

The Evolution of Digit Form in *Gonatodes* (Gekkota: Sphaerodactylidae) and its Bearing on the Transition From Frictional to Adhesive Contact in Gekkotans

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ABSTRACT Although the phenomenon of adhesion in geckos has been intensively studied for over 200 years, our understanding of how the morphological apparatus associated with this arose is less clear. Indeed, whether or not all of the intricate morphological hierarchy that is implicated in the attachment and removal of the adhesive setae originated at the same time is unknown. To explore whether setae may have arisen prior to the other parts of this structural hierarchy, we undertook morphological observations of *Gonatodes*, an ancestrally padless, sphaerodactylid genus known to exhibit the expression of incipient subdigital pads in some species. Focusing on this geographically and morphologically well-circumscribed genus, for which intraspecific relationships are adequately known and ecology is quite well documented, allowed us to deduce trends in digit proportions, shape, scalation, and skeletal structure, and associate these with the micro-ornamentation of the subdigital surfaces. Our findings indicate that in *Gonatodes*, setae capable of inducing adhesion are present without the modifications of the digital musculotendinous, circulatory and skeletal systems that are generally considered to be necessary for the operation of a functional adhesive apparatus. The acquisition of these latter characteristics (independently in many lineages of gekkotans, and incipiently so in *Anolis*) may have been preceded by a suite of modifications of the digits that enhanced static clinging in relation to sit-and-wait predation and the ability to take refuge on surfaces unavailable to other taxa. These possibilities await further testing. *J. Morphol.* 276:1311–1332, 2015.

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INTRODUCTION

Recent interest in gekkotan adhesion has been driven by two major influences: as a vehicle to help understand the evolution of functional complexes at the anatomical level (Russell, 2002; Autumn and Gravish, 2008; Gamble et al., 2012), and as a focus for attempts to co-opt and adapt its principles to human applications and to serve as a

model system for integrative biology and interdisciplinary science (Autumn et al., 2000, 2014; Autumn, 2006a; King et al., 2014). It is evident that the gekkotan adhesive system has been both gained and lost on multiple occasions (Gamble et al., 2012). It is possible, therefore, that somewhere within this broad and dynamic evolutionary nexus lie clues to how the transition from nonadhesive to adhesive capabilities occurred, and under what ecological circumstances this shift was favored. Peattie (2008) opined that the discovery of “an extant intermediate” (interpreted here as a taxon displaying epidermal characteristics consistent with the transition between the exploitation of frictional and adhesive interactions) would greatly

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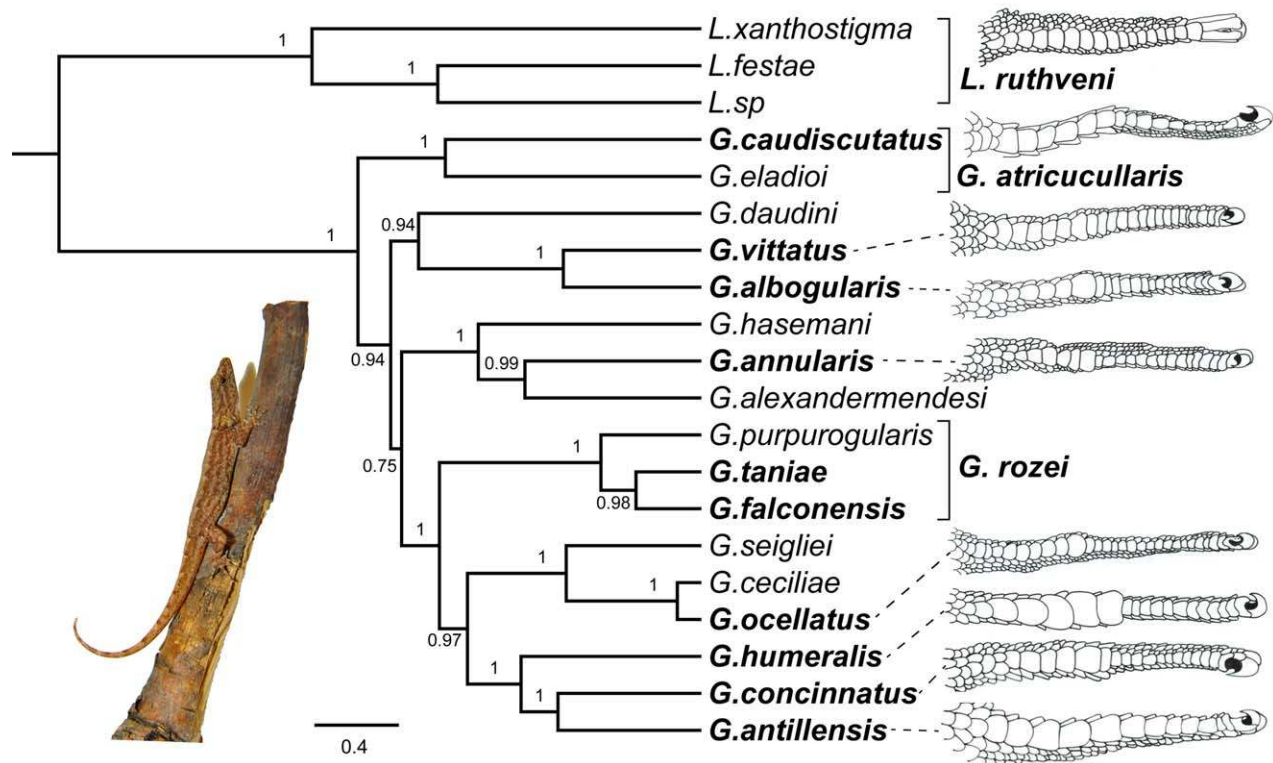


Fig. 1. Phylogeny of *Gonatodes* using *Lepidoblepharis* as the outgroup. Numbers at nodes are posterior probabilities from the Bayesian species tree analysis. *G. rozei* and *G. atricucularis* lack any published DNA sequences but their likely positions in the phylogeny have been inferred on the basis of morphological and biogeographic affinities with other *Gonatodes* species (see results). Bold-faced species names indicate species examined in this study. The illustrations of the digits provide an overview of the range of digit form in *Lepidoblepharis* and *Gonatodes*. More detail about the form of the digits of *Gonatodes* is provided in Figure 3. *Gonatodes humeralis* sitting on a branch is depicted at the bottom left. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

enhance our understanding of how the gekkotan adhesive system arose.

Heretofore, gekkotan clades have been identified in which unambiguous gains of the adhesive system have occurred, and within these, the basic morphological characteristics associated with such origins have been identified. The most completely documented example is that of the *Hemidactylus* + (*Cyrtodactylus* + *Geckoella*) clade, as presented by Russell (1976), and elaborated upon by Gamble et al. (2012: Fig.3), who posited that the likely initial key modification in this transition was the elaboration of subdigital spinules into setae (Russell, 1976; Peterson, 1983; Peattie, 2008), resulting in enhanced traction. This would then act as the focus for the integration of further morphological modifications related to the control of adhesive attachment and release, such as the broadening of the subdigital lamellae, changes in phalangeal form and proportions, and modifications of the digital muscular and tendon systems. Such attributes are associated not only with the ability to adhere to surfaces but also with control of the application and release processes (Peattie, 2008; Russell and Higham, 2009; Higham et al., 2015). We herein investigate digital form in a gek-

kotan genus we consider to be the best candidate for exploring subtle but important differences of digit form and epidermal micro-ornamentation that might provide insights into the means of transition to an adhesive system (of the sort typical of pad-bearing geckos with basal pads; Gamble et al., 2012).

For setae, some headway has been made in understanding how they relate to features of the locomotor substrata that they naturally interact with (Hiller, 1968; Russell and Johnson, 2007, 2014; Johnson and Russell, 2009). Relative to setae, however, much less is known about the variation in form, functional properties and roles of their likely precursors, epidermal spinules. These have been inferred to enhance traction (Russell et al., 2007; Peattie, 2008; Collins et al., 2015). Data gleaned from the properties of synthetic filamentous arrays indicate that simple fibrils can greatly increase frictional interactions between surfaces (Majidi et al., 2006; Bhushan and Sayer, 2007; Santos et al., 2007). A detailed investigation of the variation in form of spinules, even within the confines of single scales, of the subdigital surfaces of *Gekko gekko* (Russell et al., 2007: Figs. 2 and 4–6, Table 1) led to the proposition that the examination of candidate

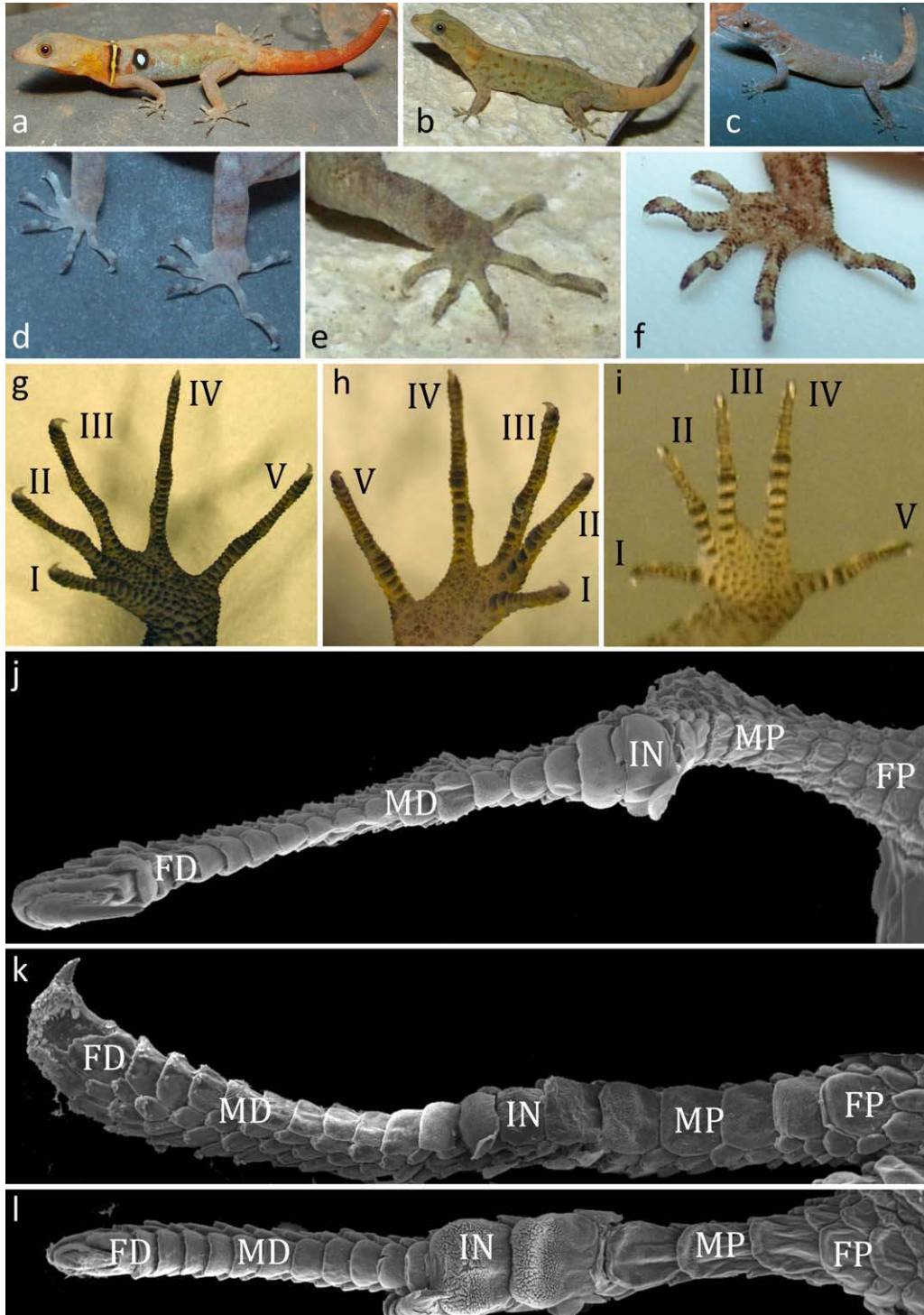


Fig. 2. The three species of *Gonatodes* studied in-depth in this contribution – (a) *G. ocellatus*; (b) *G. vittatus*; (c) *G. humeralis*. Panels (d), (e), and (f) illustrate, respectively, for *G. ocellatus*, *G. vittatus*, and *G. humeralis*, the external form of the digits when resting on a horizontal, flat, unyielding surface (lm = left manus; lp = left pes). Panels (g), (h), and (i) depict, respectively, for *G. ocellatus*, *G. vittatus*, and *G. humeralis*, the ventral aspect of the left pes. Panels (j), (k), and (l) illustrate, respectively, for *G. ocellatus*, *G. vittatus* and *G. humeralis*, the ventral aspect of Digit IV of the left pes as seen at low SEM magnification. For panels (g), (h), and (i) the Roman numerals I–V indicate the digits. For panels (j), (k), and (l), the abbreviations FP (far proximal infraproximal), MP (mid-proximal infraproximal), IN (inflection), MD (mid-distal infradistal), and FD (far distal infradistal) indicate the sampling points along the digits that were subjected to detailed study of the form and disposition of the epidermal micro-ornamentation of the subdigital surfaces. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

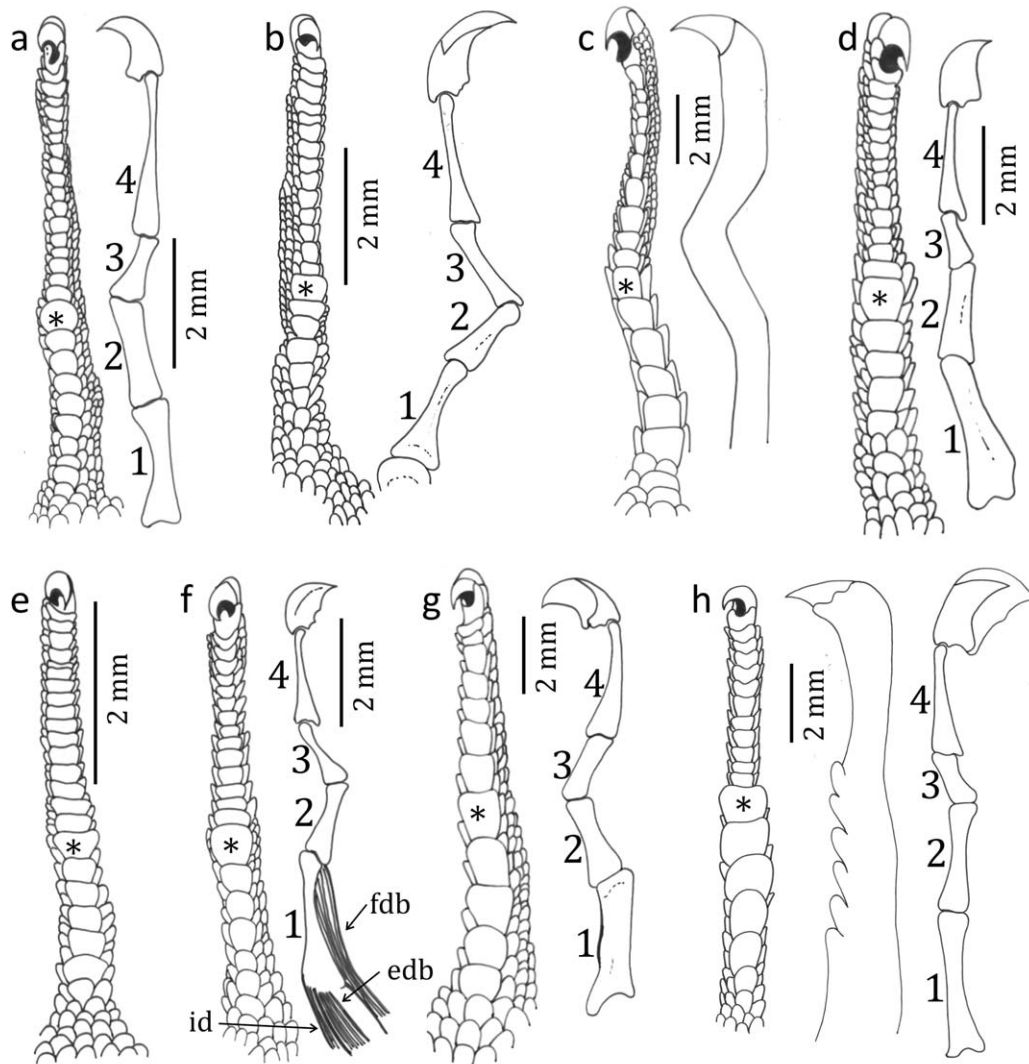


Fig. 3. Form of Digit IV, pes in select species of *Gonatodes* investigated in this study. “BMNH” designations indicate specimen numbers in the collections of the Natural History Museum, London. Asterisks denote the main friction plate, or its equivalent, at the point of inflection of the digit. The numbers 1–4 indicate the first to the fourth phalanx, respectively, on skeletal depictions. Scale bars for each species refer to all depictions for that species. (a). *G. ocellatus*, ventral aspect, Digit IV, right pes, and lateral aspect, skeleton, Digit IV, left pes; (b). *G. annularis*, ventral aspect, Digit IV, left pes, and lateral aspect, skeleton, Digit IV, right pes; (c). *G. atricucullaris*, ventral aspect, Digit IV, right pes, and profile, Digit IV, right pes showing the digital inflection; (d). *G. concinnatus*, ventral aspect, Digit IV, left pes, and lateral aspect, skeleton, Digit IV, right pes; (e). *G. vittatus*, ventral aspect, Digit IV, right pes; (f). *G. albogularis*, ventral aspect, Digit IV, left pes, *G. albogularis*, and lateral aspect, skeleton, Digit IV, left pes – extensor digitorum brevis (edb), interossei dorsalis (id), and flexor digitorum brevis (fdb) muscles depicted, from dorsal to ventral; (g). *G. antillensis*, ventral aspect, Digit IV, right pes, and lateral aspect, skeleton, Digit IV, right pes; (h). *G. humeralis*, ventral aspect, Digit IV, right pes, profile, Digit IV, right pes, and lateral aspect, skeleton, Digit IV, right pes. Specimen numbers upon which the illustrations are based are provided in the supplemental information (Supporting Information Appendix 1).

taxa that show differential degrees of expression of epidermal outgrowths would be useful for a more complete understanding of how the gekkotan adhesive system might have originated from a friction-enhancing precursor.

The proposition that epidermal spinules may enhance traction has been bolstered by recent experimental demonstration that seta-like outgrowths of the subdigital and subcaudal epidermis of chameleons (Lange, 1931; Ruibal and Ernst, 1965; Schleich and Kastle, 1979; Muller and Hil-

denhagen, 2009; Spinner et al., 2013) are friction-enhancing, even though they lack adhesive properties (Khannoon et al., 2013). Chameleon spinules increase frictional interactions regardless of the direction of loading. An increase in contact surface area is brought about by the filaments distorting and meeting the substrate along their sides, in a similar fashion to that observed for synthetic seta-like filaments (Majidi et al., 2005). Khannoon et al. (2013) suggested that such filaments represent what might be expected of a morphological

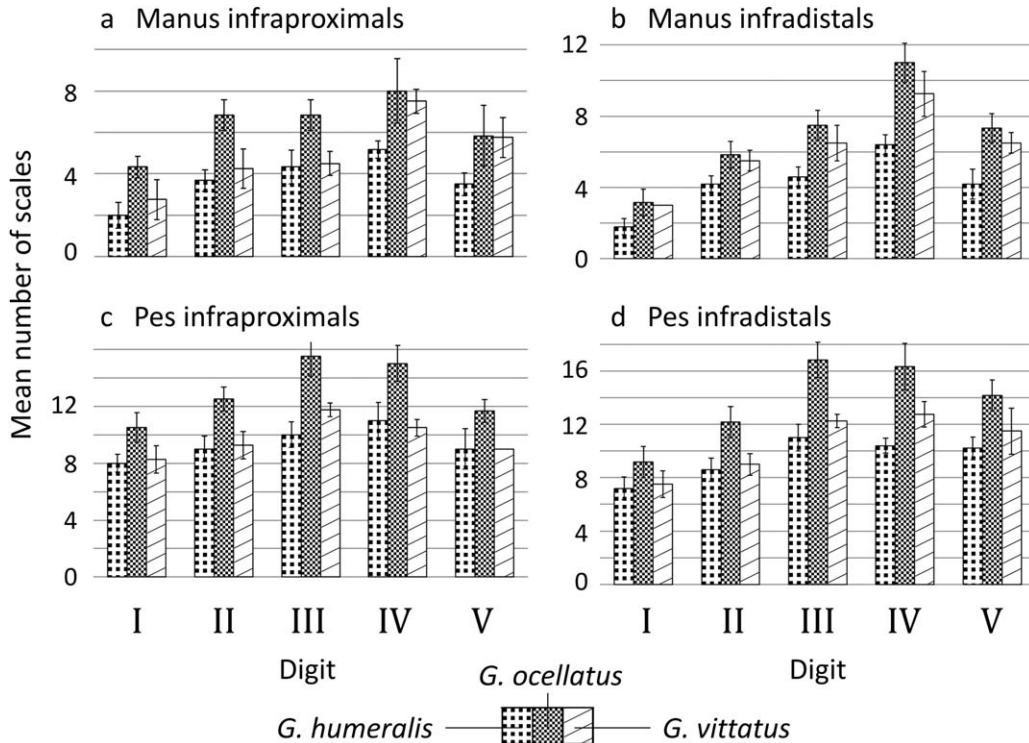


Fig. 4. Mean numbers (\pm sd) of infraproximal and infradistal scales on all digits of the left manus and pes of (from left to right on each graph) *Gonatodes humeralis* ($n = 6$), *Gonatodes ocellatus* ($n = 6$), and *G. vittatus* ($n = 4$).

transitional stage in the evolution of gekkotan adhesive setae.

Enlarged, thickened, robust scales, known as friction plates (Padian and Olsen, 1984; Russell et al., 2013; Khannoon et al., 2013), and larger and more densely packed than those on the scales that bridge the intervals between friction plates. Furthermore, we seek evidence for the possibility that subdigital friction plates are the precursors of scansors (Russell, 2002). This implies that, for taxa with digital inflections, the initial sites of the expression of putatively adhesive setae will be located on the friction plates at these points (Peattie, 2008), and that changes in scale form will be consistent with the morphological characteristics of scansors.

On the basis of a broad survey of digit form within the Gekkota (Russell, 1972), we identify *Gonatodes* as showing the greatest promise (Russell, 1972) for exploring the morphological features of digits to provide clues as to the transition from

that they will have integumentary micro-ornamentations that are similar in form, dimensions and density to those of chameleons (Spinner et al., 2013; Khannoon et al., 2013), and larger and more densely packed than those on the scales that bridge the intervals between friction plates. Furthermore, we seek evidence for the possibility that subdigital friction plates are the precursors of scansors (Russell, 2002). This implies that, for taxa with digital inflections, the initial sites of the expression of putatively adhesive setae will be located on the friction plates at these points (Peattie, 2008), and that changes in scale form will be consistent with the morphological characteristics of scansors.

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TABLE 1. Relative mean digit lengths (I–V) for the manus and pes of *Gonatodes ocellatus* ($n = 6$; SVL range 35.6–43.0 mm, mean 39.5 mm), *G. vittatus* ($n = 4$; SVL range 29.1–32.5 mm, mean 31.5 mm), and *G. humeralis* ($n = 6$; SVL range 26.9–34.0 mm, mean 31.9 mm) expressed as percentages of SVL (percras of Werner, 1971)

Species	Manus					Pes				
	I	II	III	IV	V	I	II	III	IV	V
<i>G. ocellatus</i>	6.6	8.7	9.9	11.4	9.3	5.9	9.2	11.7	13.7	11.4
<i>G. vittatus</i>	5.1	7.2	9.1	9.9	7.2	6.3	10.0	11.9	13.8	10.7
<i>G. humeralis</i>	5.2	7.4	8.3	9.3	7.6	5.0	7.5	9.6	11.5	9.5

friction-enhancement to potential adhesive capacity. *Gonatodes* is a reasonably diverse (27 species are currently recognized – Kok, 2011), ancestrally padless (Gamble et al., 2012) clade of mostly diurnal sphaerodactylines, that is sister to *Lepidoblepharis*. It is relatively well understood phylogenetically (Gamble et al., 2008; Schargel et al., 2010), has been studied intensively ecologically (Vitt et al., 1997, 2000; Persaud et al., 2003; Fuenmayor et al., 2006; Carvalho et al., 2008; Fernandes et al., 2009), and exhibits a broad array of subtle variation in digital morphology. Given this, we undertake a broad-scale examination of the form of the digits of *Gonatodes*, and subsequently a more in-depth examination of digit form in three species of *Gonatodes* as exemplars that may be taken to illustrate the morphological changes in a hypothesized shift from friction-enhancing to adhesion-enhancing digits. We assess this evidence in light of what is known about the ecology of *Gonatodes*.

MATERIALS AND METHODS

Estimating Phylogenetic Relationships Among *Gonatodes* Species

We generated a new *Gonatodes* phylogeny to provide the context for examining digit trait evolution. Previously published molecular phylogenies of *Gonatodes* lack either sufficient taxonomic sampling to incorporate our data about digits (Gamble et al., 2008, 2011, 2012) or employ relatively few characters and suffer from poor resolution and nodal support (Schargel et al., 2010). We combined data from these previous studies, along with newly generated sequences from material collected in Trinidad and Tobago (Permits FW: 4/10/1 and 009/2012), for a total of 5,712 bp of aligned molecular genetic data from fragments of six nuclear protein coding genes (RAG1, RAG2, ACM4, C-MOS, PDC, and NT3) and three mitochondrial genes (ND2 and associated tRNAs, 12S, and 16S). We included 17 species of *Gonatodes*, incorporating all but two species for which we had morphological data, *G. atricucullaris* and *G. rozei*, for which no genetic data are available. Three species of *Lepidoblepharis* were used as the outgroup. New sequences were generated using methods from Gamble et al. (2012). The aligned data file and GenBank IDs (for both see Supporting Information, sequence data file) are provided.

We generated a species tree from individual gene trees in a coalescent framework using the *BEAST method in BEAST 1.8.0 (Heled and Drummond, 2010; Drummond et al., 2012). We applied a strict clock with uniform rates across branches, the Hasegawa-Kishino-Yano (HKY) plus gamma model for each of the nuclear genes, and an uncorrelated relaxed clock (Drummond et al., 2006) with general time-reversible (GTR) plus gamma model for the mitochondrial data. We ran two Markov chain Monte Carlo (MCMC) analyses for 100 million generations each, sampling every 5,000th generation. Convergence and burn-in were determined using Tracer 1.5 and a consensus species tree (Fig. 1) was produced using TreeAnnotator 1.8.0 (Drummond et al., 2012).

Overall Aspects of Digital Morphology and Variation

We examined the external and internal morphology of the digits of a broad representation of species of *Lepidoblepharis*, *Pseudogonatodes* (the third primitively padless sphaerodactyl-line genus), and *Gonatodes* using specimens from museum collections (see Supporting Information, Appendix 1), including all

of the major lineages within *Gonatodes* (Fig. 1). Through dissection, we examined the muscles and tendons of the digits. These examinations, published accounts of digit form and scalation in *Gonatodes* (Günther, 1859; Boulenger, 1885; Noble, 1923; Carr, 1939; Smith, 1944; Vanzolini and Williams, 1962; Powell and Henderson, 2005; Cole and Kok, 2006; Schargel et al., 2010) and our newly generated phylogeny, allowed us to select the species employed in our more detailed examination of digit morphology in *Gonatodes*.

Selected Focal Species for Detailed Examination

We chose to examine *Gonatodes ocellatus*, *G. vittatus*, and *G. humeralis* (Fig. 2) in more detail (see Supporting Information). These represent, respectively, a species with elongate, slender digits with a marked inflection beneath which reside enlarged friction plates; a species with relatively shorter digits with a less marked inflection, fewer infradigital scales, and a flatter proximal portion; and a species that lacks a marked digital inflection, and bears noticeably enlarged infraproximal (*sensu* Schargel et al., 2010) scales.

Measurement and Scanning Electron Microscopy of Focal Species

Sacrificed specimens (collected in Trinidad and Tobago under permits FW: 4/10/1 and 009/2012, and maintained and euthanized under University of Minnesota animal use protocol 1108A03545; see Supporting Information, Appendix 1, specimens prefixed “TG,” which are deposited in the James Ford Bell Museum, University of Minnesota, Minneapolis) were fixed in 10% neutral buffered formalin, stored in 70% EtOH, and the following measurements (each feature measured thrice and the mean calculated) taken (with electronic callipers to the nearest 0.1 mm): snout-vent length (SVL) from the tip of the rostrum to the anterior border of the vent; length of each digit (left side, manus and pes) from the base of the digit at the cleft with adjacent digit(s) to the distalmost extremity of the claw (these lengths were expressed as percentages of SVL [percras: Werner, 1971], see Table 1); length of the proximal portion of Digits II–V (left side, manus and pes) from the basal cleft between digits (as described above) to the distal end of the scale demarcating the distal end of the inflection (there is no inflection in Digit I because it bears only two phalanges and so was not measured for this trait); length of the distal portion of Digits II–V (left side, manus and pes) from the distal end of the scale demarcating the inflection (as described above) to the distalmost extremity of the claw.

To allow comparison of integumentary micro-ornamentation of the ventral aspects of the digits with that of other body regions, 0.5-mm square skin samples were removed from the dorsum of the metapodial region of the manus and pes, and from the sagittal region of the back near the sacrum. The left manus and pes were then severed at the wrist/ankle and prepared for scanning electron microscopy (SEM) observation. All foot and skin samples were affixed to strips of cardboard using fine entomology pins, surface debris removed by immersing the samples in 70% EtOH in a sonicating bath for 5 min, fully dehydrated by immersion (for 30 minutes each) in 80, 90, and 100% (twice) EtOH, then 20% Hexamethyldisilazane (HMDS), 40, 60, 80, and 100% (twice) HMDS, and placed on an absorbent surface (Kimwipes[®], Kimberly-Clark, Roswell, GA) in a fume hood to air dry overnight. Subsequently they were affixed with carbon tape to aluminum SEM stubs, sputter coated with gold alloy (2-nm thick gold/palladium film, 82% Au/18% Pd) in a Polaron SC7640 (Quorum Technologies, Lewes, East Sussex, UK) sputter coater, and examined in a Zeiss EV060 SEM at the Microscopy and Imaging Centre, Cumming School of Medicine, University of Calgary. Images were used to acquire information about scale sizes and counts, and the form, dimensions, and density of epidermal micro-ornamentation.

For all three focal species, all digits were examined. Measurements of the feature being examined were taken using the

measuring tool in tpsDig 2.16 (Rohlf, 2010). Means of three measurements were calculated for all features examined. Approximate areas of infradigital scales were calculated by multiplying their length by their width.

Integumentary micro-ornamentation of the dorsum of the manus and pes, the back, selected stations along the ventral surface of each digit (Fig. 2j: far proximal [FP]; mid-proximal [MP]; beneath the inflection [IN]; mid-distal [MD]; and far distal [FD]), and palmar and plantar scales was examined. The intervening scales between sampling stations on each digit (Fig. 2j–l) were visually inspected to check for any regional anomalies, but their surface micro-ornamentation was not measured. For Digit I, which lacks an inflection, equivalently spaced stations along the digit were selected. Lengths of epidermal outgrowths were recorded, as well as their diameter (measured at 5 μm above their base). Spacing between the outgrowths was obtained by measuring the distance between the adjacent outer edges of neighboring filaments in the plane of the image. Their density was approximated as their number per mm^2 , determined by counting the number of filaments along a 32 μm transect, squaring that number and multiplying the product by 1,000 (Johnson and Russell, 2009). Average values for the parameters for individual epidermal outgrowths were calculated from 10 measurements taken at each station along the digit. Data were pooled for each species to obtain mean values for each of the dimensions measured.

RESULTS

Phylogenetic Relationships Among *Gonatodes* Species

Phylogenetic relationships among *Gonatodes* species (Fig. 1) were found to be largely congruent with previous studies at well-supported nodes (Gamble et al., 2008, 2011, 2012; Schargel et al., 2010), and thus are confirmed as providing the most appropriate framework for our comparative observations. Several short internal nodes deep in the phylogeny that have shown conflicting patterns between previous studies, however, also exhibit low posterior probabilities here. *Gonatodes atricucularis* and *G. rozei* were not included in the phylogenetic analysis, but their likely positions in the phylogeny are inferred (Fig. 1). *Gonatodes atricucularis* has morphological similarities with *G. eladioi* (Nascimento et al., 1987), whereas *G. rozei* has morphological similarities to, and biogeographic affinities with, the clade consisting of *G. falconensis*, *G. taniae*, and *G. purpurogularis* (Riviero-Blanco and Schargel, 2012).

General Survey of Digit Form

The digits of *Lepidoblepharis*, the sister taxon of *Gonatodes* (Fig. 1), are free, clawed, straight, and lack adhesive pads and digital inflections, although there is a slight angulation between phalanges 2 and 3 on manual and pedal Digit IV. Ventrally, they bear a single series of broad transverse plates, none of which are obviously enlarged relative to the others as distinct friction plates (Fig. 1). Their musculature is as reported for *Gonatodes* (see below). The digits of all species of *Lepidoblepharis* (and *Pseudogonatodes*) are essentially identical in their morphology.

The range of external digit form in *Gonatodes* is depicted in Figure 3. The relatively longest, slenderest (as determined by the relationship between width and length) configuration is displayed by *G. ocellatus* (Fig. 3a), and the relatively shortest and stockiest form is displayed by *G. humeralis* (Fig. 3h). These two taxa constitute the extremes of our more detailed comparison (see below), with *G. vittatus* (Fig. 3e) being selected as a morphological intermediate between them. The clade to which *G. humeralis* belongs (Fig. 1) incorporates taxa that exhibit the spectrum of the digit form depicted in Figure 3, and includes *G. concinnatus* (Fig. 3d), a species with digits very similar in configuration to those of *G. vittatus* (Fig. 3e). Our phylogenetic hypothesis (Fig. 1) provides us with the basis for setting the polarity for changes in digital form in *Gonatodes*; the evidence for the genus being ancestrally padless is very strong (Gamble et al., 2012).

All of our assessments refer to Digit IV of the pes, but all other digits (manus and pes) exhibit the same basic form in each species. The digits of *Gonatodes ocellatus* (Figs. 1, 2a,d,g,j, and 3a) are long, slender, and the inflection between phalanges 2 and 3 (Fig. 3a) is strongly marked. The number of infraproximal and infradistal scales (10/17 in the specimen illustrated) is relatively high, and the infraproximals are only slightly larger than the infradistals. The distal part of all digits is laterally compressed (Figs. 2g and 3a).

The short digital extensor muscles of *Gonatodes ocellatus* (extensor digitorum brevis – illustrated for *G. albogularis* [Fig. 3f] but identical for all species of *Gonatodes* examined, as are all other aspects of the musculature that are described) give rise to tendons at the metapodial-phalangeal joints, and these traverse the digits mid-dorsally to insert at the claw. The short flexor muscles (m. flexor digitorum brevis, see Fig. 3f for an illustration of this in *G. albogularis*) insert fleshily at the distal end of phalanx 1. No musculature extends beyond the distal extremity of the first phalanx. No muscle bellies or tendons in any of the species examined associate with any infraproximal scales, and the skin of the digits is easily removed without damage, unlike the situation for true scansors, which are firmly bound by the lateral digital tendon complex and cannot be stripped from the digits (Russell, 1986).

Taking *Gonatodes ocellatus* as the starting point of our survey, the following observations are evident, as depicted in Figure 3b–h. (Those species of *Gonatodes* that were examined morphologically [see Supporting Information, Appendix 1] but that are not illustrated in Figure 3 [*G. caudiscutatus*, *G. falconensis*, *G. rozei*, *G. taniae*] exhibit digit morphology closely resembling that of *G. albogularis* [Fig. 3f]). There is a reduction in the number of infraproximal and infradistal scales and a tendency for the largest friction plate, beneath the

TABLE 2. Relative mean lengths of (a) the proximal and (b) distal portions of Digits II–V, manus and pes, of *Gonatodes ocellatus* ($n = 6$), *G. vittatus* ($n = 4$), and *G. humeralis* ($n = 6$) expressed as percentages of SVL (percras of Werner, 1971)

Species	Manus				Pes				
	II	III	IV	V	II	III	IV	V	
(a) Proximal									
<i>G. ocellatus</i>	3.7	3.4	4.2	3.2	3.5	3.9	5.2	3.5	
<i>G. vittatus</i>	3.4	3.7	4.5	3.8	4.3	4.7	5.9	3.7	
<i>G. humeralis</i>	3.1	3.7	4.4	2.9	4.1	4.2	5.5	3.0	
(b) Distal									
<i>G. ocellatus</i>	4.5	5.8	5.3	4.6	4.7	6.8	6.5	6.1	
<i>G. vittatus</i>	3.9	4.8	4.3	4.1	3.9	5.2	5.2	5.6	
<i>G. humeralis</i>	3.9	4.2	4.2	4.1	3.9	5.0	4.9	5.1	

digital inflection, to become further enlarged, together with the series of infraproximal scales immediately adjacent to it. The infraproximal scales become increasingly imbricating and develop overlapping free distal edges. The proximal region of the digit (carrying the infraproximal scales) becomes proportionally longer, and the distal region proportionally shorter and less compressed. The inflection angle between phalanges 2 and 3 becomes more obtuse, and phalanges 1 and 2 become increasingly colinear. These trends culminate with *G. humeralis* (Fig. 3h), which has greatly enlarged infraproximal scales, especially in the region of the inflection, that carry a recognizably pilose distal free margin even at low SEM magnification (compare Fig. 2l with 2j and 2k).

These trends in digit form are associated with differing patterns of contact of the digits when standing on a flat, horizontal surface (Fig. 2d–f). In *Gonatodes ocellatus*, the infraproximal and infradistal scales do not contact the substratum (Fig. 2d), the points of contact being restricted to the scales at the base of the digit, the friction plate at the apex of the inflection (Fig. 2j, IN) and the claw. *G. vittatus* (Fig. 2e) has a more moderate digital inflection, but the digit contact pattern is the same as that for *G. ocellatus*, although both the proximal and distal parts of the digit are less arched (Fig. 2d,e). In *G. humeralis* (Fig. 2f), the digits are depressed proximally and the entirety of this region contacts the substratum, whereas the distal portion is held clear.

Detailed Assessment of Digit Form in *Gonatodes ocellatus*, *G. vittatus*, and *G. humeralis*

Relative length of digits. *Gonatodes ocellatus* has relatively the longest digits (Table 1). The manual digits of *G. vittatus* are relatively shorter than those of *G. ocellatus*, but its pedal digits (except for Digit V, which is relatively shorter) are of approximately the same relative length. Compared to *G. vittatus*, manual Digits III and IV and all pedal digits of *G. humeralis* are relatively shorter. These data indicate that the digits of the manus and pes are differently proportioned in dif-

ferent species. Digits III and IV of the manus, the longest digits, show a consistent trend toward relative shortening (Table 1) across these three species, and *G. humeralis* also exhibits wholesale relative shortening of all digits of the pes.

Within-digit proportions. For manual and pedal Digits II–V (those bearing an inflection), the relative length of the proximal (up to and including the inflection) and distal (distal to the inflection) regions (see Fig. 3) were assessed against SVL (Table 2). Although there are minor variations in the trends (Table 2), in general, *G. vittatus* has relatively longer proximal and shorter distal digit sectors compared to *G. ocellatus* (Table 2). *Gonatodes humeralis* exhibits a similar, and more marked, relative shortening of the distal portions of the digits, but also has relatively slightly shorter proximal digit sectors than *G. vittatus*. Thus, proportions of the entire digits (see above) are reflected in their intradigital proportions.

Phalangeal proportions. Because the digits of some species of *Gonatodes* are more markedly inflected than others (Figs. 2 and 3), simple linear measurement of intradigital proportions (see above) may not fully represent proportional differences. Here, we assess data taken from skeletal material for phalanges 1–4 of pedal Digit IV (Fig. 3) of *G. ocellatus*, *G. concinnatus* (skeletal material was not available for *G. vittatus*, but the digits of *G. concinnatus* are very similar in overall form: Figs. 1 and 3d,e), and *G. humeralis*.

In comparison to *G. ocellatus*, phalanx 1 is relatively longer in *G. concinnatus* and *G. humeralis* (Table 3), whereas the relative length of phalanx 2 is similar in all three species. Relative lengthening of the proximal portion of the digit is thus contributed to mostly by the proximalmost phalanx. For the distal part of the digit, the third phalanx exhibits little difference in relative length between the three species, and most of the relative shortening of this part of the digit in *G. concinnatus* and *G. humeralis* is contributed to by a relatively shorter fourth phalanx (Table 3).

The differences in relative lengths of the proximal (phalanges 1 and 2) and distal (phalanges 3 and 4) portions of the digits (Table 3) thus result

TABLE 3. Percentages of the combined lengths of phalanges 1–4 of Digit IV of the pes of *Gonatodes ocellatus*, *G. concinnatus*, and *G. humeralis* contributing to digit length (as expressed by the sum of the lengths of all four phalanges)

Species	Phalanx					
	1	2	3	4	1 + 2	3 + 4
<i>G. ocellatus</i>	27.6	21.8	14.9	35.6	49.4	50.5
<i>G. concinnatus</i>	38.1	22.2	14.3	25.4	60.3	39.7
<i>G. humeralis</i>	34.3	23.5	14.1	26.3	59.6	40.4

The combined percentage values for phalanges 1 + 2 and 3 + 4 represent the proximal and distal portions of the digit, respectively.

from maintenance of the relative proportions of the phalanges constituting the inflection (phalanges 2 and 3, Fig. 3), a relative lengthening of phalanx 1 and a relative shortening of phalanx 4. These differences, together with an alteration in the angles between phalanges 1 and 2, and 2 and 3 (Fig. 3a,h), render the combination of phalanges 1 and 2 flatter, more linear and collectively relatively longer (Table 3), and phalanges 3 and 4 collectively relatively shorter in *G. concinnatus* and *G. humeralis* when compared to *G. ocellatus*.

Mean number of infraproximal and infradistal scales by digit. The number of infraproximal and infradistal scales (see above) varies between species (Figs. 1 and 3). Counts of these for all digits of the manus and pes of *G. ocellatus*, *G. vittatus*, and *G. humeralis* (including Digit I) reveal that *Gonatodes ocellatus* (Figs. 2d,g,j and 3a), with relatively the longest, slenderest digits, has the highest scale count for both the proximal and distal regions (Fig. 4). Overall, *G. humeralis* has the lowest mean counts for infraproximal and infradistal scales for both manual and pedal digits (Fig. 4). As was the case for the intradigital proportions (Table 2), the scale counts for the manus and pes differ.

Mean length of infraproximal and infradistal scales by digit. The digits of *Gonatodes ocellatus*, *G. vittatus*, and *G. humeralis* exhibit a common pattern with regard to infradigital scale length (Fig. 5). The infraproximals are longer than the infradistals on both the manus and pes. For Digits II–V (manus and pes), which bear an inflection, the scales beneath the inflection are the longest (Fig. 5 – the inflection point is represented by the datum demarcating the longest scale for Digits II–V), and are markedly so in *G. humeralis*. The difference in length between the infraproximal and infradistal scales is greatest in *G. humeralis* (Fig. 5), and is considerably less in *G. ocellatus* and *G. vittatus*, although this varies by digit (Fig. 5). Although infradigital scale counts for *G. vittatus* and *G. humeralis* are quite similar (Figs. 4 and 5), they exhibit differentiation in the length of the infraproximal scales, most notably so in Digits III–V of the manus and pes. The mean length of the infradistal scales is very similar for all three species (Fig. 5), even though *G. ocellatus* has a greater overall body size (Table 1) resulting in a considerably greater number of such scales (Figs. 4 and 5).

Mean width of infraproximal and infradistal scales by digit. The mean width of the infradigital scales (Fig. 6) of *Gonatodes ocellatus*, *G. vittatus*, and *G. humeralis* exhibits a different pattern from their mean length (Fig. 5). The widest scales in both the manus and pes reside under the digital inflections (or their equivalent in Digit 1 – Fig. 6). The friction plates (those scales directly beneath the inflection) of *G. ocellatus* are the widest scales on all digits, and are generally absolutely wider than those of *G. vittatus* and *G. humeralis* (Fig. 6), consistent with the larger size of this species (Table 1). In the latter two species, the width of the infradigital scales in general is quite similar at all points along the length of the digits (Fig. 6), although the inflection point occurs relatively more distally in *G. vittatus* (Figs. 5 and 6), especially in the pes. There is thus an offset between these two species in the transition between the wider infraproximals and the narrower infradistals, and this is most evident for Digits IV and V of the manus, and all digits of the pes (Fig. 6). A similar offset is evident between the plots for *G. vittatus* and *G. ocellatus* (Fig. 6).

Mean area of infraproximal and infradistal scales by digit. The approximated area of the infradigital scales provides a means of estimating their potential contribution to the surface area available for frictional or adhesive interactions. Some of the infraproximals (those located in the region of the digital inflection) of Digits II–IV of the manus of *G. humeralis* (Fig. 7) have a moderately to considerably greater surface area than the equivalent scales of *G. vittatus* and *G. ocellatus*, even though it has a noticeably smaller overall body size than the latter (Table 1). The same is so for Digits III and IV of the pes. In contrast, the areas of the infradistal scales do not vary greatly between species, but *G. ocellatus* has longer digits and higher scale counts, so the overall combined area of the infradistals is greater than that for *G. vittatus* and *G. humeralis* (Fig. 7).

Calculating the surface area of the infraproximals available per mm of SVL (Table 4) provides a means of comparing differences in total surface area. These data are very similar for all three species for all digits of the manus and pes, even though this area is distributed across different numbers of scales (Figs. 4, 5, and 6). Thus, any functional differences in the capabilities of these scales are not

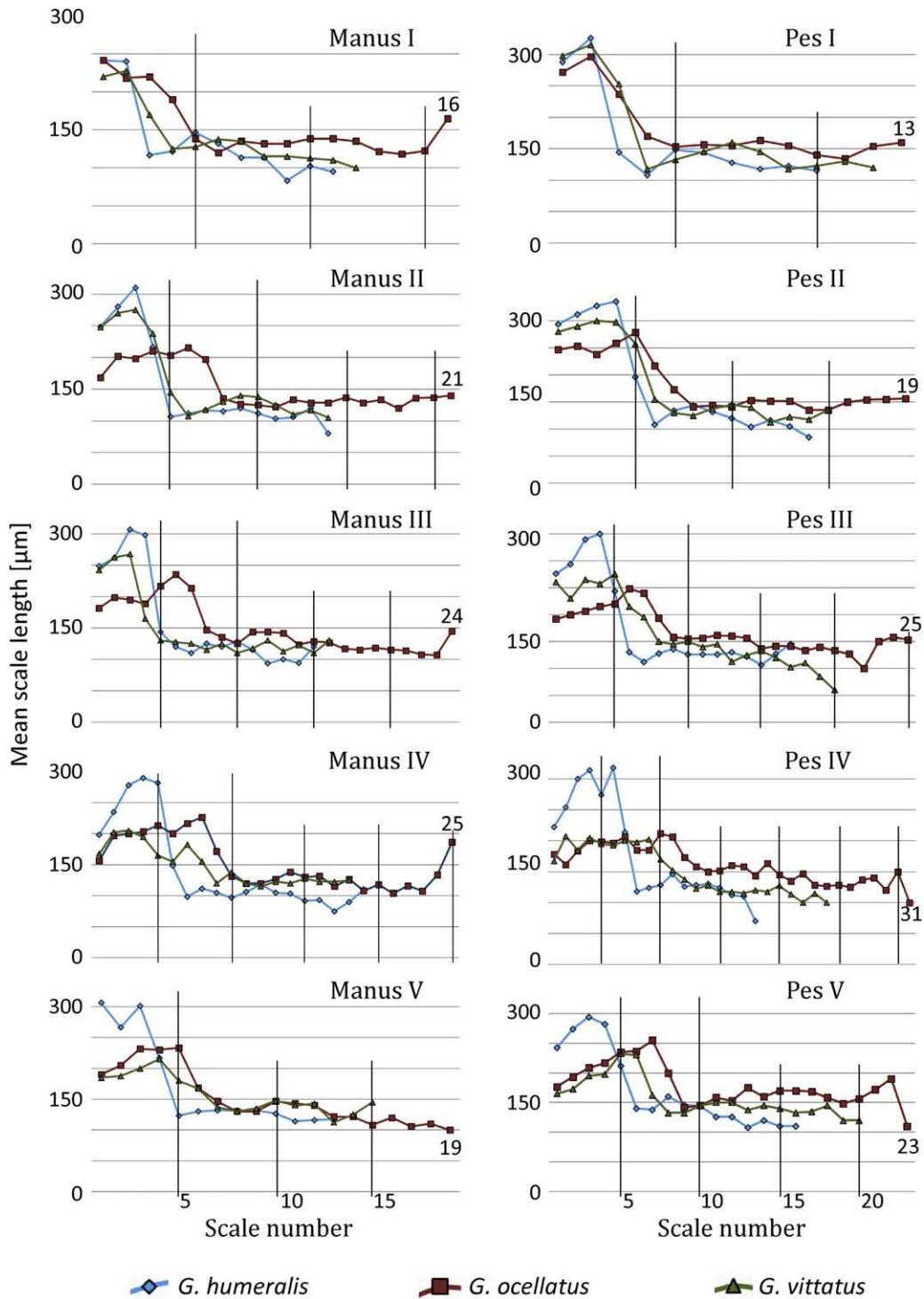


Fig. 5. Mean values for the lengths (in μm) of the left manual and pedal infradigital scales of all digits of *Gonatodes ocellatus* ($n = 6$, squares), *G. vittatus* ($n = 4$, triangles), and *G. humeralis* ($n = 6$, diamonds). The inflection points on Digits II–V (manus and pes) of each species are coincident with the distalmost point along the digit that represents the datum for the longest scale. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

derived from changes in the overall relative total surface area, which does not differ, but instead are attributable to the shape, form and location of specific scales (Figs. 2, 3, and 5–7), and to the micro-ornamentation that they bear (see below).

Form and dimensions of epidermal micro-ornamentation. For *Gonatodes ocellatus*, *G. vittatus*, and *G. humeralis*, we report mean data for epidermal outgrowths for Digit IV, manus and pes (Table 5), although all digits have equivalent

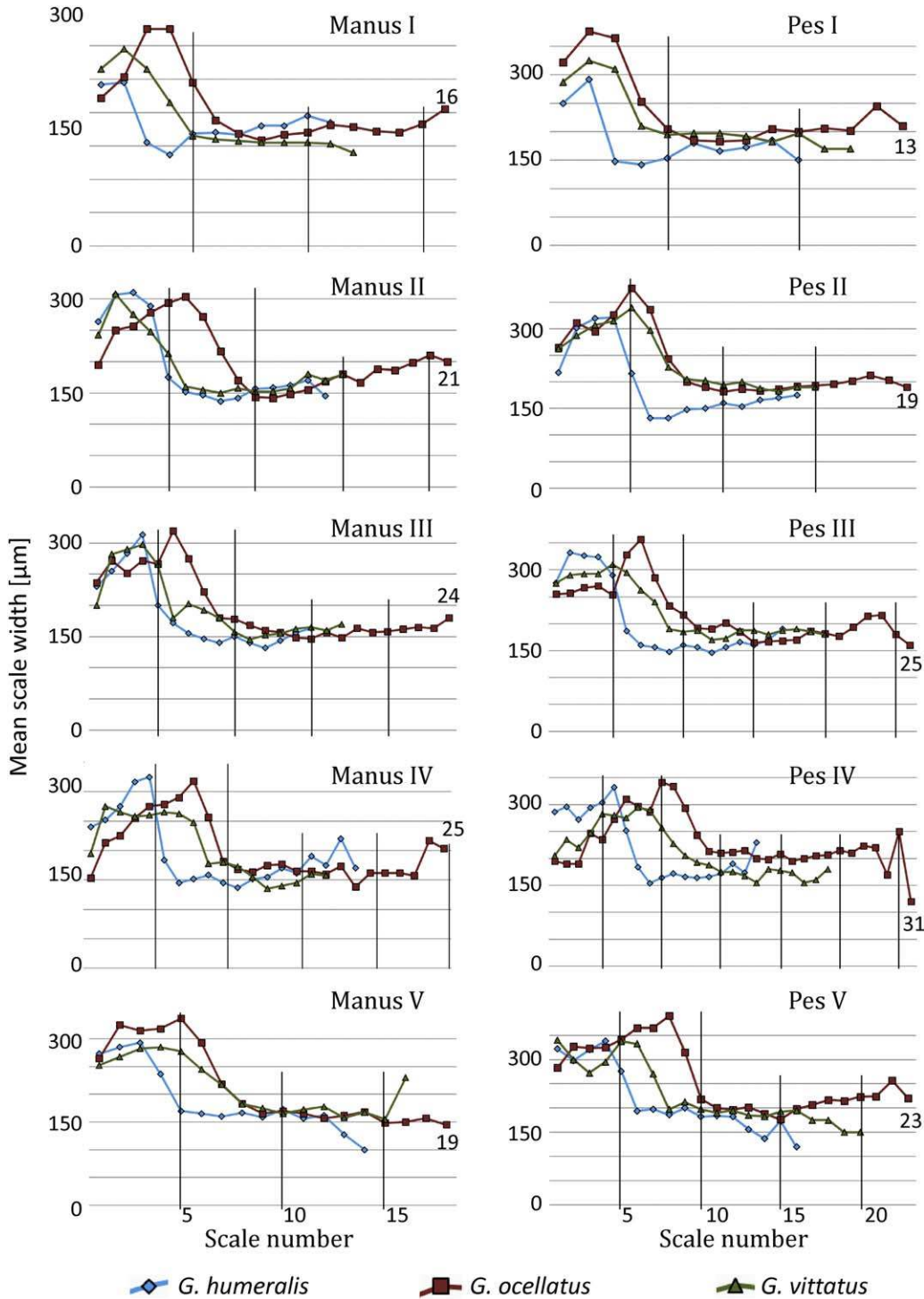


Fig. 6. Mean values for the widths (in μm) of the left manual and pedal infradigital scales for all digits of *Gonatodes ocellatus* ($n = 6$, squares), *G. vittatus* ($n = 4$, triangles), and *G. humeralis* ($n = 6$, diamonds). The inflection points on Digits II–V (manus and pes) of each species are coincident with the distalmost point along the digit that represents the datum for the longest scale. Note the proximal offset of this point in *G. humeralis* relative to that of *G. vittatus* for Digits IV and V of the manus and II–V of the pes. A similar proximal offset for *G. vittatus* is evident when compared to *G. ocellatus* for Digits II–IV of the manus and III–V of the pes. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

dimensions of the micro-ornamentation for equivalently positioned scales.

The spinules on the dorsum of the body of *Gonatodes ocellatus* are very small and sparse

(Fig. 8a). Its subdigital spinules taper and at rest their flexible tips are directed toward the proximal end of the digit (Fig. 8c–e). Those on the subdigital scales are longer and more densely packed than

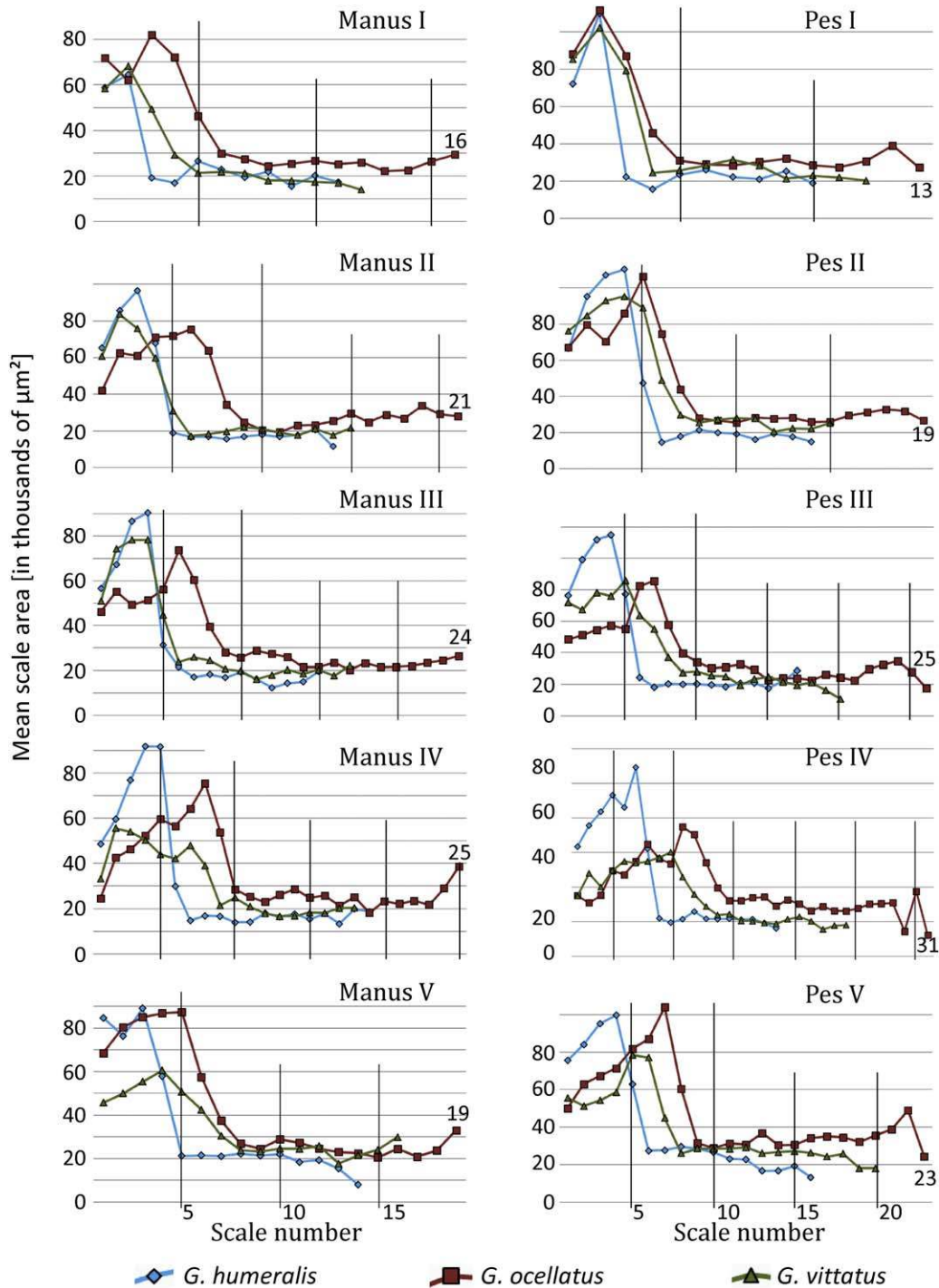


Fig. 7. Mean values for the surface area (in μm^2) of the left manual and pedal infradigital scales of all digits of *Gonatodes ocellatus* ($n = 6$, squares), *G. vittatus* ($n = 4$, triangles), and *G. humeralis* ($n = 6$, diamonds). The inflection points on Digits II–V (manus and pes) of each species are coincident with the distalmost point along the digit that represents the datum for the greatest surface area. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

those on the palmar and plantar scales (Fig. 8b), although they have the same overall form. Along the length of the digits, the lengths of the spinules vary moderately (Fig. 8; Table 5: manus 2.21–3.23 μm ; pes 2.30–5.46 μm). Whereas the mean values for the manus are generally smaller than those for

the equivalent stations on the pes (except for the far proximal infraproximals; Table 5), there is a relatively consistent pattern, and the spinules are longest on the friction plates beneath the inflection (Fig. 8c–e.g; Table 5). For *Gonatodes ocellatus*, therefore, the spinules on the digits are relatively

TABLE 4. Mean surface area (in μm^2) per mm of SVL (see Table 1) for the infraproximal scales of all digits of *Gonatodes ocellatus* ($n = 6$), *G. vittatus* ($n = 4$), and *G. humeralis* ($n = 6$)

Species	Manus					Total
	I	II	III	IV	V	
<i>G. ocellatus</i>	8,266	11,643	10,644	11,834	11,311	53,718
<i>G. vittatus</i>	5,732	9,112	9,807	11,007	9,618	45,276
<i>G. humeralis</i>	3,872	9,657	10,074	11,395	9,258	44,256
	Pes					Total
	I	II	III	IV	V	
<i>G. ocellatus</i>	7,781	12,238	12,123	15,072	12,012	59,226
<i>G. vittatus</i>	8,470	15,049	15,418	15,168	12,807	66,192
<i>G. humeralis</i>	5,610	12,735	14,705	17,674	11,409	62,133

short (see below), and their diameter is reasonably consistent from station to station. Spacing and density exhibit regional variation (Table 5), and the friction plates carry the longest spinules.

The subdigital scales of *Gonatodes vittatus* (Fig. 9a) carry tapering spinules with their flexible distal tips oriented, at rest, toward the digital base (for which illustrations of the condition in *G. ocellatus* suffice – Fig. 8c,d,f,g). Again these are more densely packed and longer than those on the palmar, plantar (Fig. 9b), and dorsal (Fig. 9c) scales. As for *G. ocellatus*, the length of the spinules does not change greatly along the length of the digits (Table 5), and the longest spinules are again located on the friction plates, beneath the inflections (Table 5; Fig. 2k: IN). As for *G. ocellatus*, the shortest spinules reside beneath parts of the digit that are held clear of the substratum (Fig. 2e,k: the FP, MP, MD, FD stations; Table 5). Relative to the situation in *Gonatodes ocellatus*, however, the spinules beneath the digital inflection of the pes deviate from the form seen elsewhere. They are 4.0–6.0 μm in length and have bifid tips (Fig. 9d),

dividing at a point about two thirds of their height from the base (Fig. 9d). Up to the point of bifurcation, the shaft has a constant diameter of about 0.7–0.8 μm (Table 5), but after the division, the branches have a basal diameter of about 0.3 μm , and from here, they taper to a rounded point or to an incipient spatular plate (Fig. 9d). The bifid nature of the spinules was not observed on the manus. Patterns of density and spacing of spinules along the digits are quite variable, but density is lowest at the mid-distal infradistal and mid-proximal infraproximal locations (Table 5), the regions of the manual and pedal digits that are held furthest from the substratum (Fig. 2e,k).

The lengths, diameters, spacing, and form of the subdigital spinules of *Gonatodes humeralis* are similar to those of *G. ocellatus* and *G. vittatus* for the far distal and mid-distal infradistal stations (Fig. 8c,d; Table 5). At the inflection locations (Figs. 2l and 10a), however, the epidermal outgrowths differ markedly in length from those of *G. ocellatus* and *G. vittatus* (Table 5), and even at low SEM magnifications (Fig. 10a) a pilose distal

TABLE 5. Mean (\pm sd) values for the length, diameter, and spacing (in μm) and mean values for density (number of outgrowths per mm^2) of epidermal micro-ornamentations (spinules and setae) at five stations along Digit IV, manus and pes of *Gonatodes ocellatus* ($n = 6$), *G. vittatus* ($n = 4$), and *G. humeralis* ($n = 6$)

Station along digit	Datum	<i>G. ocellatus</i> manus/pes	<i>G. vittatus</i> manus/pes	<i>G. humeralis</i> manus/pes
Far distal infradistal	Length	2.71 \pm 0.23/2.30 \pm 0.23	1.47 \pm 0.15/1.29 \pm 0.08	2.00 \pm 0.35/2.37 \pm 0.46
	Diameter	0.54 \pm 0.05/0.53 \pm 0.05	0.39 \pm 0.02/0.48 \pm 0.06	0.32 \pm 0.03/0.34 \pm 0.03
	Spacing	0.69 \pm 0.12/0.89 \pm 0.22	0.56 \pm 0.14/0.59 \pm 0.11	0.25 \pm 0.06/0.41 \pm 0.12
	Density	653,523/498,739	1,098,761/901,869	3,110,526/1,773,047
Mid-distal infradistal	Length	2.28 \pm 0.25/3.15 \pm 0.39	2.51 \pm 0.30/2.56 \pm 0.27	2.14 \pm 0.26/2.72 \pm 0.39
	Diameter	0.51 \pm 0.04/0.61 \pm 0.12	0.61 \pm 0.12/0.94 \pm 0.22	0.53 \pm 0.11/0.37 \pm 0.02
	Spacing	0.63 \pm 0.17/1.10 \pm 0.26	0.84 \pm 0.27/1.03 \pm 0.14	0.99 \pm 0.12/0.65 \pm 0.15
Inflection scale	Density	772,175/343,994	480,916/257,934	433,396/968,752
	Length	3.23 \pm 0.40/5.46 \pm 0.72	2.64 \pm 0.47/4.86 \pm 0.38	14.09 \pm 0.78/13.16 \pm 1.12
	Diameter	0.61 \pm 0.03/0.52 \pm 0.05	0.41 \pm 0.07/0.45 \pm 0.07	0.66 \pm 0.05/0.78 \pm 0.09
	Spacing	0.73 \pm 0.17/0.85 \pm 0.19	0.43 \pm 0.09/0.66 \pm 0.15	0.72 \pm 0.13/0.87 \pm 0.19
Mid-prox infraprox	Density	557,749/530,468	1,410,509/814,555	525,100/370,897
	Length	3.21 \pm 0.36/4.79 \pm 0.32	2.27 \pm 0.47/2.88 \pm 0.51	10.34 \pm 1.69/9.58 \pm 2.18
	Diameter	0.71 \pm 0.12/0.76 \pm 0.15	0.56 \pm 0.16/0.55 \pm 0.09	0.67 \pm 0.04/0.72 \pm 0.16
	Spacing	1.22 \pm 0.18/1.39 \pm 0.31	1.00 \pm 0.34/0.98 \pm 0.15	1.15 \pm 0.33/1.16 \pm 0.32
Far prox infraprox	Density	268,741/217,952	412,499/425,516	301,896/283,235
	Length	2.21 \pm 0.15/3.42 \pm 0.40	2.04 \pm 0.27/2.41 \pm 0.40	4.09 \pm 0.55/1.15 \pm 0.12
	Diameter	0.59 \pm 0.08/0.50 \pm 0.03	0.41 \pm 0.03/0.46 \pm 0.06	0.36 \pm 0.04/0.28 \pm 0.03
	Spacing	0.72 \pm 0.14/0.70 \pm 0.18	0.57 \pm 0.14/0.49 \pm 0.10	0.35 \pm 0.12/0.33 \pm 0.07
	Density	577,415/672,135	1,106,194/1,101,068	2,000,604/2,777,778

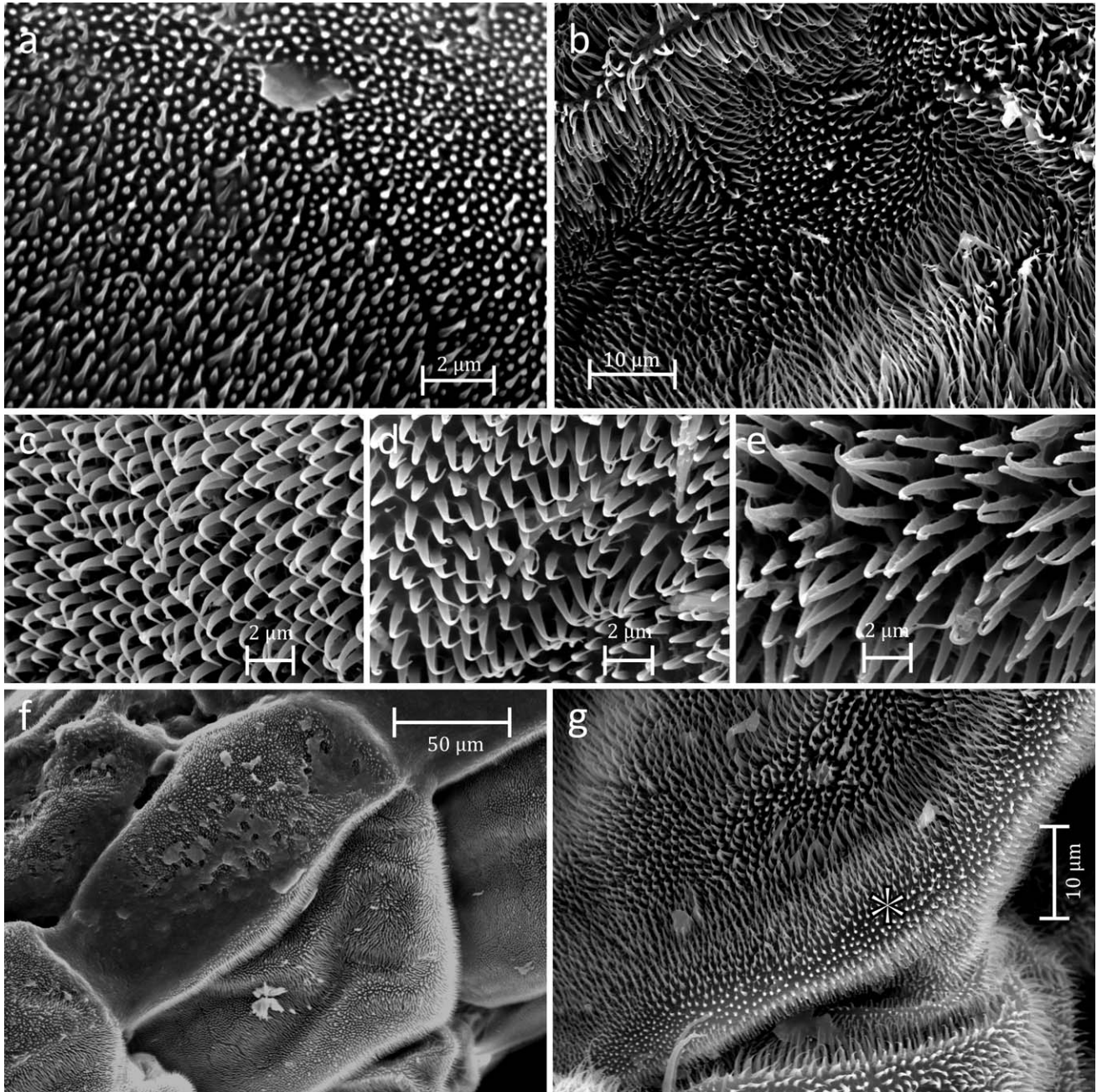


Fig. 8. Scanning electron micrographs of the epidermal micro-ornamentation of *Gonatodes ocellatus*. (a) Scales from the dorsum of the body, near the hips, showing the spinulate nature of the epidermis, the minute spinules (averaging $0.5\mu\text{m}$ in length) that are spaced relatively widely apart (average interspinule distance $0.25\mu\text{m}$). (b) A palmar scale at low magnification showing the fine pile of spinules on the surface. The concave appearance of this scale is artifactual and results from water loss during sample preparation. (c)–(g), Spinules on the infradigital scales of Digit IV, manus. (c) Spinules at the far distal station (Fig. 2j: FD). (d) Spinules at the mid-distal station (Fig. 2j: MD). (e) Spinules beneath the inflection point (Fig. 2j: IN). (f) Scale of the mid-proximal region (Fig. 2j: MP) showing the fine pile of the spinules investing this area. (g) Scale of the far proximal region (Fig. 2j: FP) showing the field of spinules in this region. Note the sparse spacing and small size of spinules in the hinge region between scales (asterisk), the pattern here being similar to that on the dorsal scales (Panel a). Scale bars are in μm . Dimensions of the digital epidermal outgrowths, their density, and spacing are provided in Table 5.

border on such scales is evident. Here, the epidermal outgrowths range from 10.0 to $15.0\mu\text{m}$ in length (Tables 5 and 6), their density is relatively low and the spacing relatively great (Table 5). The longest of these, on the basis of their morphology,

are true setae (Fig. 10c,d), being multiply branched distally with flattened, spatulate tips of about $0.12\mu\text{m}$ in width (Fig. 10c). Spinule form varies greatly even within the confines of a single scale at the inflections (Fig. 10). A transect (Fig.

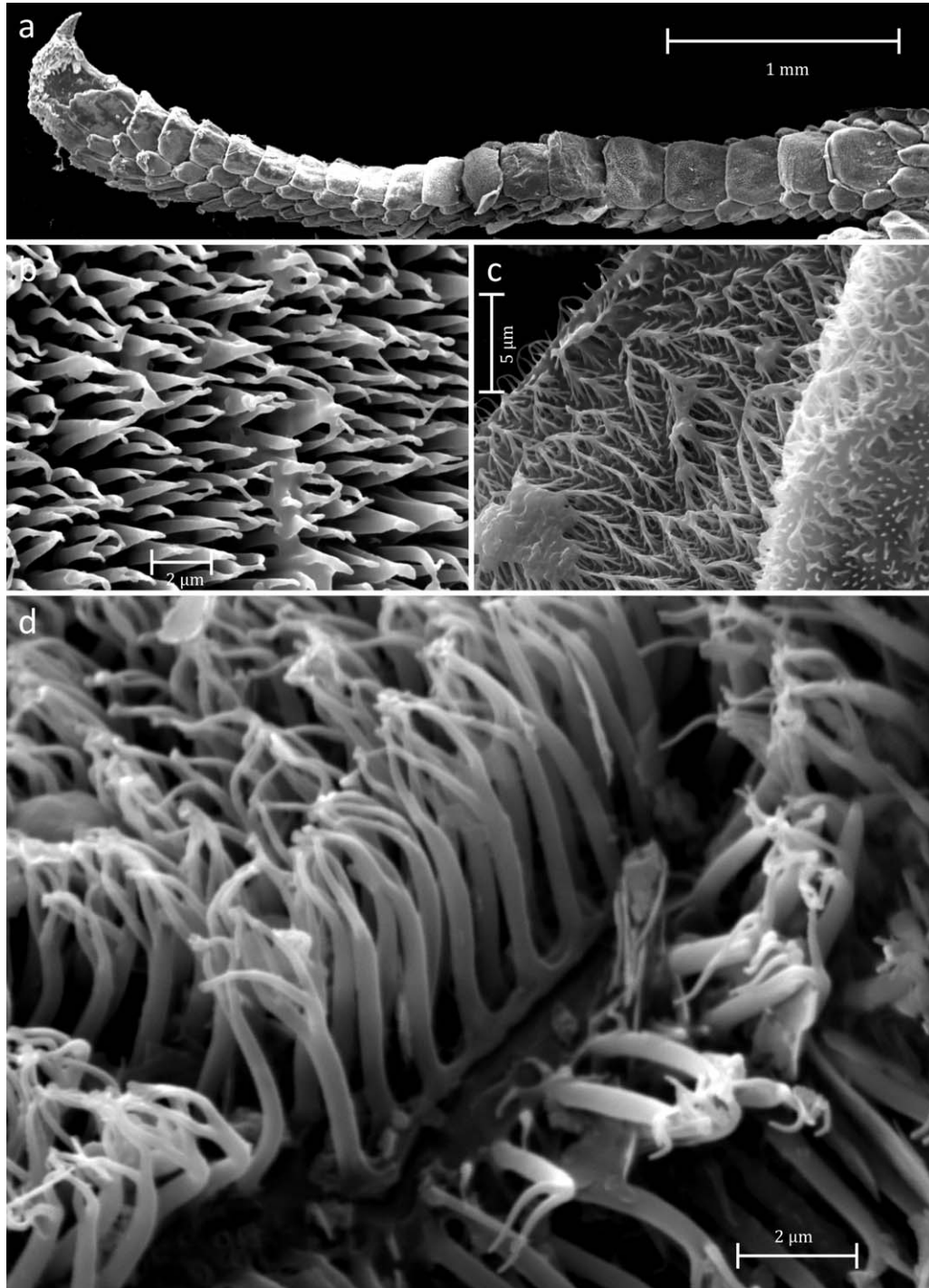


Fig. 9. Scanning electron micrographs of epidermal micro-ornamentation of *Gonatodes vittatus*. (a) Ventral aspect of Digit IV, left pes illustrating the difference in size (length and width) of the infraproximal versus infradistal scales and the imbricating nature of the infraproximals. (b) Spinules of the plantar scales. (c) Spinules on the dorsal region of the body, near the sacrum. (d) Spinules at the inflection point of Digit IV, left pes, showing their bifid nature and their arrangement in ranks and rows. Scale bars are in μm . Dimensions of the digital epidermal outgrowths, their density, and spacing are provided in Table 5.

10b) along such a scale reveals that branched, spatula-bearing setae occur only at the distal end (Fig. 10c,d). More proximally (Fig. 10e–g), these give way to spinules that diminish in length from distal to proximal (Table 6). Far proximally on

such scales the length (Tables 5 and 6) and form of these spinules is similar to those of the inflection scales of *G. vittatus*, with evidence of bifurcated and tapered to flattened termini (Fig. 10g). Transition from simple tapered spinules (there is a

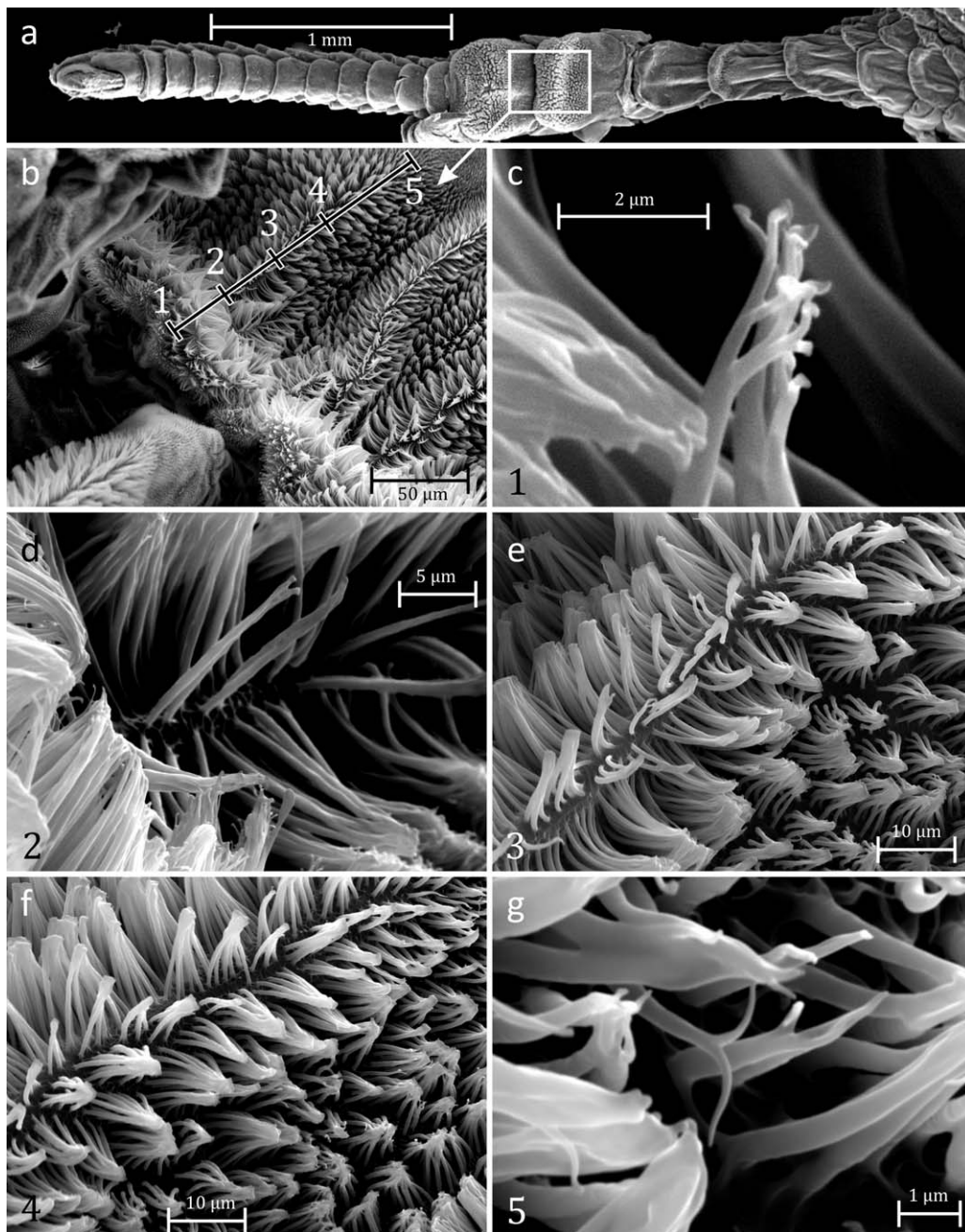


Fig. 10. Scanning electron micrographs of subdigital form and epidermal micro-ornamentation of *Gonatodes humeralis*. (a) Ventral aspect of Digit IV, left pes illustrating the size (length and width) of the scales along the length of the digit, and the strong imbrication and evident free distal margin of the scales in the region of the inflection. A distinctive pilose field is evident at the distal extremity of the scales beneath the inflection point (as demarcated by the box overlying one such scale), even at this low level of magnification. The box depicts the area enlarged in Panel b. Surface wrinkles on these scales are specimen preparation artifacts resulting from water loss. (b) A portion of the inflection scale demarcated by the box in Panel a, showing the range of form of epidermal outgrowths on this scale. The transect line with numbered stations (1–5) identifies the regions depicted in Panels c–g. (c) Epidermal outgrowths near the distal border of an elongated inflection scale (Panel b, Station 1) at its free distal margin. Here, the outgrowths have multiply branched tips bearing spatulate ends and are true setae. (d) Setae close to the distal end of an elongated inflection scale (Panel b, Station 2) at the posterior end of the free distal margin. (e) Spinules on an enlarged inflection scale at Station 3, Panel b. (f) Spinules on an enlarged inflection scale at Station 4, Panel b. (g) Spinules on an enlarged inflection scale at Station 5, Panel b. Here, bifurcated tips of the spinules are evident, and are very similar to those seen on the inflection scales of the pes of *G. vittatus* (Fig. 9d). The numbers 1–5 in the lower left corners of Panels c–g represent the equivalently numbered position on the transect depicted in Panel b. Scale bars are in μm . Dimensions of the digital epidermal outgrowths, their density, and spacing are provided in Tables 5 and 6.

TABLE 6. Mean values for the length, diameter, spacing, and density of the epidermal micro-ornamentations at five locations along a distal to proximal transect of an inflection scale of Digit IV, pes of *Gonatodes humeralis* (see Fig. 10c–g for images of the epidermal outgrowths)

Station along scale (see Fig. 10c–g)	Length	Diameter	Spacing	Density/mm ²
Station 1	12.98	0.66	0.86	437,418
Station 2	15.12	0.64	1.03	358,994
Station 3	9.58	0.67	1.16	299,991
Station 4	7.14	0.62	1.18	308,299
Station 5	4.78	0.51	0.90	505,140

mixture of unbranched and branched spinules far proximally on such scales – Fig. 10g) to setae is thus evident within the confines of a single scale. The mid-proximal infraproximal scales exhibit spinule dimensions similar to those of the inflection scale (Table 5), indicative of proximal encroachment of the spinule to seta transition along the digit, in accord with the change in morphology of the scales in this region (Figs. 4–8), and the flattening of the proximal portion of the digit.

DISCUSSION

Morphological Trends in the Digits of *Gonatodes*

Although regarded as an ancestrally padless genus (Gamble et al., 2012), *Gonatodes* expresses sufficient variation in the form of its digits (Figs. 1–3), to demonstrate changes related to the potential acquisition of basally located (Gamble et al., 2012) adhesive subdigital pads typical of many gekkotan clades. As such, it can be regarded as an example of an extant taxon that exhibits intermediate stages between frictionally and potentially adhesively functional digits (Peattie, 2008). Much of the anatomical specialization of the digits of geckos that have fully functional basal adhesive pads (Dellit, 1934; Hiller, 1968, 2000; Russell, 1976, 1979, 2002; Autumn et al., 2000; Autumn, 2006a,b) is, however, absent from *Gonatodes*, indicating that these are not necessarily associated with the initial stages of adhesive interactions. The pattern of musculature and tendinous insertions is consistent with the ancestral pattern for lizards in general (Russell, 1976) and exhibits no means of actively hyperextending the digits through actions of the dorsal interossei muscles (Russell, 1975, 2002).

That integumentary modifications associated with adhesive capabilities can be present without the more extensive anatomical modifications of the digits is also the case for *Anolis*, an iguanomorph genus well-known for its possession of a functional adhesive system. Only in pad-bearing geckos does digital hyperextension precede the raising of the heel region of the manus and pes during the stance phase of locomotion, and in *Anolis* digital hyperextension is achieved as a result of the digits

rolling off the substratum at the end of lift-off (Russell and Bels, 2001). Such a mechanism would be fully consistent with the initiation of adhesive capabilities in the Gekkota as well.

Our broad survey of digit form in *Gonatodes* (Figs. 1 and 3) revealed an array of expression that indicates trends toward relative enlargement of scales in the proximal region of the digits, culminating in the presence of incipient subdigital pads. Assembling our broad-scale observations into a series suggests the following tendencies from the primitive condition to the expression of incipient pads: reduction in the number of infraproximal and infradistal scales; a greater discrepancy between the size of the infraproximals and infradistals; increasing imbrication of the infraproximals; a relative shortening and increased stoutness of the digits; a flattening and relative elongation of the proximal region of the digits that results in greater contact with the substratum; a lessening of the lateral flattening of the distal region; relative enlargement of the scales beneath the digital inflection; and changes in the orientation of the phalanges such that the proximal pair (in Digit IV) become more aligned, and the “v” of the inflection is transformed into a stair-like rise between the proximal and distal regions of the digit.

These tendencies were explored in more detail using *Gonatodes ocellatus*, *G. vittatus*, and *G. humeralis* as exemplar species. The above-mentioned generalities were confirmed and were supplemented by further information, as follows: the trend of shortening of the digits is especially evident for Digits III and IV of the manus and all digits of the pes, and is accompanied by a change in the relative proportions of the proximal versus the distal regions of the digits, with the former becoming relatively longer and the distal region relatively shorter—these changes are more marked in the pes (indicative that the hand and foot are functionally different [Fontanarrosa and Abdala, 2013]); the relative lengthening of the proximal region of the digits is contributed to by an increase in length of the basal phalanx, and the distal shortening results from a relative truncation of the penultimate phalanx (these findings relating to Digit IV of the pes), with the intervening phalanges exhibiting essentially constant proportions in all

three species; associated with these proportional changes are differences in scalation patterns, with the number of infraproximal and infradistal scales being reduced, and the infraproximals being differentiated from the infradistals by becoming relatively larger, and especially longer; there is an associated trend toward greater imbrication of the infraproximals, with the distal margin developing a free border; the overall combined surface area of the infraproximals does not change markedly, but the scales in the vicinity of the digital inflection are disproportionately enlarged in *G. humeralis*; as was the case for the proportions of the digits, there are differences in scalation patterns and in trends between the manus and pes, with the latter showing the above-mentioned changes in a greater number of digits.

Examination of the subdigital micro-ornamentation of the three exemplar species revealed the following features that are associated with the trends in gross morphology of the digits: the spinules of *Gonatodes ocellatus* are largest on the friction plates, implying that longer spinules enhance frictional interactions (Peattie, 2008); in *G. vittatus*, the subdigital spinules are generally similar to those of *G. ocellatus*, although the longest spinules that are situated on the friction plates are bifurcated (as also reported for *G. albogularis* by Peattie, 2008), their morphology being consistent with the ability to deform and distort more when driven into close contact with the substratum, thus increasing the contact area; in *G. humeralis*, this trend is carried further, the spinules in the vicinity of the digital inflection are even longer and are expressed as branched, spatulate-tipped setae on the free distal margin of these scales (also seemingly noted, but not elaborated upon by Hiller, 1968); the density of the setae is relatively low and their spacing relatively wide (contra our predictions, although densities are comparable to those of chameleon spinules; Khannoon et al., 2013), possibly in relation to the accommodation of their branched, arborescent distal tips; within the confines of a single, enlarged subinflection scale of *G. humeralis* the entire spectrum of epidermal filaments, from small, hooked spinules to setae, is evident and there is gradation from one type to the next.

The panoply of changes summarized above can be placed into context by comparing the epidermal outgrowths of *Gonatodes ocellatus*, *G. vittatus*, and *G. humeralis* with patterns of variation found in other geckos that have fully expressed subdigital adhesive pads. In *G. ocellatus*, the subdigital spinules are of similar size and form to the spinules on the nonadhesive regions of the digits of *Gekko gecko* (Russell et al., 2007), and the digits of narrow-toed gekkotans (Peattie, 2008). They are largest on the friction plates, indicating that these enlarged scales do indeed exhibit micro-ornamentation associated with friction-enhancement (Peattie, 2008), and resemble the artificial filaments fabricated by vari-

ous research groups (Majidi et al., 2006; Northern and Turner, 2006; Bhushan and Sayer, 2007) that generate frictional interactions in proportion to the loading force. In *G. vittatus*, the spinules on the inflection scale (friction plate) are bifurcated (Fig. 9d), and have a form and length very similar to those on the summit of domed scales on the palmar and plantar region of *Gekko gecko* (Russell et al., 2007: Fig 4), and the friction-enhancing ventral tail tip of *Phelsuma madagascariensis* (Hiller, 1968). Similarly sized bifurcated spinules are also found on the proximal regions of the enlarged infraproximal and subinflection scales of *G. humeralis* (Fig. 10g). The distal regions of these same scales in *G. humeralis* carry true setae (Fig. 10c) with multiple spatulate terminal branches. There is a gradation in the form of epidermal outgrowths across a longitudinal transect on such scales (Fig. 10c–f).

Variation in form and dimensions are considerable across setal fields in gekkotan taxa having a fully expressed adhesive system (Johnson and Russell, 2009), and the variation of form of epidermal outgrowths on the scales beneath the digital inflection of *Gonatodes humeralis* are consistent with this pattern of gradational variation. 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. The basal lamellae of the Tokay gecko (*Gekko gecko*) carry spinules 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 that lack the characteristics of scansors. Such scales bear a strong structural resemblance to the seta-bearing scales of *G. humeralis* and serve to further 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 of actively controlling the adhesive process via digital hyperextension (Russell and Bels, 2001). Thus, the postulation that adhesive pads require complex morphological elaborations within the digits (Peattie, 2008) does not necessarily hold (Russell and Bels, 2001), and it is likely that adhesive lamellae alone can promote attachment and permit release at rest and during locomotion. The locomotor kinematics of species of *Gonatodes* requires investigation, and the adhesive capabilities of *G. humeralis* must be explored further. We predict that *G. humeralis* will achieve digital hyperextension as a result of the primitive lacertilian pattern of digit plantar flexion (Brinkman, 1980), whereby the putative adhesive apparatus is

detached from base to tip, as in *Anolis* (Russell and Bels, 2001).

Broadening of the subdigital lamellae (Gamble et al., 2012) is also not necessarily an early event in the development of adhesive scales, although their lengthening is. Changes in phalangeal proportions are evident, but are localized and are associated with an overall diminution of relative digit length. The elaboration of spinules into setae is localized to specific regions on modified scales (Peattie, 2008), and furthermore occurs on their imbricating distal margins, which later become prominent at the free margins of the scansors of pad-bearing geckos (Russell, 2002). Positionally and structurally, the subinflection friction plates of *Gonatodes* can be regarded as the homologs of lamellae, and ultimately scansors.

The Ecology of *Gonatodes* in Relation to the Expression of Incipient Digital Pads

Gonatodes ocellatus, our model of ancestral scansorial digit morphology of the genus, preferentially inhabits boulders, tree trunks, caves, and large, hollow trees (Underwood, 1962; Murphy, 1997), but has also been encountered in rainwater drainage culverts and buildings (Murphy, 1997; Persaud et al., 2003). It prefers rocky surfaces, which is consistent with the strongly inflected form of its digits (Arnold, 1998) and the presence of large friction plates (Figs. 2g,j and 3a). *Gonatodes vittatus* has been encountered on trees with loose bark (Underwood, 1962), within arboreal cactus (Marcuzzi, 1950), and in the litter at the base of coconut trees (Lynn, 1959; Test et al., 1966; Murphy, 1997). Its relatively shorter digits (Figs. 3e and 9a), with a slightly less intense inflection, may be suited to such habitats, but our understanding of the potential habitat-specificity of small differences in digit form is lacking.

In contrast to the aforementioned species, much has been written about the habitat preferences of *Gonatodes humeralis*. Some of this is quite general (Beebe, 1944; Underwood, 1962; Vanzolini, 1968; Carvalho et al., 2008), but other treatments provide more detail. It is the most widely distributed species in its genus (Vanzolini, 1955) and is sympatric over its range with at least 10 other *Gonatodes* species. It is associated with both primary and secondary forest, where it exploits the trunks of a wide variety of forest tree species (Hoogmoed, 1973; Vanzolini and Williams 1981; Vitt et al., 2000; Persaud et al., 2003), as well as branches and bushes (Dixon and Soini, 1986; Avila-Pires, 1995; Vitt et al., 1997). We, and others (Costa et al., 2009), have also observed it resting on leaf surfaces, palm leaf spathes (Murphy, 1997), and sleeping at night on leaves (Hoogmoed, 1973; Avila-Pires, 1995; Henle and Knogge, 2009). It employs bromeliads, conspicuous and abundant

components of Neotropical environments that are exploited by many species of anurans but few squamates (Henle and Knogge, 2009), as locomotor surfaces and egg deposition sites (Maciel et al., 2005), up to 9 m above the forest floor (Avila-Pires, 1995; Nunes, 2002; Maciel et al., 2005).

Gonatodes humeralis thus uses a higher part of the canopy than has been recorded for any of its congeners, and it is the only species known to exploit leaf surfaces. It is on such low friction substrata that adhesive capability may be particularly useful for holding station, maneuvering, and for occupying areas that are out of reach of many predators.

Digital adhesive mechanisms have been considered key innovations in lizards, opening new ecological opportunities and ultimately leading to speciation and morphological diversification (Russell, 1979; Losos, 2010; Gamble et al., 2012). However, opportunities to examine key innovations early in their evolution are rare. We hypothesize that the novel digital features of *Gonatodes humeralis* are associated with its expanded spatial niche breadth and broad geographical distribution. Therefore, the expression of setae in *G. humeralis* provides us with a potential opportunity to observe the early ecological consequences of a functional digital adhesive mechanism. Rigorous testing of the hypothesis that this ecological opportunity led to ecological release (Yoder et al., 2010; Des Roches et al., 2011) will be a fruitful topic for additional study.

That setae first appear in locations where frictional loading would be highest in the primitive configuration of the digits (beneath the inflection), and that the surface area available for adhesive contact would be increased by elongation of the subdigital scales in this region, are consistent with the transition to the form of the digits seen in *G. humeralis*. Thus, we hypothesize that static clinging in sit-and-wait foragers such as *Gonatodes* (Vitt et al., 1997; Persaud et al., 2003) may have been the precursor of the more active mode of employment of adhesive capabilities typical of many other gekkotan lineages (Gamble et al., 2012).

The friction-enhancing epidermal filaments of chameleons (Khannoon et al., 2013) are nondirectional, but this is associated with the feet being modified as prehensile grasping structures supporting the animal by using a tong-like grip on narrow, cylindrical perches (Anderson and Higham, 2013). Although the seta-like structures of chameleons are of similar length (7.5–16.0 μm) and density (370,000–900,000 filaments per mm^2) (Khannoon et al., 2013) to those of *Gonatodes* (Table 5), they have considerably greater diameters (1.3–1.8 μm) and take the form of rods or flattened, blade-like plates capable of being adpressed to the surface through compression via apposition of the digits (Herrel et al., 2013). *Gonatodes*, in contrast, essentially hangs from its digits on vertical surfaces

(Persaud et al., 2003), and frictional and adhesive interactions are thus much more likely to be associated with specific directions of loading along the long axes of the digits. The spinules on the digits of such species (Fig. 8c–e) show an arrangement consistent with directionality and potentially with gravity-induced frictional loading along the digital long axes. The bifurcation of the epidermal spinules on the friction plates of *G. vittatus* (Fig. 9d) likely enhances frictional capabilities by reducing the bending stiffness of the terminal branches, thereby increasing the available surface area of contact (Khannoon et al., 2013) when the spinules are distorted as the friction plates are pushed against the substratum. Such bifurcated spinules are also present in *G. humeralis* (Fig. 10g) in locations proximal to true setae (Fig. 10c) on the subinflection scales (the friction plates), suggesting that the branching of setae is inherited from structures that were already branched (Russell et al., 2007; Peattie, 2008).

Overall, our findings show that the range of digit form in the ancestrally padless gekkotan genus *Gonatodes* is diverse, as are the habitat preferences and mode of substratum exploitation among its species. This diversity enabled us to assess how changes of digit proportions, scalation, and epidermal micro-ornamentation have been integrated in the transition from friction enhancement to the ability to adhere via subdigital setae. Changes in the pes and manus have proceeded somewhat differently, in association with the structural differences between these two renditions of the tetrapod autopodium. The transitional arguments set forth for *Gonatodes* are corroborated by our observations of the digits of the adhesively well-studied *Gekko gecko*, which exhibits on its subdigital lamellae (lying proximad of its muscularly controlled scanners) the entire array of subdigital micro-ornamentation evident on the incipient subdigital pads of *Gonatodes humeralis*. Furthermore, we note that *G. humeralis* exploits habitat higher in the canopy than any of its congeners, and is able to cling to low friction surfaces (as well as to the vertical walls of glass and plastic terraria), which is atypical of the genus. This suggests that the acquisition of adhesive functionality may be associated with ecological release, and that the sit-and-wait foraging strategy of gekkotans may have been instrumental in establishing the directionality typical of the gekkotan adhesive apparatus.

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