae, which retains the proportions evident in the outgroups examined (character J, Fig. 3, branches 4, 5; Table 1) (Russell and Bauer 2008). The ancestral state reconstruction for the Diplodactylidae, and the Eublepharidae + (Sphaerodactylidae + [Phyllodactylidae + Gekkonidae]) indicates a relative shortening of the intermediate phalanges (phalanges 2 and 3 of digit IV, Powell et al. 2018), which is associated with the overall relative shortening of the digits of geckos when compared with other lizards (Russell et al. 1997). A difference in the extensor musculature of the digits distinguishes the Diplodactylidae + Carphodactylidae from the remainder of the Gekkota (Fig. 3, branch 2) and precedes the appearance of toe pads in all extant gekkotan lineages.

The instances of toe pad loss indicated for *Pachydactylus rangei* and *Chondrodactylus angulifer* (Gekkonidae), and *Lucasium damaeum* (Diplodactylidae) (Fig. 1) are characterized by reduction of seta-bearing toe pads accompanied by retention of modified internal anatomy of the digits consistent with modular digit structure and the prior presence of toe pads and their mechanisms of control (Haacke 1975; Russell 1976, 1979; Johnson et al. 2005; Lamb and Bauer 2006; Garcia-Porta and Ord 2013; Higham et al. 2015). Such instances of loss are associated with adaptation to newly-occupied ecological settings (Ree 2005; Heinicke et al. 2017). Reversion to the padless condition from a prior pad-bearing state for *Cnemaspis kandiana* + *C. podihuna*, *Narudasia festiva*, and *Ptenopus garrulus* among the Gekkonidae (Fig. 1A) is currently not explainable on anatomical grounds. These taxa are relatively long-branched (see Daza et al. [2012] with regard to the first two of these) and further investigation is needed. In studies in which the actual structure of purported re-evolved features have been examined (e.g., Ober 2003; Kohlsdorf and Wagner 2006; Wagner et al. 2018), anatomical differences have been noted compared with the original condition. Re-evolution of entire structural complexes in their exact original configuration is generally considered unlikely (Kearney and Stuart 2004; Goldberg and Igić 2008; Wake et al. 2011).

Insights into the evolutionary assembly of the gekkotan adhesive system

The case for transition from adhesively non-competent to competent digits deep within the sphaerodactylid genus *Gonatodes* (Fig. 1A) (Russell et al. 2015; Higham et al. 2017) indicates that the initial stages of this transition, allowing the organism to interact with the environment in a fundamentally different way (Rabosky 2017), can be achieved with relatively simple alterations of setal form, scale structure, digital proportions, and phalangeal modifications. Such changes seemingly underpinned further modifications of the adhesive apparatus in other lineages, leading to exaptive radiations (Pianka and Sweet 2005; Simões et al. 2016). The additional anatomical shifts (Table 1) that characterize more evidently discernible toe pads of geckos are thus not necessary for the establishment of adhesive competency, which is accommodated with relatively unchanged locomotor kinematics. Such evidence lends support to arguments for more than a single origin of toe pads within the Gekkota. Furthermore, digit form in various lineages of geckos lacking toe pads suggests that other taxa might exhibit adhesive competence in a similar fashion to that of *Gonatodes humeralis* (Russell et al. 2015; Higham et al. 2017). Among others, the gekkonids *Cnemaspis littoralis*, *Cnemaspis quattuorseriatus*, *Cyrtodactylus khasiensis*, *Cyrtodactylus novaeguineae*, *Cyrtodactylus brevipalmatus*, and the sphaerodactylid *Quedenfeldtia trachyblepharus* (Fig. 4) exhibit morphology suggestive of this possibility. Such morphological trends are clearly evident in the digits of the Melanesian radiation of *Cyrtodactylus* (Oliver et al., 2012; Fig. 2).

Our analysis reveals a commonality of basic functional organization (Table 1) of toe pads and their associated mechanisms that relate to the employment of a reversible adhesive and its integration with lizard locomotor mechanics and kinematics. Following the establishment of these basic attributes (Frazzetta 1982), various lineages embellished them in similar, but not identical, ways (Desutter-Grandcolas et al. 2005). The underlying similarity of these basic components is seemingly related to the manner in which directionally-oriented adhesive setae must operate in attachment and detachment (Autumn 2006; Tian et al. 2006; Peattie 2009; Gillies and Fearing 2011; Cheng et al. 2012). Indeed, lizard digits are inherently directionally-organized tensile structures, and it is onto this fundamental organizational plan that the adhesive apparatus has been superimposed. The tensile loading characteristics, structural modifications, close surface contact, and hyperextensive release attributes associated with digits are also encountered in the adhesively-competent tail tips of geckos (Tornier 1899; Bauer 1998), which are sporadically distributed across the Gekkota (in several genera of the Diplodactylidae; the sphaerodactylid *Eulpetes*; and the gekkonid genera *Lygodactylus* and *Urocotyledon*—Bauer 1998). Thus, tail tips, as well as digits, exhibit independent origins of adhesive competence in different parts of the tree.

Structurally relatively simple patterns of expression of the adhesive apparatus (Fig. 3, branches 4, 8A, 8B; Table 1) are yet to be explored kinematically to determine whether they exhibit the distoproximal pattern of digital hyperextension seen in geckos with anatomically more complex adhesive toe pads (Russell 1975; Russell and Higham 2009), or employ proximodistal hyperextension, similar to that seen in *Anolis* (Russell and Bels 2001) and *G. humeralis* (Higham et al. 2017). Such observations are needed to explore potential functional differences between variants of digital structure. Furthermore, Table 1 reveals that *Anolis* exhibits only five of the character state changes that, in various combinations, characterize gecko toe pads. These relate to the structure of the phalanges and the association of the lamellae (scansors) with the lateral digital tendons. No specialized muscular or other modifications encountered in pad-bearing phyllodactylid or gekkonid geckos (Fig. 3, branches 10A, B, 11A, B; Table 1) are evident in *Anolis* (Russell 2017; Russell and Eslinger 2017), and the extent of their morphological “sophistication” resembles more closely that displayed by pad-bearing sphaerodactylid geckos (Fig. 3, branches 8A, 8B; Table 1), especially that of the *Aristelliger* lineage (Fig. 3, branch 8A; Table 1). Indeed, toe pad expression in *Anolis* is not structurally greatly different from that of the incipiently-padded sphaerodactylid *G. humeralis* (Russell et al. 2015). Locomotor kinematics relating to toe pad application and release are also similar in *Anolis* and *G. humeralis* (Russell and Bels 2001; Higham et al. 2017), indicating that what is necessary and sufficient for the carrying out adhesive attachment and release has been achieved with only relatively minor modifications of the digits and locomotor kinematics.

Collectively changes in the above-mentioned characters (Fig. 3 and Table 1) are suggestive of sequential stages (Frazzetta 1982; Lee 1996; Deméré et al. 2008) in the elaboration and further modification of adhesively competent toe pads and their associated operating mechanisms. Phalangeal modifications, including the loss of the large posteroventral flexor processes (character I, Fig. 3; and [Supplementary Document S2](#)) and depression of the intermediate phalanges (character H, Fig. 3; and [Supplementary Document S2](#)) precede other changes in the morphology of the digits and are evident in at least one species of the sphaerodactylid genus *Gonatodes* (Russell et al. 2015), where they are integrated with a relatively unchanged pattern of locomotor kinematics (the absence of distoproximal digital hyperextension) that permits reversible adhesive attachment allowing controlled movement on smooth, low-friction, vertical surfaces (Higham et al. 2017).

Arching of the penultimate phalanx (character M, States 1 and 2, [Supplementary Document S2](#)) occurs early in the transition to recognizable toe pads (Fig. 3 and Table 1), and is associated with a flattening of the more proximal region of the digits, resulting in the loss of the digital inflection (Fig. 4A, D, F; character B, and [Supplementary Document S2](#)) and relative lengthening of the proximal part of the digits (Russell et al. 2015). The arching of the penultimate phalanx results in a modified means of raising the distal part of the digits,

including the claws, above the substratum (Fig. 4A, D, F), allowing the claws to make effective purchase while accommodating associated morphological shifts of the depression of the proximal region of the digits (Peterson 1983). This feature is carried through most of the pad-bearing lineages ([Supplementary Document S2](#)).

Associated to some extent with changes in the form of the penultimate phalanx is the connection of the lateral digital tendons to the ventral digital scales, which become hypertrophied into scansors (Rosenberg et al. 1992; Alibardi 1997; Khannoon 2015; Russell et al. 2015; van der Vos et al. 2018). Their association with the lateral digital tendons integrates the tensile control of the emergent scansors (Russell 1986) with the application of frictional adhesive force associated with setal attachment (Tian et al. 2006).

The suite of features (characters T, U, V, Z, AD, AE—Fig. 3; Table 1; and [Supplementary Document S2](#)) that, in modified form, characterize the various lineages of pad-bearing taxa in the Phyllodactylidae and Gekkonidae (Fig. 3 and Table 1) seemingly relate to the enhancement of promotion of contact of the setal tips with the substratum (T, U, V; [Supplementary Table S2](#)), and to the muscular features (Z, AD, AE; [Supplementary Table S2](#)) necessary for driving distoproximal hyperextension of the digits. These are not universal among pad-bearing taxa (Fig. 3 and Table 1) and indicate that aspects of finer control have embellished the features that are minimally necessary and sufficient for enabling adhesion-assisted locomotion (Russell et al. 2015). Beyond this the operational boundary conditions relating to setal attachment and detachment (Tian et al. 2006) appear to limit the overall disparity and morphological variation expressed along multiple evolutionary pathways (Bock 1959) leading to gecko adhesion. As for several other taxa (Dean et al. 2007; Konow et al. 2008; Ord et al. 2015; Büscher et al. 2018), these variants have basic functional equivalence (Young et al. 2007; Wake et al. 2011) expressed within a functionally stable region of morphospace (Martinez and Sparks 2017), although they may have quite different performance capabilities. Clinging performance (Irschick et al. 1996) and locomotor performance and versatility are not necessarily directly correlated. Kinematic analysis of a wider range of adhesively-competent geckos negotiating low-friction surfaces is needed to explore this relationship.

Beyond the origin of toe pads (basal-type pads, as discussed above) there is evidence of transition between visibly-recognizable toe pad types. Terminally-situated leaf-like pads appear, in several (but not all) instances to have been derived from a basally-padded configuration (Fig. 1A; [Supplementary Document S2](#)). Changes in toe pad disposition may be related to the differential effectiveness of different toe pad types on substrata that provide distinctive challenges (Russell and Delaugerre 2017). Currently, however, we have a very limited understanding of the functional and ecological significance of the variants of toe pad configuration (Autumn et al. 2014).

The distribution of putatively ancestrally naked-toed taxa across the gekkotan phylogeny (Fig. 3), the inference that this is the ancestral state for the Gekkota as a whole, and the variation evident in toe pad structure (Fig. 3 and Table 1) argue for multiple origins of the gekkotan adhesive system, which is consistent with the current emergence of adhesive competency in incipient form in some gekkotan lineages (Fig. 4; see also Higham et al. 2017; Russell et al. 2015). Collectively this implies that toe pads in various gekkotan clades are non-homologous and that the presence of a spinulate Oberhäutchen layer of the epidermis is the deep homology (Russell 1979) that, under appropriate environmental stimulus, leads to the elaboration of adhesively-competent setae, followed by the expression, in various combinations in various lineages, of anatomical specializations associated with their control and deployment.

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Supplementary data

[Supplementary data](#) are available at *ICB* online.

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