



Setal Field Transects, Evolutionary Transitions and Gecko–Anole Convergence Provide Insights Into the Fundamentals of Form and Function of the Digital Adhesive System of Lizards

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Recent years have witnessed a multitude of studies focusing on gekkotan adhesion. Intense interest in this phenomenon was triggered by the discovery of the manner and magnitude of the forces generated by the hair-like filaments (setae) on the toe pads and inspired the development of the next generation of smart, reversible synthetic adhesives. Most studies pursuing these goals have concentrated on the generalized form and properties of gekkotan setae outlined in those key early studies, resulting in the fabrication of synthetic filaments of uniform dimensions. Although there are over 1,800 species of extant geckos, and hundreds of species of anoles (a separate lizard lineage that has convergently evolved adhesive toe pads), most investigations have used relatively few species as the source of basic information, the Tokay gecko (*Gekko gecko*) being the most prominent among these. Such exemplar taxa generally exhibit structurally intricate setae and morphologically complex configurations of the adhesive apparatus. Setal structure taken to be characteristic of these taxa is generally reported by singular statements of maximal length, diameter, density and branching pattern. Contemporaneous work focusing on the configuration of setae at locations across the toe pads and upon the evolutionary origin of adhesively competent digits in anoles and specific lineages of geckos, however, has revealed extensive variation of setal structure within individuals, information about how setae may have arisen from non-adhesive filamentous precursors, and how newly adhesively competent digits have been integrated into pre-existing patterns of locomotor mechanics and kinematics. Such observations provide insights into what is minimally necessary for adhesively competent digits to function and reveal the simplest configuration of components that make this possible. We contend that information gleaned from such studies will assist those seeking to employ the principles of fibrillar-based adhesion, as exemplified by lizards, for bio-inspired applications.

Keywords: *Anolis*, biomimetics, convergent evolution, fibrillar adhesion, Gekkota, synthetic adhesives

INTRODUCTION

Recent years have witnessed a deluge of studies focusing on gekkotan adhesion, a remarkable phenomenon whereby geckos can attach to, and move on, smooth, low friction surfaces using series of expanded scales (scansors or lamellae) that possess arrays of hair-like fibers (setae) carrying multiple flattened, triangular-shaped tips (spatulae) (Ruibal and Ernst, 1965; Autumn et al., 2000; Autumn et al., 2002). Intense interest in this was triggered by the discovery of the manner and magnitude of the forces generated by a single seta of the Tokay gecko (*Gekko gecko*) (Autumn et al., 2000). These revelations served as inspiration for the development of the next generation of smart, reversible synthetic adhesives. The structure and dimensions of the setae examined by Autumn et al. (2000) have become the exemplar for gecko filaments. Attempts to simulate their attributes through fabrication of synthetic fibrils have been guided by these findings.

It is sobering to realize, however, that there are over 1,800 species of extant geckos (Uetz et al., 2020), as well as hundreds of species of anoles (a separate group of lizards that has convergently evolved adhesive toe pads—see below; Poe et al., 2017). Relatively few species, however, have been employed as the source of basic information about setal structure, and those that have generally exhibit structurally intricate setae and morphologically complex configurations of the entire adhesive apparatus (Garner et al., 2020; Russell et al., 2019; Russell and Gamble, 2019). The setal structure taken to be characteristic of these taxa is usually represented by a singular statement of seemingly important dimensions: length, diameter, density and branching pattern. Collectively these oft-repeated properties have led to setal arrays being conceptualized as organized assemblages of fibrils of essentially identical configuration (Garner and Russell, in review).

Work focusing on the form of setae at locations across toe pads, and on the evolutionary origin of adhesively-competent digits in specific lineages of geckos has, however, shed light on (1) the variation of setal structure within individuals (Russell et al., 2007; Johnson and Russell, 2009; Webster et al., 2009; Russell and Johnson, 2014); (2) the manner in which setae may have arisen from non-adhesive filamentous precursors (Russell et al., 2015; Higham et al., 2017); and (3) the way digits exhibiting the first stages of adhesive competence (in that they can support the animal during static clinging and locomotion on vertical, low friction substrata) have been integrated into pre-existing patterns of locomotor mechanics and kinematics (Russell et al., 2015; Higham et al., 2017). More recently, similarly-focused investigation of the structure of setae and the configuration of the adhesive apparatus of anoline lizards have provided insights into which structural and functional attributes are shared with geckos (Garner et al., 2020), thereby enhancing our understanding of which features appear to be of fundamental mechanical importance for the operation of a digit-based adhesive system. We contend that information gleaned from such studies can be of assistance to those seeking to adapt the principles of fibrillar-based adhesion of lizards for technological applications by revealing what is minimally necessary and

sufficient for adhesively competent digits to function. Recognition of such attributes should help to simplify the pathway to the development of effective synthetic setae and mechanical mechanisms to operate them (as assessed against the performance of the actual structures being mimicked). As Niewiarowski et al. (2016) note, “no synthetic mimic can yet perform as well as a gecko”.

TRANSECTS OF SETAL FIELDS

Large numbers of publications dealing with the attributes of the adhesive setae of geckos provide information about their dimensions and morphology (**Table 1**). Parameters such as setal length, diameter, density, and spatular width and length have been documented. There is, however, considerable inconsistency in such reports (**Table 1**), this perhaps being attributable to the actual variation expressed between setae, both within and between species (see below). Generalizations about the numbers of terminal branches (hundreds to thousands) that setae bear also abound. Collectively these reports provide little in the way of insight into which of these features are particularly important, or why they should be so. Comparative observations between species (**Table 2**) intimate that there are species-specific differences in setal structure (Peattie, 2007), with even closely-related species seemingly exhibiting quite different dimensional properties (**Table 2**—see the data for the three species of *Gekko*). Questions arise, therefore, as to what this enormous variation might mean and what aspects of it, if any, might be critical for the development of artificial simulacra.

The sources cited in **Tables 1** and **2** (apart from Ruibal and Ernst, 1965) do not mention the location on the toe pad from which the exemplar setae were sampled (scansors closer to or farther from the toe tip) and give little or no information about whether setal features vary predictably along the toe pads. Transects along the entire length of toe pads, however, reveal that variation of setal length, basal diameter and stalk density is extensive within individuals of a given species (**Figures 1–4**), and that this variation is regularized and predictable both along the length of the entire toe pad, as well as locally along the length of each scansor (Russell et al., 2007; Johnson and Russell, 2009; Webster et al., 2009; Russell and Johnson, 2014). There are similarities in the patterns evident in the transect data of the setal fields of *Chondrodactylus bibronii* (**Figure 1**) and *Gekko gecko* (**Figures 2–4**), with the lengths of the setae decreasing from distal to proximal along the length of each scansor and along the length of the toe pad as a whole, and with the setal stalk diameters (and thus the aspect ratio of the setae) changing in a regularized fashion (**Figures 1** and **2**). There are also notable differences between *C. bibronii* and *G. gecko* with regard to setal and stalk diameters, with the setae of the former increasing in diameter from distal to proximal on each scansor (**Figure 1**) and those of the latter doing the opposite.

The extent of the variance of setal form and stalk density within a single species becomes more poignant when compared to the single seta statements for other species. Variation in setal length, basal diameter and stalk density of *Chondrodactylus bibronii* (**Figure 1**) when compared to those parameters reported by Peattie (2007) for eight other species of gecko

TABLE 1 | Data reported for setal dimensions for geckos in general and for *Gekko gecko*, indicating the variability in the values. For *Gekko gecko*, which has been used extensively in research focusing on gecko adhesion, the values reported span large ranges but generally are not accompanied by information as to where on the toe pad the measurements were taken from. Apart from a few early investigations, most of the values reported are taken from papers published between 2005 and 2016.

Setal length (μm)	Setal basal diameter (μm)	Setal density (mm ⁻²)	Spatula width (μm)	Spatula length (μm)
Geckos				
20–100 ²⁸	1–2 ²⁸		0.2 ^{8,24,31}	0.5 ^{6,7}
30–120 ^{10,30}	1–5 ²³		0.2–0.3 ^{6,7,18}	
30–130 ^{6,7,11,16}	5–10 ^{6,7}		0.2–0.5 ^{11,13}	
80–120 ¹²	20 ²⁴			
100 ²³				
110 ²⁹				
<i>Gekko gecko</i>				
30–130 ^{1,20,25}	1–2 ²	5300 ²⁷	0.1 ²⁷	0.2 ^{3,4}
80–100 ²⁶	2.5 ¹⁸	14000 ⁶	0.1–0.2 ²⁵	0.3 ⁹
90 ²²	3–5 ¹⁹		0.2 ^{4,5,9,15,17,19,21}	
110 ^{3,4,15}	4.2 ^{3,9,15}		0.2–0.5 ^{1,20}	
120 ⁹	5 ⁴			
	5–10 ²⁵			
	10 ²²			

The sources of the data are indicated by superscript numbers in the table and refer to the following publications: ¹Alexander (2006); ²Allibardi and Toni (2005); ³Autumn and Gravish (2008); ⁴Autumn and Hansen (2006); ⁵Autumn et al. (2006); ⁶Bhushan (2007); ⁷Bhushan and Sayer (2007); ⁸Kellar and Bogue (2008); ⁹Chen et al. (2008); ¹⁰Dalla Valle et al. (2007); ¹¹Del Campo and Arzt (2007); ¹²Dellit (1934); ¹³Filipov and Popov (2006); ¹⁴Gao et al. (2005); ¹⁵Gravish et al. (2008); ¹⁶Hallahan et al. (2008); ¹⁷Hansen and Autumn (2005); ¹⁸Hiller (1968); ¹⁹Huber et al. (2005); ²⁰Hui et al. (2007); ²¹Lee et al. (2007); ²²Maderson (1964); ²³Niewiarowski et al. (2016); ²⁴Northen et al. (2008); ²⁵Pugno and Lepore (2008); ²⁶Rizzo et al. (2006); ²⁷Sun et al. (2005); ²⁸Toni et al. (2007); ²⁹Yao and Gao (2006); ³⁰Yu et al. (2006); ³¹Xu et al. (2015).

TABLE 2 | Data ranges furnished by (1) Ruibal and Ernst (1965), (2) Schleich and Kästle (1986) and (3) Bauer (1998) for setal dimensions of individual species of geckos.

Species	Family	Setal length (μm)	Setal basal diameter (μm)	Setal density (mm ⁻²)	Source
<i>Amalosa lesueurii</i>	Diplodactylidae	17+	1.5–3+	150,000	(2)
<i>Bavayia cyclura</i>	Diplodactylidae	32*+	1.3+	429,000	(3)
<i>Bavayia sauvagii</i>	Diplodactylidae	31*+	1.5+	335,000	(3)
<i>Correlophus sarasinorum</i>	Diplodactylidae	36*+	1.3+	134,000	(3)
<i>Dactylocnemis pacificus</i>	Diplodactylidae	17.5–20+	1.5+	200,000	(2)
<i>Dactylocnemis pacificus</i>	Diplodactylidae	17+	1.5+	280,000	(3)
<i>Eurydactyloides vieillardii</i>	Diplodactylidae	19+		363,000	(3)
<i>Naultinus elegans</i>	Diplodactylidae	15+	0.8	621,000	(3)
<i>Naultinus rudis</i>	Diplodactylidae	21+	0.8	490,000	(3)
<i>Pseudothecadactylus lindneri</i>	Diplodactylidae	37*+	1.2+	142,000	(3)
<i>Rhacodactylus auriculatus</i>	Diplodactylidae	38*+		172,000	(3)
<i>Toropuku stephensi</i>	Diplodactylidae	17+	0.8	458,000	(3)
<i>Woodworthia maculata</i>	Diplodactylidae	13+	0.6	342,000	(3)
<i>Chondrodactylus bibronii</i>	Gekkonidae	96*+	3.5*+	16,000*	(2)
<i>Hemidactylus bouvieri</i>	Gekkonidae	10–50+	1.5–2.5+	110,000	(2)
<i>Gekko gecko</i>	Gekkonidae	75–108+ 30–130+	3–4.5*+2.2–4.7*	14,400*	(2)
<i>Gekko kuhli</i>	Gekkonidae	24–91+			(2)
<i>Gekko vittatus</i>	Gekkonidae	37–78*+	3.5*+	25,600*	(2)
<i>Tarentola caboverdiana</i>	Phyllodactylidae	27–68+	4–4.5*	26,000*	(2)
<i>Thecadactylus rapicauda</i>	Phyllodactylidae	50–60*+	1.8+	6,000	(2)
<i>Aristelliger praesignis</i>	Sphaerodactylidae	46–57*+	1.3+		(1)
<i>Sphaerodactylus cinereus</i>	Sphaerodactylidae	10–65			(1)

Values that fall entirely within the ranges of setal dimensions reported for *Chondrodactylus bibronii* in **Figure 1** are denoted by an asterisk (*), and those that fall entirely within the ranges of setal dimensions reported for *Gekko gecko* in **Figure 2** are denoted by a plus sign (+).

(encompassing representatives of three families, each of which has independently evolved adhesive toe pads—Russell and Gamble, 2019), reveals that the majority of the variation reportedly encompassed by these eight species (Peattie, 2007) is subsumed within the range of variation displayed by *C. bibronii*. The same is true (even more so) for the setal length and setal stalk diameter variation shown by *Gekko gecko*

(**Figure 2**). Further evidence of this overlap of setal dimensions between *C. bibronii*, *G. gecko* and other species of gecko is evident from the data compiled by Ruibal and Ernst (1965) and Schleich and Kästle (1986), as presented in **Table 2**.

Although the clinging performance of whole animals (Irschick et al., 1996) has been correlated with toe pad area, it is evident from transect surveys of the toe pads that setae in different

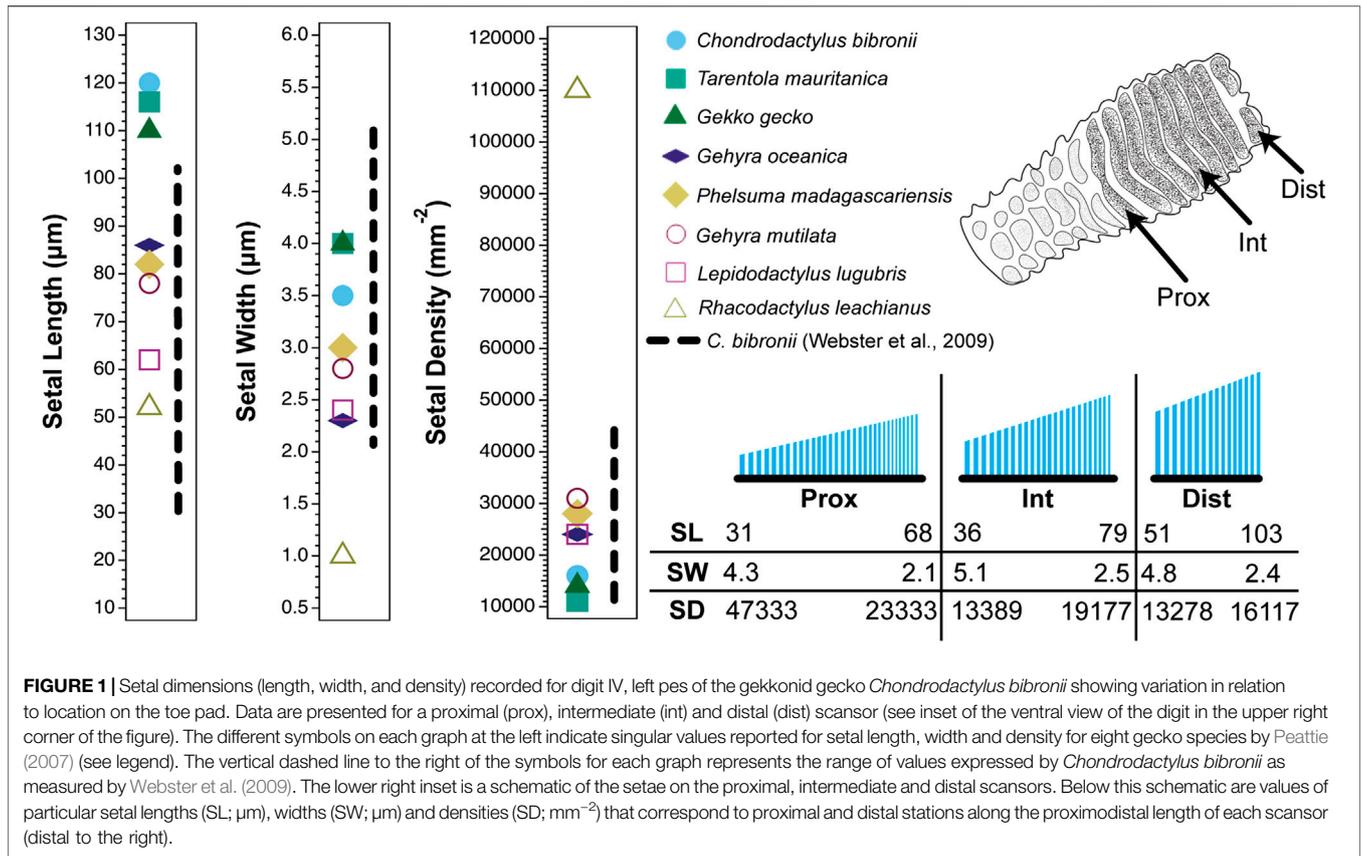


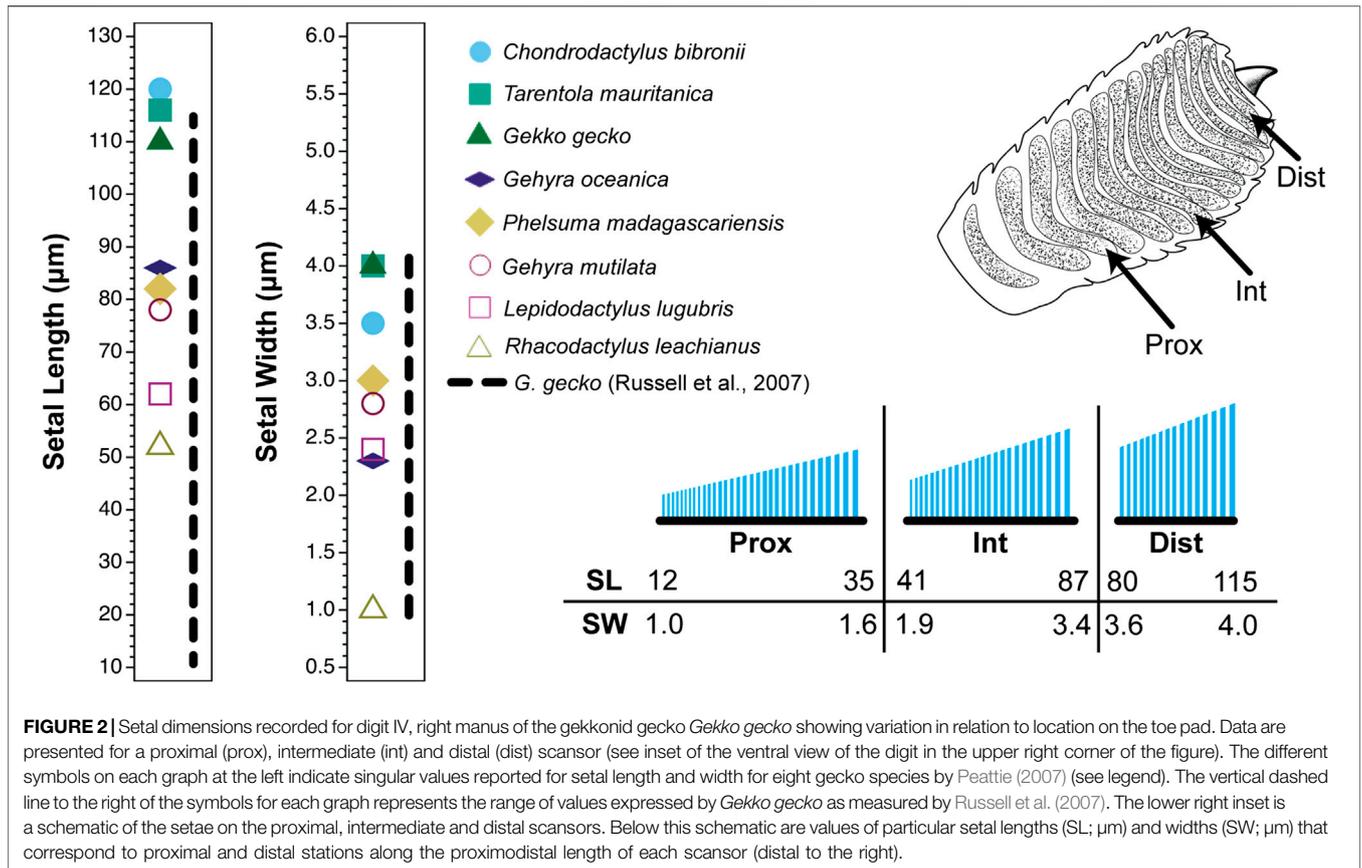
FIGURE 1 | Setal dimensions (length, width, and density) recorded for digit IV, left pes of the gekkonid gecko *Chondrodactylus bibronii* showing variation in relation to location on the toe pad. Data are presented for a proximal (prox), intermediate (int) and distal (dist) scensor (see inset of the ventral view of the digit in the upper right corner of the figure). The different symbols on each graph at the left indicate singular values reported for setal length, width and density for eight gekko species by Peattie (2007) (see legend). The vertical dashed line to the right of the symbols for each graph represents the range of values expressed by *Chondrodactylus bibronii* as measured by Webster et al. (2009). The lower right inset is a schematic of the setae on the proximal, intermediate and distal scensors. Below this schematic are values of particular setal lengths (SL; μm), widths (SW; μm) and densities (SD; mm^{-2}) that correspond to proximal and distal stations along the proximodistal length of each scensor (distal to the right).

locations differ in aspect ratio (and therefore bending stiffness) (Figures 1 and 2) and the number of spatulate tips that the setae carry (Figure 4) (Russell et al., 2007). For *Gekko gekko*, the most proximal fibrils recognizable as true setae (with spatulate tips) are carried on scensor/lamella numbers 14 and 15 (Figure 4H,I). These bear relatively few tips (Figure 4H,I) (certainly not the hundreds to thousands typically stated to characterize the setae of this species). They are relatively short and range down to less than 25 μm at the proximal ends of these plates (Figure 3E). Bending stiffness and the number of adhesive contacts likely directly influence adhesive force production, thus we find it probable that setae from various regions of the toe pad differentially contribute to total adhesive force capacity. In addition to variability in dimensions, fibrillar outgrowths on the subdigital surface of gecko vary considerably in form. The 16th subdigital plate (Figure 4J) of *Gekko gekko* bears filaments that are short, bifid at their distal tips and lack spatulae. Such forms may very well be capable of generating considerable van der Waals interactions, but whether such interactions are capable of supporting whole animal attachment and locomotion is not known.

Beyond the setae themselves, the data summarized in Figure 4 for the Tokay gecko indicate that there are major differences in the surface area of the individual scensors/lamellae that make up the toe pad, with this increasing from distal to proximal. If all

setae are idealized as identical structures along the length of the toe pads, this would suggest that those scensors with the greatest surface area contribute a proportionally greater amount of the total adhesive force available to the digit. Average setal tip width and average setal tip area gradually decrease from distal to proximal along the length of the toe pad, however, as does total setal tip area. Together with changes of setal density and setal stalk diameter along the length of the toe pad (Figures 1 and 2), the variation of setal structure along the digital transect is bewilderingly complex. What this means for the potential generation of adhesive force at any station within the toe pad is unknown. It is evident, however, that bringing setae into close enough contact with the locomotor substratum to enable them to generate van der Waals and frictional adhesive attachment will be restricted to certain patches on any given footfall (Russell and Johnson, 2007; Russell and Johnson, 2014) rather than the entirety of the toe pad creating such engagement. It is possible that there is compensatory tradeoff along the length of the toe pad with regard to setal dimensions and configuration such that each localized area has the same potential for adhesive force generation (Russell et al., 2007), but we know nothing about the relative force generation attributes of these different setal configurations.

Such patterns of variation have consequences for the way in which we conceive and design simulacra of setae. Our understanding of the adhesive capacity of individual setae is



based upon a single set of observations of filaments taken from an undisclosed part of a digit (Autumn et al., 2000). These observations have neither been repeated for setae with other configurations in the same species, nor for those from other species. There is still much to learn about the mechanical properties of gecko setae and it is unlikely that the single available set of observations (Autumn et al., 2000) suffices to explain the properties of all observed configurations. The current perception of the total clinging ability of a single digit of the Tokay gecko (*Gekko gecko*), as extrapolated from multiplying the adhesive force of a single (idealized) seta (Autumn et al., 2000) by the stated number of setae carried on such a digit (Sun et al., 2005; Autumn et al., 2006; Tian et al., 2006; Hui et al., 2007) is likely a considerable overestimate. Whole animal observations of clinging force per digit result in performance values lower by an order of magnitude or more (Irschick et al., 1996; Autumn et al., 2000, 2002; Autumn and Peattie, 2002). The discrepancy between these two approaches may reside, to some extent in the variability of the number of spatulate tips per seta along the length of the toe pad (Figure 4), differences in setal density at different stations on the toe pad (Figures 1–3), and the number of setae actually making contact with the surface (which may be reduced based on the surface roughness of the substratum).

There is still much to learn about how individual setae perform and how that performance relates to their structural properties. It is likely that much of this can be achieved through modeling, but

the variation must be assessed and appreciated before it can be incorporated into such models. Much of the variation seen (at least within a single species) likely relates to the functioning of the entire setal field and the way in which it is applied to and released from the substratum. It is the entire setal field upon which the animal relies to ensure that, upon each footfall, sufficient contact is made to ensure effective attachment. A deeper understanding of the local regional variation in structure of the setae and their patterning into fields is required for more effective (and purpose-specific) fields of artificial biomimetic fibrils to be developed (Russell et al., 2019). Finding ways of simplifying such surveys of variation is paramount and we here turn to taxa that exhibit, within their ranks, evolutionary transitions from non-adhesively to adhesively competent digits. Such transitions offer the promise of determining what is minimally necessary and sufficient for a functional digital adhesive system to become incorporated into the pre-existing locomotor mechanics of lizards.

EVOLUTIONARY TRANSITIONS

The gekkotan adhesive system has been both gained and lost on multiple occasions (Gamble et al., 2012; Gamble, 2019). Although geckos are widely known for their possession of adhesive toe pads, somewhere in the region of 40% of the 1800+ living species lack them. Peattie (2008) opined that the discovery of “an extant

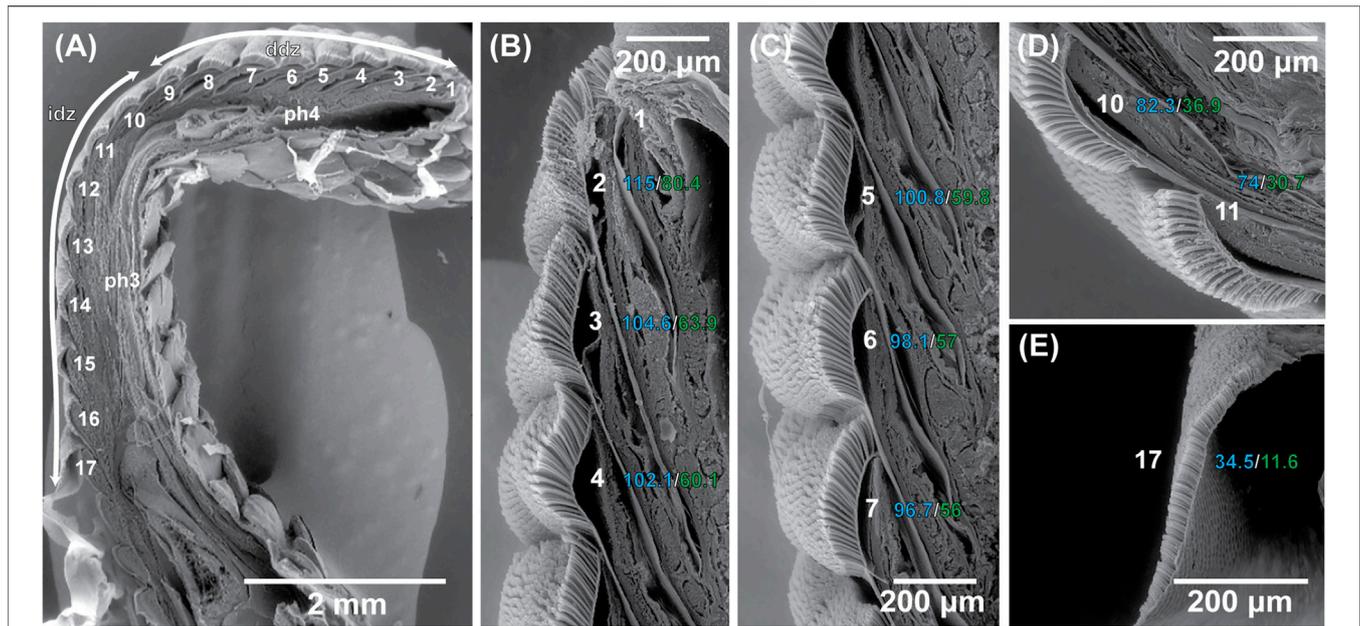


FIGURE 3 | Scanning electron microscopic visualization of the sagittally-sectioned fourth digit of the right manus of the Tokay gecko, *Gekko gekko*. **(A)** Visualization of the entire toe pad showing the location and relative dimensions of the scansors and lamellae (numbered sequentially 1–17 from distal to proximal). The distal region of the digit (ddz) carries a series of scansors (1–9) that lie beneath the fourth phalanx (ph4). The intermediate region of the digit (idz) carries a series of scansors and lamellae (10–17) that lie beneath phalanx 3 (ph3), the transition from scansor to lamella occurring between plates 13 and 14. Lamellae are distinguished from scansors by not being served by branches of the lateral digital tendon system. Panels **(B)–(E)** depict enlargements of the individual scansors and lamellae, showing the relative lengths of the plates and the configuration of the fields of setae carried on their outer surfaces. On each plate the lengths of the filaments decrease from a maximum at the distal end to a minimum at the proximal end, and from distal to proximal along the toe pad the lengths of the filaments decrease, although there is overlap of the span of lengths between adjacent plates. For plates 1–7, 10–11, and 17 maximum filament length (in μm) is indicated in blue and minimum filament length (in μm) in green. Data from Russell et al. (2007).

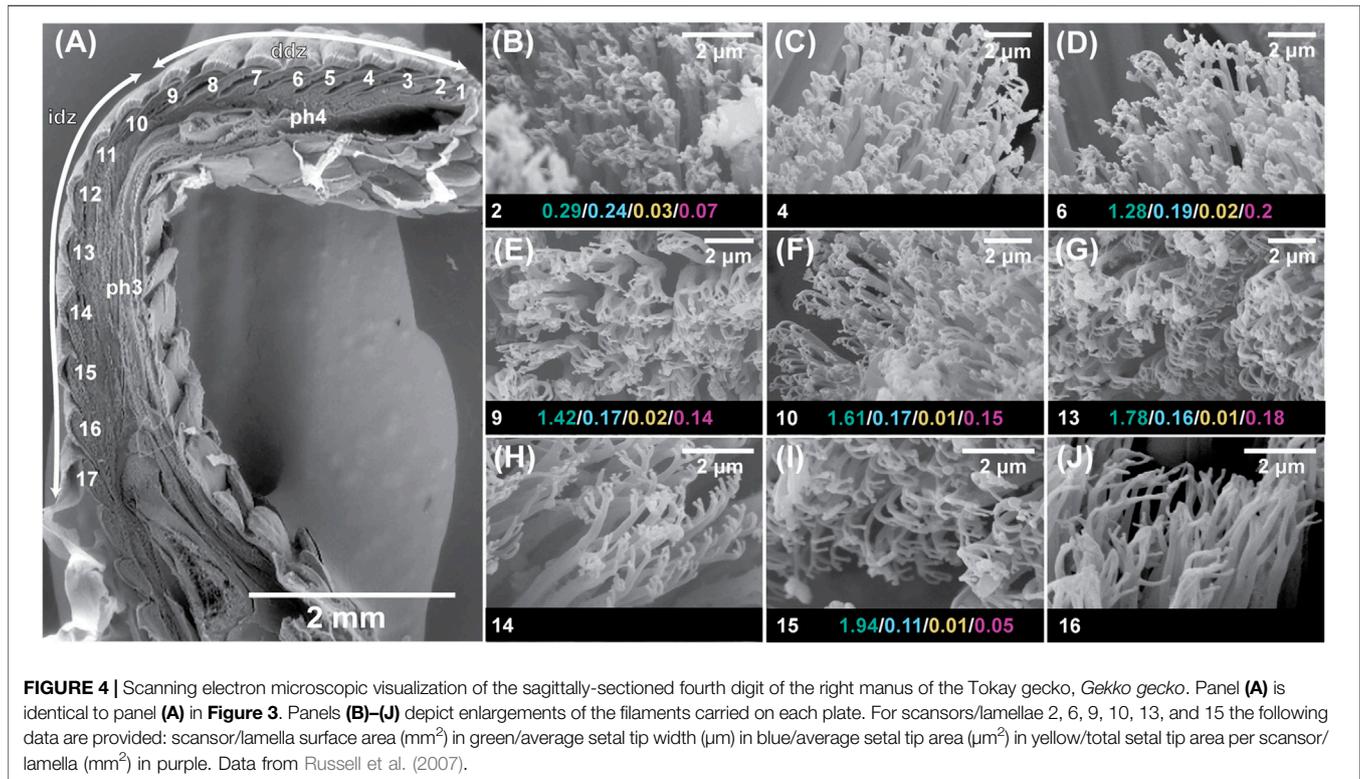
intermediate” would greatly enhance our understanding of how the gekkotan adhesive system arose. Russell and Gamble (2019) identified a number of candidate taxa for exhibiting such a transition, but only the genus *Gonatodes* has been studied in detail in this regard (Russell et al., 2015; Higham et al., 2017).

Examination of the setal fields of *Gekko* (see above), reveals that the simplest of its spatulated setae are relatively short and subdivided into few terminal branches (Figure 4H). We do not know how effective these are in contributing to the total adhesive effectiveness of that species. We do know, however, that the relatively short, sparsely-branched setae of *Gonatodes humeralis* (Russell et al., 2015) are sufficiently developed and numerous to permit support of its own body mass at rest and during steady vertical locomotion on a low-friction substratum (Higham et al., 2017). Equivalent locomotor capabilities are not present in any of its close relatives (Higham et al., 2017). Thus, *Gonatodes* provides the opportunity, using appropriate phylogenetic comparison and the establishment of evolutionary polarity (Russell et al., 2015), to establish what might be the minimal set of modifications for the emergence of a functioning digital adhesive system that is effective at the whole organism level.

Trends in digit evolution within the genus *Gonatodes* are depicted in Figure 5, which shows the pertinent digital features of three exemplar species. *Gonatodes ocellatus* has digits that are elongate and slender with a marked inflection,

beneath which reside enlarged friction plates (Figure 5A–C). *Gonatodes vittatus* (Figure 5F–H) has relatively shorter digits with a less marked inflection, fewer ventral scales, and a flatter proximal portion. *Gonatodes humeralis* (Figures 5L–N) lacks a marked digital inflection and bears noticeably enlarged scales at the base of the digits. Full details of the morphological features of the digits of these three species are provided by Russell et al. (2015). The salient points of the transition to adhesive competence constitute a correlated suite of small shifts leading to the rather dramatic functional outcome of whole animal adhesive competency (Higham et al., 2017).

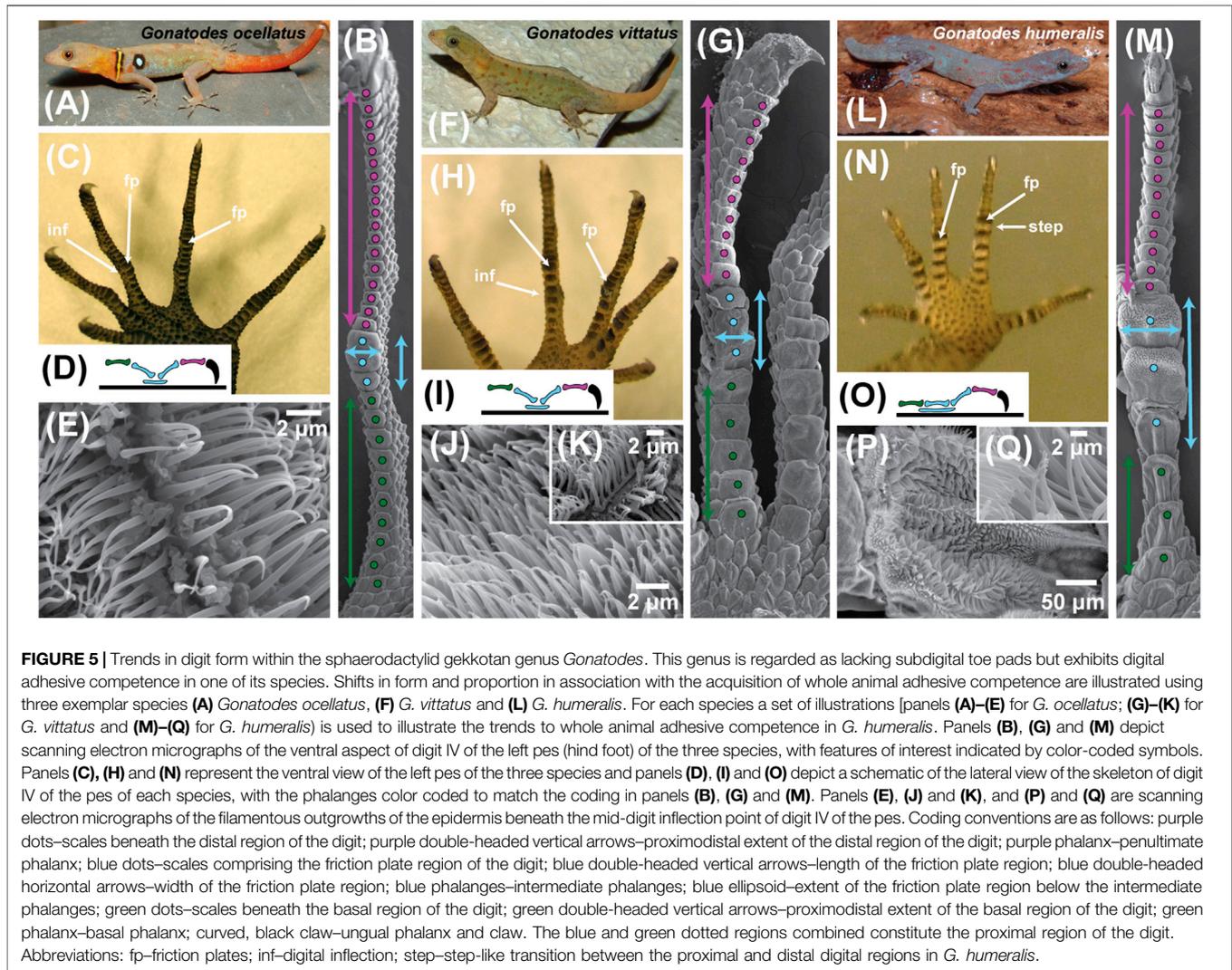
In the shift from strongly inflected digits, in which friction plates at the midpoint of the digit (Padian and Olsen, 1984; Russell and Bauer, 1990; Peattie, 2008) enhance traction (Figures 5A–C and 6A–D), to the adhesively-competent digits of *G. humeralis* (Figures 5L–N and 6E,F), the digits become relatively shorter (in relation to overall body size; Figure 5A,C,F,H,L,N). This shift is associated with a change in the relative proportions of the proximal and distal regions of the digits (Figure 5B,G,M) and a greater discrepancy in size between the scales on the underside of the digits in their proximal and distal regions (Figures 5B,G,M and 6A,C,E). Those of the proximal zone become relatively larger (both longer and wider), markedly fewer in number and exhibit greater overlap between successive scales (Figure 5B, 5G, and 5M). The relative



enlargement of the subdigital scales is particularly evident for the friction plates (Padian and Olsen, 1984; Russell and Bauer, 1990) (Figures 5B,G,M and 6C,E) that lie beneath the digital inflection (labeled “inf” on Figures 5C,5H and 6C). In *G. humeralis* (Figure 5M), this enlargement is accompanied by a flattening of the proximal part of the digit such that all of the scales on the underside of the proximal region (Figure 5M) are co-planar and contact the substratum as a continuous strip. The inflection of the digit thus shifts from a “v”-like configuration when viewed in profile (Figure 5D,I) to a step (Figure 5N,O and 6E).

Within the digits, the changes in digital proportions and configuration are accompanied by changes in the arrangement of the phalanges. The basalmost phalanx (Figures 5D,I,O and 6C,E) increases in relative length whereas the penultimate phalanx (Figures 5D,L,O and 6C,E) becomes relatively shorter. The intermediate phalanges (Figures 5D,L,O and 6C,E) retain their relative proportions but become reoriented such that the proximal one becomes linearly aligned with the proximalmost phalanx (Figures 5D,L,O and 6E) and the distal one becomes more vertically-oriented, resulting in the “v”-like configuration of these two phalanges (Figures 5D and 6C) transforming into a step (Figures 5O and 6E). This transition is associated with a proximal extension of the friction plate area (Figures 5D,L,O and 6E) to become more extensive beneath the proximal part of the digit, resulting in the formation of an incipient toe pad (Figures 5M,N and 6E).

In all three exemplar species (Figure 5), the epidermal filaments on the underside of the toes are longest on the friction plates. In *G. ocellatus*, they are tapered spinules, the longest being about 3.2 μm in length (Figure 5E). In *G. vittatus*, the longest of these filaments are about 4.0–6.0 μm in length, with bifid tips, the split occurring at a point about two thirds of their height from the base (Figure 5K), appearing much like the filaments on the proximal lamellae of the digits of *Gekko gecko* (Figure 4). This bifurcation is thought to be associated with friction enhancement (Lange, 1931; Ruibal and Ernst, 1965; Schleich and Kästle, 1979; Peattie, 2008; Müller and Hildenhagen, 2009; Spinner et al., 2013; Russell et al., 2015). In *Gonatodes humeralis*, the lengths, diameters, spacing and form of the subdigital spinules are similar to those of *G. ocellatus* and *G. vittatus* for the scales on the underside of the distal region of the digit (Russell et al., 2015). On the incipient toe pads, however, the distally-situated epidermal outgrowths range from 10.0 to 15.0 μm in length, their density is relatively low and the spacing relatively great (Russell et al., 2015). These are true setae that are divided terminally and carry spatulate tips of about 0.12 μm wide (Figure 5P,Q). Such setae are similar in form to those on the most proximal scansors of *Gekko gecko* (Figures 3E and 4H). Unlike the latter, however, the setae on each plate are shorter distally than they are more proximally (13.0 vs 15.1 μm), a pattern also observed in *Anolis* (see below; Garner et al., 2020). The branched, spatula-bearing setae occur only at the

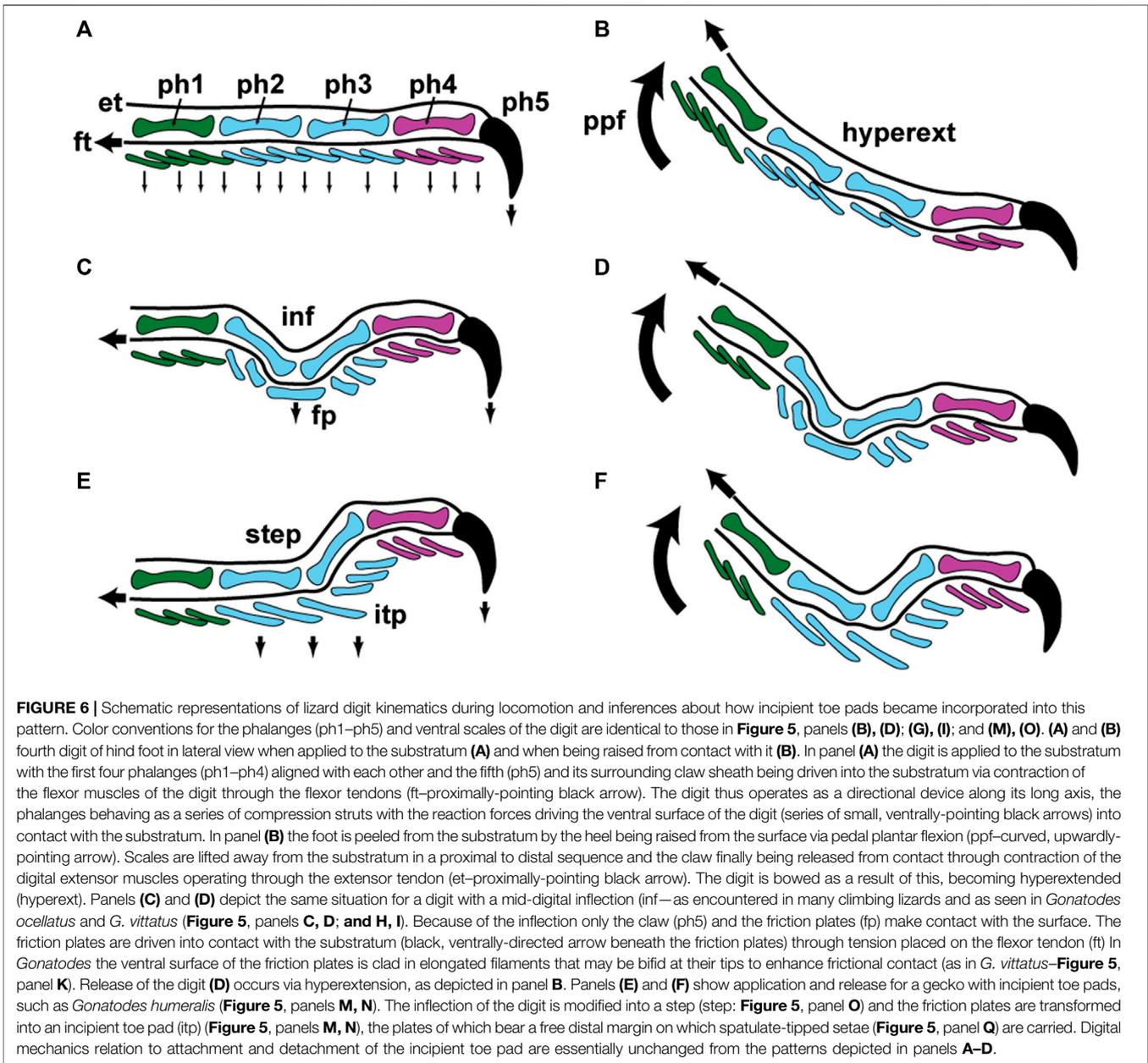


distal end of the incipient toe pad plates (Figure 5M) and give way to spinules more proximally. Transition from simple tapered spinules (there is a mixture of unbranched and branched spinules far proximally on such scales) to setae is thus evident within the confines of a single scale.

Although Peattie (2008) suggested that “true adhesive pads require complex morphological elaborations within the toe” to enable operation of an adhesive system, *Gonatodes humeralis* demonstrates that this is not so, there being no modifications of the digital musculotendinous, circulatory and skeletal systems that are generally considered to be necessary (Peattie, 2008) for the operation of a functional adhesive system in geckos. In terms of their anatomy, the seta-bearing scales of *G. humeralis* are not scansors (Russell, 2002), but instead are more akin to the basal lamellae found in many geckos. The latter bear elaborate epidermal outgrowths, but are not associated with a lateral digital tendon network (see below). The lamellae of the Tokay gecko (*Gekko gecko*) carry epidermal outgrowths that range in length from 1.2 μm at their proximal end to over 12.0 μm distally

(Russell et al., 2007: fig. 5), the latter being multiply branched and carrying spatulate tips. Thus, Tokay geckos also possess setae that are carried on highly modified scales (lamellae–Figure 3A,E) that lack the characteristics of scansors. Such scales bear a strong structural resemblance to the seta-bearing scales of *G. humeralis* and serve to support the idea of a transition from friction-enhancing to adhesion-promoting structures prior to the widening of the digits and the acquisition of features that provide the capability for actively controlling the adhesive process via distoproximal digital hyperextension (Russell and Bels, 2001).

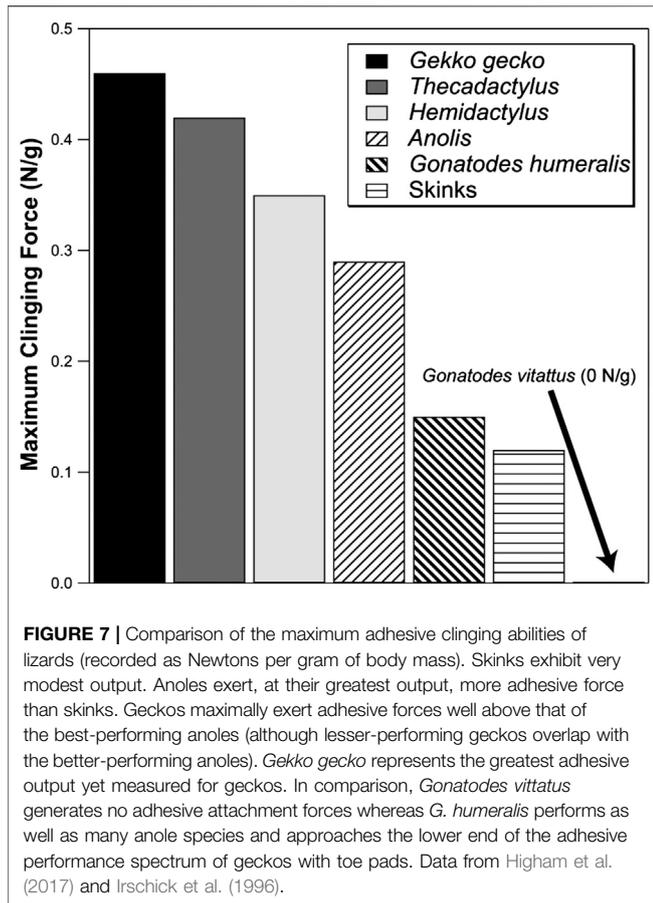
When climbing vertical, low friction substrata (Higham et al., 2017), *Gonatodes humeralis* employs limb and digit kinematics that are essentially unchanged from those of lizards in general (Brinkman, 1980; Russell and Bauer, 2008) (Figure 6A,B). The digits are placed onto the substratum and withdrawn from contact with it such that the distal ends of the digits are the last regions to be withdrawn from it. In *Gekko gecko*, the opposite occurs, enabled by the specialized musculature of the digits that



allows their distal ends to be raised from the substratum while their proximal ends remain in contact (Russell, 2002), a process known as hyperextension. When the digits of *Gekko gekko* make contact with the substratum, they do so with their proximal ends first. The distal parts, carrying the toe pads, are unfurled after this. *Gonatodes humeralis*, however, like lizards in general (**Figure 6A–D**), removes its digits from the locomotor surface by raising its heel first and rising onto the tips of the digits, thereby removing the ventral surface of the digits from contact with the substratum in a proximal to distal sequence (Higham et al., 2017). This results in hyperextension of the digits (as it does in lizards in general), and thus hyperextension is involved with

removal of the incipient toe pads from adhesive contact with the substratum (**Figure 6E and F**). This breaking of adhesive contact is accommodated within a pre-existing pattern of digit kinematics (**Figure 6**). Adhesive competence of the digits of *G. humeralis* has been subsumed into an essentially unchanged pattern of digit mechanics. Geckos with incipient toe pads provide insights into the most basic aspects of digit configuration and kinematics compatible with the deployment of an effective adhesive system that can assist locomotion (**Figure 6**).

Gonatodes humeralis, unlike other species of *Gonatodes*, can scale smooth, low friction vertically-oriented substrata (Higham et al., 2017). Although the adhesive forces generated are rather

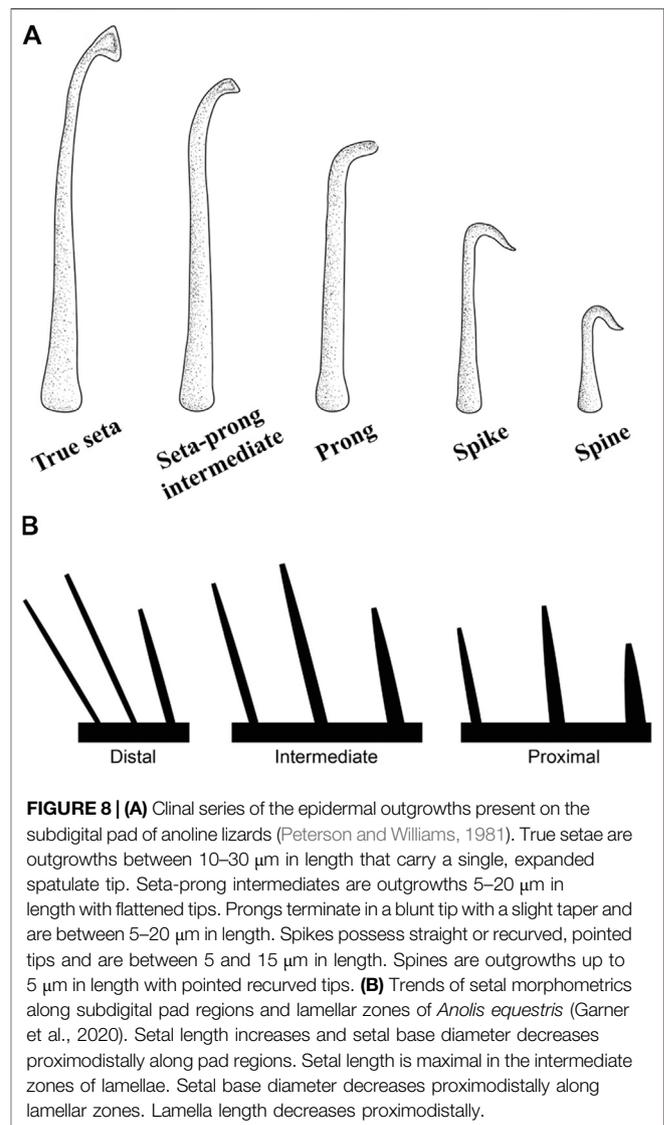


low by gecko standards, they are comparable to those generated by anoles (Figure 7). Given that the setae of *G. humeralis* are similar in form to the simplest setae of *Gekko gecko* (Figure 4H), it can be inferred that the latter are also capable of generating adhesive interactions.

To this point, we have established the following. (I) That the setae of geckos with structurally complex toe pads, such as *Gekko gecko* and *Chondrodactylus bibronii*, exhibit clinal variation in setal dimensions and form along the length of the digit, with the setae located proximally on the toe pad being relatively short and only modestly branched. (II) That similarly built setae are present on the incipient toe pads of geckos such as *Gonatodes humeralis*, which exhibits little in the way of the “complex morphological adaptations” thought to be required for the operation of an adhesive system (Peattie, 2008). The adhesive capabilities of *G. humeralis* suggest that the simpler setae occurring more proximally on the digits of *Gekko gecko* (Figure 4H,I) are also adhesively effective. These observations demonstrate that an operational adhesive system is possible in the absence of either complexly branched setae bearing “100–1,000... spatulae” (Autumn and Hansen, 2006) and complex anatomical modifications promoting attachment and detachment. We now ask (III) whether such basic levels of organization are evident in toe pads of other taxa, turning our attention to the dactyloid iguanian genus *Anolis* to explore this possibility.

GECKO-ANOLE CONVERGENCE

The evolutionary phenomenon of convergence (the independent acquisition of form and function—Kuhn et al., 2020) potentially provides evidence for determining the most fundamental attributes of complex adaptations (*sensu* Frazzetta, 1975). Independent but structurally similar “solutions” to challenges imposed by the environment provide insights into the evolutionary responses possible. The adhesive toe pads of geckos and anoles are regarded as convergent adaptations (Russell and Garner, in review), their adhesive toe pads having arisen completely independently. This provides the opportunity to examine which attributes are repeated in the two lineages and thus to attempt to establish what is necessary and sufficient for adhesively competent digits to be incorporated and integrated into the lacertilian pattern of locomotion.



Convergence of the Adhesive Fibrils of Geckos and Anoles

As in geckos, the epidermal outgrowths of the subdigital pads of *Anolis* (Figure 8A) vary considerably in form along the proximodistal axis of the digit (Figures 3–5) and five morphotypes have been recognized (Peterson and Williams, 1981): (1) true setae, outgrowths 10–30 μm in length with expanded, spatulate tips, (2) seta-prong intermediates, 5–20 μm in length with flattened tips, (3) prongs, 5–20 μm in length terminating in blunt tips with a slight taper, (4) spikes, 5–15 μm in length with straight or recurved, pointed tips, and (5) spines, up to 5 μm in length with recurved, pointed tips. All lamellae (scales bearing true setae) of *Anolis* with well-developed subdigital pads are thought to display a proximodistal clinal gradation of all 5 morphotypes (from spines to setae) on each lamella, similar to the clinal variation of epidermal outgrowths on the scales of the incipient toe pads of *Gonatodes humeralis* (Russell et al., 2015). As in gekkotans, it is the true setae and their spatulae that are responsible for the majority of adhesive force capacity in *Anolis*. In *Anolis*, however, the setae are unbranched (Ruibal and Ernst, 1965; Williams and Peterson, 1982; Stork, 1983).

A recent investigation of the morphometrics of the setal arrays of the Cuban knight anole (*Anolis equestris*), a species similar in size to *Gekko gecko*, reveals that its setae increase in length and decrease in basal diameter proximodistally along regions (proximal, intermediate, distal) of the subdigital pad (Figure 8B) (Garner et al., 2020). Within a single lamella, however, setal length is greatest in the intermediate region, whereas setal basal diameter decreases proximodistally (Figure 8B), a pattern similar to the dimensions observed on the incipient toe pads of *Gonatodes humeralis* (see above). Setal density remains relatively consistent along the entire subdigital pad and along regions (proximal, intermediate, distal) of individual lamellae.

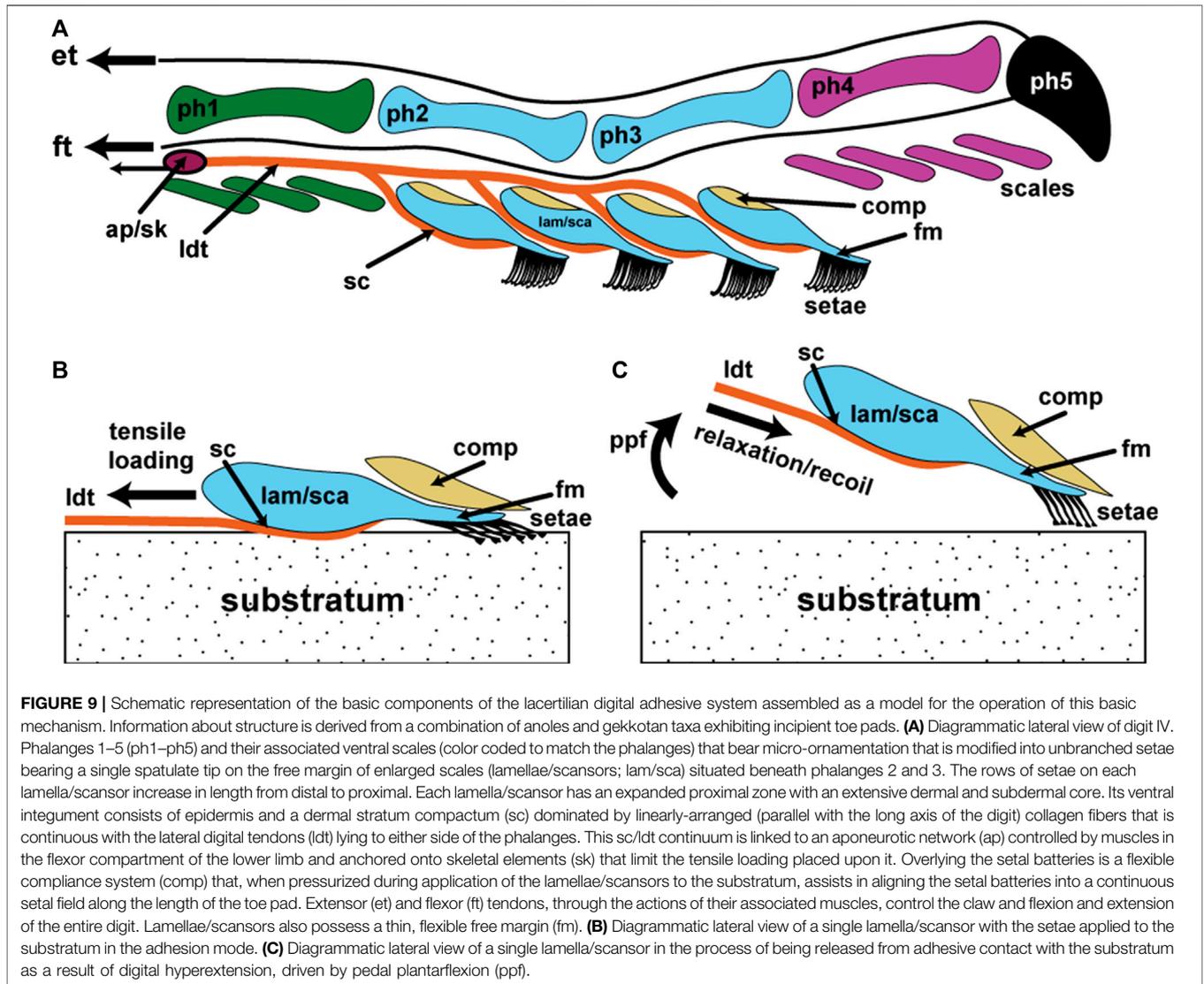
The profuse branching noted for the archetypal gecko seta (Autumn et al., 2000) should result in greater adhesive force production compared to an unbranched seta of similar size, such as those of *Anolis* (Arzt et al., 2003; Peattie and Full, 2007; Murphy et al., 2009; Garner et al., 2020). Thus, if geckos and anoles differed only in the nature of the structural hierarchy of their setae, the setal fields of gekkotans, when scaled against body mass, should be able to induce greater adhesive forces. Gekkotan and anoline setae and setal fields, however, differ not only in setal size and number of spatulae per seta, but also in the number of fibrils present per unit area (Garner et al., 2020). Indeed, when compared to setal density patterns in *Chondrodactylus bibronii*, those of *Anolis equestris* are 33.3–78 times as densely packed. Application of the Johnson-Kendall-Roberts (JKR) theory of elastic contact to the assessment of adhesive performance of gekkotan and anoline setal arrays, in conjunction with the comprehensive morphological data obtained for the setal fields of *Gekko gecko* (Russell et al., 2007) and *Anolis equestris* (Garner et al., 2020), reveal that adhesive performance of gekkotan and anoline setal arrays should theoretically be similar when taking the differences in the morphology and configuration of their

setae and setal fields into consideration. Anoles appear to compensate for the lack of structural hierarchy of their setae by possessing greater setal density compared to geckos (Garner et al., 2020), although structural hierarchy of setae may be important in other aspects of the gekkotan adhesive system (Persson, 2003; Yao and Gao, 2007). Peterson et al. (1982) also note that anoles appear to combat increased adhesive demands related to increases in body size by possessing greater setal densities. Not all geckos, however, are characterized by such densities, and the setae of *A. equestris* are only 1.75–2.5 times as densely packed as those of *Naultinus elegans*, the gecko so far examined to exhibit the highest density and shortest setae, and these are also not profusely branched (Bauer, 1998). Table 2 reveals that many diplodactylid geckos have short, slender, densely packed setae, with values greatly exceeding those for gekkonid geckos (the group to which *Chondrodactylus* and *Gekko* belong). Very little is known about the adhesive capabilities of diplodactylid geckos, although this is now beginning to be explored (Pillai et al., 2020). This again reveals that there is much more to be learned about the variation in structure and function of gekkotan setae, cautioning against making sweeping generalizations that appear to characterize geckos overall.

The above-mentioned calculations of adhesive performance of geckos and anoles, based on setal morphometrics (Garner et al., 2020), are supported by whole animal observations. Ruibal and Ernst (1965) qualitatively observed gecko and anole adhesive locomotion on a vertical raceway and noted no obvious differences in performance. More comprehensive work by Irschick et al. (1996) corroborated this finding and found that static clinging performance of geckos and anoles is not markedly different (Figure 7). The general similarity of setal form and material properties of anoles and geckos indicate the requirement for similar loading conditions (normal load followed by shear load) because measurements of whole animal adhesive performance indicate that their adhesive systems can be engaged in the same manner (Irschick et al., 1996). The means by which setal loading and unloading occurs in anoles, however, differs from that typically attributed to geckos (Russell and Bels, 2001), but is similar to that employed by *Gonatodes humeralis* (Figure 6E,F), with subdigital pad retraction progressing proximodistally (as opposed to the distoproximal pattern thought to be typical of geckos). This pattern of release of the setae is consistent with setal length increasing proximally along the length of each lamella (Figure 8B), suggesting that clinal variation in setal length is related to the biomechanics of subdigital pad peeling (Johnson and Russell, 2009; Garner et al., 2020), although further empirical work is needed to validate this.

Convergence of the Digital Anatomy of Geckos and Anoles

The anatomical modifications generally associated with the adhesive system in geckos (Peattie, 2008) are only modestly



represented by *Anolis*, being confined to skeletal (phalangeal) and tendinous features (Russell and Gamble, 2019). The digits of *Anolis* exhibit little in the way of muscular modifications akin to those exhibited by at least some gecko lineages (Russell and Gamble, 2019). *Anolis* does, however, incorporate a compliance-promoting cushioning system (Figure 9A) into its toe pads, in the form of hypertrophied lacunar cells of the epidermis (Russell, 2016). This cushioning system is unique to *Anolis* but is analogous and positionally similar to the vascular (Russell, 1981) and adipose tissue (Russell and Bauer, 1988) compliance structures found among geckos.

Modifications of the intermediate phalanges enhance both the pressing of the toe pads onto the substratum during attachment and their hyperextension during release (Figure 6E,F). The toe pads of *Anolis* are located basally on the digits, ventral to the location of the digital inflection (between phalanges 2 and 3 of digit IV) of its close relatives, in a

similar location to those of *Gonatodes humeralis* (Figures 5M,N and 6E,F). Associated with the toe pads of *Anolis* are lateral digital tendons similar to those of geckos. These course along the lateral and medial borders of the phalanges of the digit and branch to serve each lamella. As in geckos, the dense, collagen rich connective tissue of the lateral digital tendons is continuous with the stratum compactum of the dermis of the lamellae (the lamellar dermis lacking a stratum laxum). Thus, as in geckos (Russell, 1986), the lateral digital tendon/lamellar dermis complex furnishes a tensile skeleton that provides connectivity between the setae and skeleton at the metapodial-phalangeal joint capsules. This chain reinforces the junction between the integument and the underlying tissues (Russell, 1986) and permits the tensile load imposed on the setae (Peterson et al., 1982) to be channeled to points of resistance deep within the manus and pes, and to be regulated in its magnitude.

SYNTHESIS AND THE GENERATION OF A MODEL OF THE FUNDAMENTALS OF FORM AND FUNCTION OF THE DIGITAL ADHESIVE SYSTEM OF LIZARDS

Our examination of transects of setal fields constituting the toe pads of geckos, the evolutionary transition to functionally adhesive digits in the naked-toed gecko genus *Gonatodes*, and the comparison of the structure of gecko and anole adhesive systems has allowed us to deduce what we consider to represent the most basic level of organization and mechanical operation of such a system. Both setal structure, at its most elaborate, and the configuration and operation of the entire adhesive system of the Tokay gecko (*Gekko gekko*) are complex (Russell, 2002). They permit impressive feats of behavior that are assisted by the deployment of the adhesive apparatus (Autumn 2006), but are not typical of all geckos.

Examination of the variability of setal structure exhibited by several species of geckos (and anoles) across the entirety of their setal fields indicates that setae vary considerably in form and dimensions depending on the particular location on the digit (Russell et al., 2007; Johnson and Russell, 2009; Webster et al., 2009; Russell and Johnson, 2014; Garner et al., 2020). Such data indicate that there is no single morphology of setae for the toe pads of lizards bearing adhesive pads and that these parameters vary regionally, presumably reflecting the functional contribution of particular regions of the toe pads to the totality of the adhesive capabilities of the entire setal fields. A common feature, however, regardless of the particular dimensions of setae at different stations on the toe pad, is that the setae on individual scensors show gradation in length (Figures 1 and 2). In the case of *Gekko* and *Chondrodactylus*, increase in length of the setae occurs in a proximal to distal direction (Figures 1 and 2). This has been suggested to be associated with the achievement of simultaneous release of all setae on a scensor as the digit is hyperextended (Johnson and Russell, 2009). In the case of *Gonatodes humeralis* (Russell et al., 2015) and *Anolis equestris* (Garner et al., 2020), however, setal length decreases proximodistally. Interestingly, the locomotor kinematics of *Gonatodes humeralis* and *Anolis* are essentially unchanged from those typical of lizards in general, the toes being peeled from the substratum proximodistally as the ankle and wrist extend (a motion called plantarflexion) (Russell and Bels, 2001; Higham et al., 2017) (Figure 6B,D,F). Thus, a seta-based adhesive mechanism has been co-opted into a pre-existing pattern of foot and digital mechanics in both *G. humeralis* and *Anolis*.

The relatively simple setae, although still branched, at the proximal end of the setal fields of *Gekko gekko* somewhat resemble those of *Gonatodes humeralis* (Figure 5M,N). *Gonatodes humeralis* exhibits the early stages of evolutionary acquisition of adhesively-competent digits (Russell et al., 2015) and is capable of adhesively-assisted locomotion on vertical, smooth, low-friction surfaces (Higham et al., 2017). It lacks any of the major skeletal, muscular, tendinous and compliance modifications evident in the digits of the Tokay gecko (Russell, 2002), but is still able to attach and detach its adhesively-competent digits in a controlled fashion (Higham et al., 2017). The

morphological modifications that it does show are related to changes of scale size and number on the underside of the digits, alterations of in phalangeal proportions and orientation, and transformation of some of the epidermal outgrowths on the expanded scales of the incipient toe pads into setae with spatulate tips. There are no evident lateral digital tendons associated with the plates of the incipient toe pads, and it appears that tensile loading is placed upon the setae and lamellae by gravitational loading, potentially restricting the circumstances in which this rudimentary adhesive system can be engaged.

It is interesting to note that all geckos capable of supporting static and dynamic adhesion on vertical, low friction substrata, including *Gekko gekko* and *Gonatodes humeralis*, possess setae that exhibit some level of branching. Comparison of both *Gekko gekko* and *Gonatodes humeralis* with *Anolis* reveals a setal structure that is much simpler than that of *Gekko gekko* or *Gonatodes humeralis*. *Anolis* possesses unbranched setae that are relatively short and present in higher density (compared to that of gekkonid geckos—Table 2). Its clinging abilities (Figure 7) are similar to those of many geckos (Irschick et al., 1996), despite the absence of structural hierarchy that purportedly increases the adhesive capacity of a single fiber (Arzt et al., 2003; Peattie and Full, 2007; Murphy et al., 2009; Garner et al., 2020). The higher setal density of *Anolis* is thought to compensate for the lack of branching in anoline setae (Garner et al., 2020). A number of species of *Anolis* also appear to respond to the increased adhesive demands of increased in body size by increasing setal density (Peterson et al., 1982). Like *G. humeralis*, *Anolis* exhibits proximal to distal hyperextension of its digits (Figure 6) and its setae increase in length from distal to proximal on each lamella (Figure 8B), consistent with the simultaneous release hypothesis proposed by Johnson and Russell (2009). In terms of digital anatomy, *Anolis* exhibits a simpler manifestation than *Gekko*, but is more fully elaborated than that of *Gonatodes humeralis*. *Anolis* exhibits phalangeal modifications associated with application of the toe pads to the substratum and their hyperextension upon release. Beyond this it also has a lateral digital tendon system and a compliance mechanism associated with enhancing contact of the setae with the substratum.

The foregoing yields information about what is minimally necessary and sufficient for the effective operation of a lacertilian digital filamentous adhesive system. Such information should potentially be useful for simplifying approaches to the development of biomimetic derivatives. From the above-mentioned observations we can conclude that a functional adhesive system, effective at the whole animal level, can exist and operate with relatively short and unbranched or moderately branched setae, and that operational control of such a system requires only minor morphological and behavioral changes compared to lizards in general. Squamate adhesive systems do not need to be morphologically highly divergent from their ancestral non-adhesive precursors. Basic whole animal adhesive competence can be attained with relatively simple morphological and biomechanical underpinnings.

The situation evident in *Anolis* and gekkotans with incipient toe pads provides the best approximation of the necessary and sufficient components. A model for the basic functioning of a digit-based, filamentous adhesive system is presented in **Figure 9**. The presence of spatulate-tipped setae arranged in orderly ranks and rows provide the necessary adhesive interface with the substratum. Such setae do not have to be branched to be effective but must be present in sufficient numbers to enable effective support (of the animal's body mass) when using only a (potentially small) subset of them on surfaces that permit only patchy contact. If a rolling-type pattern of contact and detachment (as embodied in hyperextension of digits, whether proximodistal or distoproximal) is involved, with the filaments carried on a series of plates, then a staggering of filament length, row by row, that is geometrically integrated with the mechanics (angulation) of plate release, is needed to promote simultaneous release and attachment of the fibrils (**Figure 9**).

Digits are inherently directional devices when used to interact with the substratum during locomotion. As such they undergo tensile loading. Setae are inherently tensile (Williams and Peterson, 1982) and directional (Autumn et al., 2000) structures that require a mechanism of controllable application (**Figure 9B**) and release (**Figure 9C**) of tensile loading to exploit available attachment forces. The lateral digital tendon system of anole and gecko digits facilitates this load-bearing function (**Figure 9**). The lamellae (and scansors) bear setae that are intimately connected to such a mechanism through firm interdigitation of the epidermis with a richly collagenous, longitudinally-oriented fibrous sheet that invests the inner face of the lamella/scansor and that is continuous with the lateral digital tendons (Russell, 1986). The collagen fibers, at rest, exhibit crimp and upon loading it is likely that the crimp is straightened (**Figure 9B**), the collagenous bundles thereby shifting into their high modulus phase, preventing further extension. We suggest that the magnitude of extension allowed is tuned to the parallel preload required for the setae to be effectively adhesively engaged with the substratum (Autumn et al., 2000) and that this tensile loading is maintained until detachment is initiated. In lizards, we propose that this is accomplished by the lateral digital tendon/stratum compactum mechanism being connected deep in the foot such that constant tension can be maintained by internally regulated locking devices. We suggest that the perpendicular preload (Autumn et al., 2000) required to establish initial setal tip contact is provided by the unfurling of the hyperextended digit (**Figure 6B,D,F**), and that tension imposed through the lateral digital tendon/stratum compactum system (**Figure 9A**) places tension on the lamella/scansor and its setae, resulting in the lowering the setal angle and the bringing of the broad face of the spatulate tip(s) into contact with the substratum (**Figure 9B**). The small amount of movement required for the application of the parallel preload (Autumn et al., 2000) is likely controlled by the very limited extensibility of the lateral digital tendons/

stratum compactum. When this tension is released, the lateral digital tendons and the collagenous networks in the lamellae recoil and the crimp in the collagen fibers is restored (**Figure 9C**). This results in the setae being relieved of their tensile loading, permitting their shafts to increase their angle relative to the surface of the lamella (**Figure 9C**) and allowing them to approach their critical release angle (**Figure 9C**). This process occurs as the digit is hyperextended through actions of the extensor muscles and angular changes between the phalanges driven by pedal plantarflexion (**Figure 6B,D,F**).

Both pad-bearing anoles and geckos exhibit some sort of compliance mechanism to assist with enhancing contact with the substratum (Russell, 1981, 2002, 2017). This may chiefly assist in aligning the setal arrays on individual lamellae/scansors so that the setal field essentially forms one unified structure, with the junctions between the plates being overlain by a continuous cushioning mechanism (**Figure 9A,B**). It may also assist the setal fields to match more closely with irregularities in the substratum (Russell and Johnson, 2007). Such a compliance mechanism (differently constructed in different lineages) is a common feature of lizards with adhesive toe pads. Compliance of the setal fields with the substratum may also be assisted by the setae being carried on a relatively slender, free distal component of the lamellae/scansors (**Figure 9**). Indeed, in *Anolis*, the setae are borne on a very thin free margin that is comprised solely of epidermal tissue. The free margin of geckos is slightly more robust. In both cases, the free margin is overlain by the compliance mechanism.

CONCLUSION

The last two decades have witnessed a flood of investigations examining the form, function, and properties of the gecko adhesive system, many of them aiming, directly or indirectly, to inform the design and fabrication of the next generation of smart, reversible, fibrillar synthetic adhesives. Most of such applied research, however, has focused on relatively few species of gecko that exhibit complex manifestations of the entire adhesive apparatus, perhaps unnecessarily complicating the biomimetic process. Here we contend that studies examining setal transects of adhesive pad-bearing lizards, evolutionary transitions from non-adhesive to adhesively competent digits, and the convergent evolution of the adhesive apparatuses of geckos and anoles provide a wealth of information from which researchers may gain engineering inspiration. Specifically, these biologically focused studies collectively demonstrate what is minimally structurally necessary for an effective and functional fibrillar adhesive system that is capable of reversibly attaching to vertical, low friction substrata. We urge researchers focused on bio-inspired adhesives to consider the natural variation in both structure and function of the adhesive fibrils and their associated higher order digital anatomy exhibited by lizards with subdigital adhesive pads. Such information is likely to not only increase the available information for successful

biomimicry, but also decrease functional disparities between synthetic simulacra and their natural counterparts.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article. Further inquiries should be directed to the corresponding author.

ETHICS STATEMENT

The animal studies were reviewed and approved by the University of Calgary Animal Research and Education Executive Committee under Protocol Numbers BI2002-013, BI2008-24 for those studies completed by AR and the University of Akron Institutional Animal Care and Use Committee Protocol Number 19-07-13 NGC for those studies completed by AG.

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AUTHOR CONTRIBUTIONS

AR conceived of the approach and wrote the first draft of the paper. AR and AG developed the ideas further and contributed equally to subsequent drafts. AR developed the ideas for the figures and these were refined by AG. AR employed various aspects of his previous research on geckos and anoles to develop the synthesis of ideas and AG provided new insights into anole and gecko adhesion based upon his ongoing research.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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