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MORPHOLOGY OF CUTANEOUS SENSE ORGANS OF GEKKONID GECKOS (SQUAMATA: GEKKONIDAE): STRUCTURAL VARIATION IN THE MOST DIVERSE GEKKOTAN FAMILY

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ABSTRACT. Cutaneous sensory organs (sensilla) are mechanoreceptive structures present in the skin of squamate reptiles. In gekkotan lizards these structures are characterized by a raised eminence, the button, which bears one or more elongate hair-like bristles as well as a field of shorter spinules. Variation in the dimensions of these structures and in the number and elaborations of the bristles have been well characterized in the limbless pygopodid gekkotans and their tetrapodal relatives in the Diplodactylidae and Carphodactylidae, but patterns of variation in the Gekkonidae, by far the most diverse and species-rich clade of gekkotans, remain unexplored. We used scanning electron microscopy to examine and characterize the sensilla of 47 species representing 11 major clades of gekkonids, as well as representatives of other gecko families. Variation in morphology across gekkonid sensilla exceeds that observed in other gecko families, with bristle number varying from zero to 29 and bristle length from 3 to 50 μm . There is some phylogenetic signal in sensillar morphology, particularly within genera, but there is no association between mechanoreceptor dimensions and overall body size. In some taxa there is evidence that bristle length and bristle number are inversely related. Intraspecific variation in receptor size and configuration, both between individuals and across different body regions, is clearly present but remains insufficiently documented.

KEY WORDS: cutaneous sensilla; geckos; Gekkonidae; Gekkota; mechanoreceptors; scanning electron microscopy

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INTRODUCTION

Cutaneous sensory organs, or cutaneous sensilla (hereafter, sensilla), are microscopic structures elaborated from the corneous keratinized epidermis and immediately underlying tissues of squamate reptiles (Leydig, 1868, 1876; Cartier, 1872; Todaro, 1878; Maderson, 1965; Hiller, 1971, 1976, 1977, 1978; Düring and Miller, 1979; Bauer and Russell, 1988; Ananjeva et al., 1991; Alibardi, 2021). They are distributed variably across the body of squamates (Bauer and Russell, 1988; Riedel and Schwarzkopf, 2022) but are typically aggregated most densely on the labial (Ananjeva et al., 1991; Nikitina and Ananjeva, 2003), digital (Schmidt, 1912b; Audy, 1953; Hiller, 1968, 1971; Schleich and Kästle, 1986; Bauer and Russell, 1988), and caudal (Hiller, 1971; Bauer and Russell, 1988; Matveyeva and Ananjeva, 1995; Russell et al., 2014) scales. Each sensillum is characterized by a raised, circular, domed eminence, the button, from the center of which, in most cases, one or more hair-like structures, called bristles (Hiller, 1971, 1978), emerge. Upon mechanical deformation of the button or displacement of the bristle(s), signals are generated and transmitted by the nervous system, thereby conveying pertinent information about the environment (Miller and Kasahara, 1967; Hiller, 1978). This sensory mechanism can, for example, prompt behavioral responses such as those associated with moving in a complex environment (Spinner et al. 2013; Riedel et al., 2015; Crowe-Riddell et al., 2016) or determining at what location along the tail the autotomic reflex is initiated in response to predatory threat (Russell et al., 2014). In addition to being a source of mechanical stimuli, cutaneous sensilla have been hypothesized to be polyfunctional (Riedel et al., 2019), but the potential additional functional roles have yet to be

physiologically demonstrated. Surveys of the surface structure of the gekkotan integument (Hiller, 1971; Bauer and Russell, 1988; Matveyeva and Ananjeva, 1995; Spinner et al., 2013; Riedel et al., 2019) indicate that there is correlation between the morphology of sensilla and both familial-level phylogenetic relationships and environmental parameters.

Aside from pygopodoids (pygopodids, carphodactylids, and diplodactylids) (Riedel et al., 2019; Dujsebayaeva et al., 2021; Riedel and Schwarzkopf, 2022), which account for only 11.1% of all gekkotan species (Uetz et al., 2021), descriptions and illustrations of gecko mechanoreceptors are largely represented by isolated and taxonomically narrow studies devoid of a broader comparative framework. This shortcoming is due, in part, to the absence, until quite recently, of a well-supported gekkotan phylogeny with resolution at the familial and generic level (e.g., Gamble et al., 2008, 2015). The taxonomic extent of coverage of gekkotan sensilla structure incorporating qualitative or quantitative descriptive data, or both (including that for the Diplodactylidae and Carphodactylidae before the work of Riedel et al., 2019), is summarized in Tables 1 and 2 for non-gekkonid and gekkonid geckos, respectively.

The relatively extensive sampling of the cutaneous sensilla of the Diplodactylidae and Carphodactylidae shows that most diplodactylid sensilla are single-bristled and seemingly exhibit little structural variation (Bauer and Russell, 1988; Riedel et al., 2019; Riedel and Schwarzkopf, 2022; see also Cartier, 1872; Hiller, 1971; Russell and Bauer, 1987), whereas those of carphodactylids exhibit diverse morphologies (Bauer and Russell, 1988; Riedel et al., 2019; Riedel and Schwarzkopf, 2022), with variation in bristle number, length, surface ornamentation, and button diameter (Table 1).

TABLE 1. SUMMARY OF THE QUALITATIVE AND QUANTITATIVE DATA REPORTED IN THE LITERATURE FOR SENSILLA OF THE GEKKOTAN FAMILIES EXCLUSIVE OF THE GEKKONIDAE. THE DATA PRESENTED BY RIEDEL ET AL. (2019) FOR THE CARPHODACTYLIDAE AND DIPLODACTYLIDAE ARE NOT INCLUDED HERE AND ARE DEALT WITH IN TABLE 3 AND ELSEWHERE IN THE TEXT.^a QUANTITATIVE DATA ARE PROVIDED UNDER “BRISTLE LENGTH” AND “BUTTON WIDTH;” QUALITATIVE STATEMENTS ABOUT PROPORTIONS DERIVED FROM IMAGES ARE LISTED UNDER “BRISTLE LENGTH RELATIVE TO WIDTH OF BUTTON.” FORM OF BRISTLE IS SIMPLE, WITHOUT SIDE HAIRS OR SUBDIVISIONS, UNLESS OTHERWISE INDICATED.

Family	Species	No. of Bristles per Sensillum	Bristle Length Relative to Width of Button	Form of Bristle	Bristle Length (μm)	Button Width (μm)	Button Width to Bristle Length Ratio
Carphodactylidae	<i>Nephurus asper</i>	3 ¹³		Bristle with side hairs ¹	20 ¹	15.7–22.6 ¹	0.79–1.13
	<i>Nephurus levis</i>			Bristle with side hairs ¹³	12–22 ¹³	15 ¹³	1.25–0.68
	<i>Phyllurus caudiamulatus</i>			Bristle with side hairs ¹	22.2 ¹	19.4 ¹	0.87
	<i>Phyllurus platyrus</i>	1 ⁵		Bristle with side hairs ¹	35 ⁵	30 ⁵	0.86
Pygopodidae	<i>Uvidicolus sphyrurus</i>	9 ¹		Bristle with side hairs ¹¹	15 ¹	22.8 ¹	1.52
	<i>Lialis jicari</i>	4 ¹⁴		Bristle with side hairs ¹⁷	2.1–9.3 ¹⁷	19–20 ¹⁷	2.20–9.04
	<i>Pygopus lepidopodus</i>	7 ⁴		Bristle with side hairs ¹⁶	3.3–15.7 ¹⁶	15.7–17.5 ¹⁶	1.11–4.76
Diplodactylidae	<i>Pygopus nigriceps</i>				12–18 ⁴	12–22 ⁴	1.00–1.22
	<i>Bavayia sauvagii</i>				12 ¹	13 ¹	1.08
	<i>Correlophus sarasinorum</i>	1 ¹			20 ¹	22 ¹	1.10
	<i>Dactylocnemis pacificus</i>	1 ⁴			8 ⁴	13 ⁴	1.63
Eublepharidae	<i>Pseudothecadactylus lindneri</i>	1 ¹			30–34 ¹	14–21 ¹	0.47–0.61
	<i>Rhacodactylus auriculatus</i>	1 ¹			25 ¹	20 ¹	0.80
	<i>Woodworthia maculatus</i>				22 ¹	16 ¹	0.73
	<i>Colonyx variegatus bogerti</i>	2 ⁵			40 ⁵	20 ⁵	0.50
Phyllodactylidae	<i>Eublepharis macularius</i>	1 ^{5,18}			52 ⁵	20 ⁵	0.38
	<i>Goniurosaurus luii</i>	1 ^{11,14}	Much longer ¹⁴	Bristle with side hairs ¹¹			
	<i>Phyllodactylus guttatus</i>	1–5 ²	Longer ²		20 ³	19 ³	0.95
	<i>Phyllodactylus hasselquistii</i>	4 ⁸	Approx. equal ⁵				
Tarentolidae	<i>Tarentola annularis relicta</i>	1 ⁹	Shorter ⁹				
	<i>Tarentola boettgeri</i>	4 ⁸	Longer ⁸		60 ⁵	29 ⁵	0.48
	<i>Tarentola chazaliae</i>	1 ⁵					
	<i>Tarentola darwini</i>	2–4 ^{8,10}	Approx. equal ^{8,10}				
Tarentolidae	<i>Tarentola deserti</i>	2 ⁸	Longer ⁸				
	<i>Tarentola mauritanica</i>	1 ^{6,7,15}	Longer ⁸		18 ^{5,6}	19 ⁵	1.06
		1–4 ^{5,14}					
		5 ⁸					
Tarentolidae	<i>Tarentola neglecta</i>	5 ⁸	Shorter ⁸				
	<i>Tarentola parvicarinata</i>	6 ⁸	Longer ⁸				
	<i>Tarentola protogigas</i>	2 ^{8,10}	Much longer ^{8,10}				

TABLE 1. Continued.

Family	Species	No. of Bristles per Sensillum	Bristle Length Relative to Width of Button	Form of Bristle	Bristle Length (μm)	Button Width (μm)	Button Width to Bristle Length Ratio
Sphaerodactylidae	<i>Euleptes europaea</i>	0 ¹⁴		No bristles, just slightly longer "hairs" ¹⁴			
	<i>Sphaerodactylus cinereus</i>	2-3 ¹²	Slightly longer ¹²		10 ³	13 ³	1.30
	<i>Sphaerodactylus roosevelti</i>	1-2 ³			8 ³	13 ³	1.63
	<i>Teratoscincus scincus</i>						

^aSources of data are indicated by superscript numbers as follows: ¹Bauer and Russell (1988); ²Darwish (2012); ³Dujsebeyeva (1995); ⁴Dujsebeyeva et al. (2021); ⁵Hiller (1971); ⁶Hiller (1976); ⁷Hiller (1977); ⁸Joger (1984a); ⁹Joger (1984b); ¹⁰Joger (1984c); ¹¹Koppetsch et al. (2020); ¹²Röll (1995); ¹³Russell and Bauer (1987); ¹⁴Sammartano (1980); ¹⁵Schmidt (1912a); ¹⁶Shea (1993); ¹⁷Spinner et al. (2013); ¹⁸Whimster (1980).

TABLE 2. SUMMARY OF THE QUALITATIVE AND QUANTITATIVE DATA REPORTED IN THE LITERATURE FOR SENSILLA OF THE GEKKONIDAE. ^aRÖLL (1999) PROVIDES RANGES AND MEANS FOR THE MEASUREMENTS TAKEN—WE REPORT ONLY THE MEAN VALUES HERE. QUANTITATIVE DATA ARE PROVIDED UNDER “BRISTLE LENGTH” AND “BUTTON WIDTH.” QUALITATIVE STATEMENTS ABOUT PROPORTIONS DERIVED FROM IMAGES ARE LISTED UNDER “BRISTLE LENGTH RELATIVE TO WIDTH OF BUTTON.” FORM OF BRISTLE IS SIMPLE, WITHOUT SIDE HAIRS OR SUBDIVISIONS, UNLESS OTHERWISE INDICATED.

Clade	Species	No. of Bristles per Sensillum	Bristle Length Relative to Width of Button	Form of Bristle	Bristle Length (μm)	Button Width (μm)	Button Width to Bristle Length Ratio
<i>Gekko</i>	<i>Gekko gekko</i>	1 ^{5,6,9}			60 ⁵ 10-25 ⁹	27 ⁵ 15-22 ⁹	0.45 0.88-1.50
	<i>Lepidodactylus lugubris</i>	1-4 ⁵			23 ⁵	16 ⁵	0.70
	<i>Cyrtodactylus peguensis</i>	1 ¹⁰					
<i>Hemidactylus</i>	<i>Hemidactylus turcicus</i>	1-4 ¹²	Much longer ¹⁰				
	<i>Mediodactylus kotschyi</i>	1-4 ¹²		May be bifid or even more subdivided ¹²			
	<i>Stenodactylus petrii</i>	At least 4 ¹	Shorter ¹				
<i>Stenodactylus</i>	<i>Tropicolotes steudneri</i>	1-6 ¹⁸					
	<i>Tropicolotes tripoltanus</i>	1-2 ⁴	Longer ¹⁸				
	<i>Cyrtopodion scabrum</i>	1-3 ¹⁸					
<i>Agamura-Bumopus</i>	<i>Tenuidactylus fedtschenkoi</i>	2-4 ⁴					
		1-3 ²			20 ²	19 ²	0.95

TABLE 2. Continued.

Clade	Species	No. of Bristles per Sensillum	Bristle Length Relative to Width of Button	Form of Bristle	Bristle Length (µm)	Button Width (µm)	Button Width to Bristle Length Ratio
<i>Uroplatus</i>	<i>Uroplatus fimbriatus</i>			Many short bristles, fewer long ones ^{14,15}			
<i>Lygodactylus</i>	<i>Phelsuma andamanensis</i>	1 ¹¹			21.0 ¹¹	16.9 ¹¹	0.80
	<i>Phelsuma astriata</i>	1 ¹¹			22.2 ¹¹	13.9 ¹¹	0.63
	<i>Phelsuma guentheri</i>	1–3 ¹¹			26.7 ¹¹	17.8 ¹¹	0.67
	<i>Phelsuma guineai</i>	1–2 ¹¹			20.9 ¹¹	14.4 ¹¹	0.69
	<i>Phelsuma laticauda</i>	1 ¹⁵	Long ¹⁵				
	<i>Phelsuma madagascariensis</i>	1 ¹¹			25 ⁵ 32.9 ¹¹	22 ⁵ 14.5 ¹¹	0.88 0.44
<i>Paroedura-Ebenavia</i> <i>Blaesodactylus-Geckolepis</i>	<i>Phelsuma nigristriata</i>	1 ⁷		Trifid, one ramus longer than others ⁷			
	<i>Phelsuma ornata</i>	1–3 ¹¹			27.6 ¹¹	14.9 ¹¹	0.54
	<i>Phelsuma sundbergi</i>	1 ¹¹			25.8 ¹¹	16.5 ¹¹	0.64
	<i>Rhoptropella ocellata</i>	12–29 ¹¹			8.6 ¹¹	24.4 ¹¹	2.84
	<i>Paroedura picta</i>	1 ³			20 ³	19 ³	0.95
	<i>Geckolepis polylepis</i>	1 ^{14,16}	Very long: 7× button diameter ^{14,16}		60 ¹⁶		
<i>Pachydactylus</i>	<i>Chondrodactylus bibronii</i>						
	<i>Chondrodactylus laevis</i>	1 ¹³		Bifid ¹³			
	<i>Pachydactylus punctatus</i>	1 ¹¹	Much longer ⁸		20.7 ¹¹	13.4 ¹¹	0.65
	<i>Pachydactylus rangei</i>	3–4 ¹³		Bifid ¹³			
	<i>Rhoptropus afer</i>	1–4 ¹¹			23.1 ¹¹	16.4 ¹¹	0.71
	<i>Rhoptropus barnardi</i>	1–2 ¹⁰			25.3 ¹¹	14.6 ¹¹	0.58

^aSources of data are indicated by superscript numbers as follows: ¹Darwish (2012); ²Dujsebaveva (1995); ³Dujsebaveva et al. (2021); ⁴El-Sayyad et al. (2009); ⁵Hiller (1971); ⁶Hiller (1977); ⁷Hiller (2009); ⁸Joger (1984a); ⁹Lauff et al. (1993); ¹⁰Peattie (2008); ¹¹Röll (1999); ¹²Sammartano (1980); ¹³Sammartano (1983); ¹⁴Schmidt (1911); ¹⁵Schmidt (1912a); ¹⁶Schmidt (1912b); ¹⁷Schmidt (1920); ¹⁸Schneider (1990).

Surprisingly little is known about potential variation of cutaneous sensilla morphology within the other gekkotan families. For the Phyllodactylidae, and Sphaerodactylidae, which together account for 387 species and 18.0% of gekkotan diversity (Uetz et al., 2021), only five genera and 15 species (half of which represent a single genus—*Tarentola*) have been examined for dimensional attributes and only seven species are represented by quantitative data (Table 1). For the Eublepharidae (44 species), only three genera and three species have been examined (Table 1), although data for all six constituent genera are forthcoming (see Nazarov et al., 2021).

For the Gekkonidae, which comprise 1,469 species, accounting for 68.7% of gekkotan diversity (Uetz et al., 2021), documentation of sensilla structure is even less representative. The earliest gekkonid taxa studied were *Gekko gekko*, *Gekko kuhli*, *Cyrtodactylus* cf. *marmoratus*, “*Ptyodactylus natalensis*” [unidentifiable] (Cartier, 1872), *Phelsuma laticauda* (Schmidt, 1912a), *Phelsuma dubia* (Schmidt, 1912b), *Uroplatus fimbriatus* (Schmidt, 1912b, 1920), and *Gekko polyplepis* (Schmidt, 1912b). Such early observations were descriptive and lacked dimensional data. Later studies employing scanning electron micrographic (SEM) imaging permitted proportions to be assessed, measurements to be made, and bristles to be counted, but to date only 17 genera and 28 species (eight of which occur in a single genus—*Phelsuma*) have been examined (Table 2).

Collectively the available information for gekkotan families other than the Carphodactylidae and Diplodactylidae reveal that, compared with the data presented by Riedel et al. (2019), the width of the sensillar button falls mostly within the range reported for diplodactylids (14.6–20.2 μm), with only four species occupying the range (21.7–26.1 μm)

reported for carphodactylids (Tables 1, 2). Bristle number per sensillum is generally low, ranging up to six, revealing that some taxa exceed the reported diplodactylid maximum of two (Riedel et al., 2019) and extend into the range reported for carphodactylids (Tables 1, 2). Bristle length mostly exceeds button width (Tables 1, 2), although the reporting of this value for phyllodactylids varies considerably (Table 1). Among the sphaerodactylids, *Euleptes europaea* has been reported to lack bristles on its sensilla (Sammartano, 1980) and to bear short “hairs” only slightly longer than those covering the adjacent epidermis (Table 1). Among the Gekkonidae, *Rhoptropella ocellata* has been reported to bear 12–29 bristles per sensillum, far exceeding the maximum of nine recorded for carphodactylid sensilla by Bauer and Russell (1988) and Riedel et al. (2019), with these being much shorter than the width of the button they surmount (Röll, 1999). *Rhoptropella* is the sister taxon of *Phelsuma* (Gamble et al., 2015) but seemingly differs markedly from it in both number of bristles per sensillum and relative bristle length (Table 2). The data summarized in Tables 1 and 2 thus indicate that the structure of sensilla among geckos may vary considerably.

In light of what has so far been documented for gekkotans (Tables 1, 2; Riedel et al., 2019), we herein conduct a phylogenetically diverse comparative survey of cutaneous sense organ structure of the Gekkonidae, by far the most diverse gekkotan family, as a first foray into exploring the extent of their variation in this family.

MATERIALS AND METHODS

Our survey includes data for various regions (trunk dorsum, tail, snout, head, labial scales, etc.) of the integument for 11 major clades, 23 genera, and 47 species of the

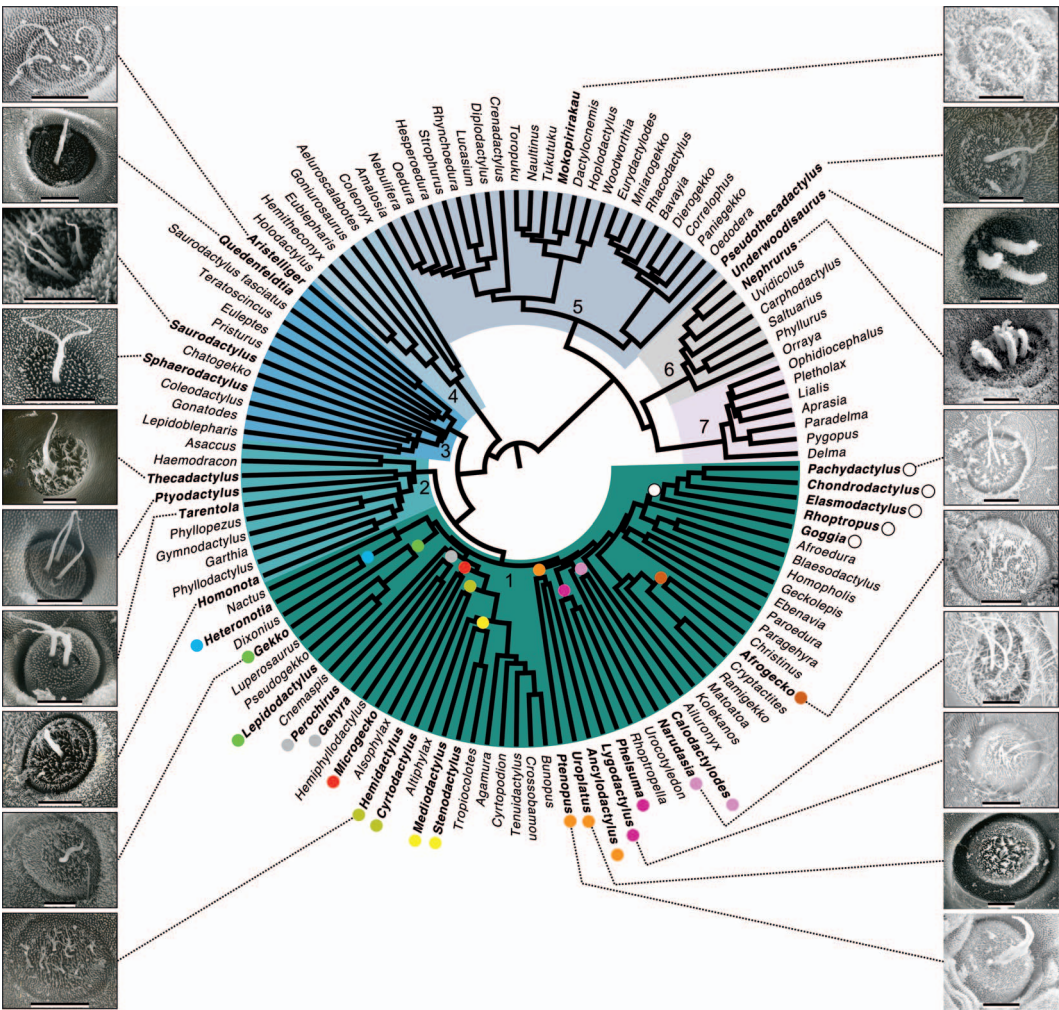


Figure 1. Overview of the diversity of form in gekkotan cutaneous sensilla as revealed by scanning electron microscopy (SEM). Generic phylogeny of the Gekkota modified from Gamble et al. (2015). Gekkotan families: 1) Gekkonidae, 2) Phyllodactylidae, 3) Sphaerodactylidae, 4) Eublepharidae, 5) Diplodactylidae, 6) Carphodactylidae, 7) Pygopodidae. Genera examined in this study are bolded. Scale bars = 10 μm. The clades within the Gekkonidae that include species examined in this study are indicated by colored circles (with equivalent circles placed adjacent to the bolded generic names represented in our data set). Counterclockwise (from left to right) the examined clades are as follows: *Heteronotia*, blue; *Gekko*, bright green; *Gehyra*, grey; *Microgecko*, red; *Hemidactylus*, olive green; *Stenodactylus*, yellow; *Uroplatus*, orange; *Lygodactylus*, purple; *Calodactylodes*, pink; *Afrogecko*, brown; *Pachydactylus*, white with black border.

Gekkonidae (Fig. 1; Table 3). Our sample includes five major clades not previously examined for sensillar structure among the Gekkonidae (Tables 2, 3) and increases the total number of gekkonid species investigated

in this regard (Table 3) by 40. Seven of the species we examine have been examined previously for sensillar structure (Tables 2, 3).

Scanning electron micrographs were acquired at Villanova University (Villanova,

TABLE 3. SPECIMENS VISUALIZED AND MEASUREMENTS TAKEN FROM GEKKOTAN CUTANEOUS SENSILLA. MEASUREMENTS WERE ONLY TAKEN FOR GEKKONID TAXA. GEKKONID TAXA ARE CLUSTERED BY CLADE (SEE FIG. 1) AND ARE LISTED IN THE SAME SEQUENCE AS DEPICTED IN FIGURE 1. ^a FOR BRISTLE DIAMETER AND BRISTLE LENGTH THE VALUES REPORTED ARE MAXIMUM VALUES IF THE SENSILLUM IN QUESTION BEARS MORE THAN ONE BRISTLE. RATIOS OF DIAMETER TO LENGTH OF BRISTLES ARE CALCULATED FROM THE MAXIMUM VALUES, WHERE APPROPRIATE. COMPARISON OF VALUES FOR THE NUMBER OF BRISTLES CARRIED BY A SENSILLUM AND SENSILLUM BUTTON DIAMETER WITH THE DATA REPORTED BY RIEDEL ET AL. (2019) FOR DIPLODACTYLID AND CARPHODACTYLID GECKOS IS ACCOMPLISHED BY SUPERSCRIPT NUMBER DESIGNATIONS. ? = NOT REPORTED IN CITED WORK; N/A = NOT APPLICABLE (NO BRISTLES PRESENT); — = CLADE NOT LISTED (NON-GEKKONID GEKKOTANS).

Family	Clade	Species	ID	Sensillum Location	No. of Bristles ^b	Diameter (µm)	Bristle Length (µm) ^c	Diameter : Bristles Ratio
G	<i>Heteronotia</i>	<i>Heteronotia spelea</i>	MCZ R158550	Unknown	1 (bifid) ²	12.54 ¹	9.88	1.27
				Unknown	1 (bifid) ²	14.44 ¹	8.74	1.65
				Unknown	1 (bifid) ²	15.84 ²	11.70	1.35
				Unknown	1 ²	16.15 ²	15.30	1.06
G	<i>Gekko</i>	<i>Gekko intermedius</i>	MCZ R166436	Unknown	1 (bifid) ²	15.40 ²	16.10	0.96
G	<i>Gekko</i>	<i>Gekko japonicus</i>	MCZ R255842	Tail	1 ²	26.78 ⁵	10.40	2.58
G	<i>Gekko</i>	<i>Lepidodactylus labialis</i>	MCZ R142948	Unknown	1 ²	19.20 ²	18.00	1.07
G	<i>Gehyra</i>	<i>Perochirus ateles</i>	MCZ R159979	Unknown	1 ²	18.88 ²	15.93	1.14
				Unknown	1 ²	15.00 ²	?	?
G	<i>Gehyra</i>	<i>Gehyra punctata</i>	APR 046	Labial	6+ ³	17.02 ²	18.40	0.93
G	<i>Gehyra</i>	<i>Gehyra variegata</i>	MCZ R79966	Snout	7 ³	13.92 ¹	6.00	2.32
				Rostrum	3+ ³	14.44 ¹	10.07	1.43
				Tail	10+ ⁴	15.36 ²	10.32	1.49
				Tail	10+ ⁴	14.08 ¹	9.84	1.43
G	<i>Microgecko</i>	<i>Microgecko helenae</i>	MCZ R84041	Unknown	5 ³	15.85 ²	5.12	3.10
				Unknown	4 ³	14.40 ¹	9.18	1.57
				Unknown	5 ³	16.50 ²	9.90	1.67
G	<i>Microgecko</i>	<i>Microgecko persicus</i>	MCZ R124315	Unknown	4 ³	15.61 ²	10.24	1.52
G	<i>Hemidactylus</i>	<i>Hemidactylus angulatus</i>	MCZ R102040	Canthal	0 ¹	13.3 ¹	N/A	N/A
				Snout	1 ²	10.36 ¹	14.42	0.72
			MVZ 75491	Dorsal	1 (bifid) ²	11.61 ¹	15.66	0.74
				Labial	1 ²	13.50 ¹	22.22	0.61
G	<i>Hemidactylus</i>	<i>Hemidactylus imbricatus</i>	MCZ R84083	Dorsal	1 ²	11.78 ¹	23.25	0.51
				Dorsal	1 ²	12.48 ¹	25.48	0.49
			Unknown	Unknown	1 ²	10.98 ¹	12.24	0.90
G	<i>Hemidactylus</i>	<i>Hemidactylus mabouia</i>	MCZ R47308	Unknown	1 ²	13.50 ¹	10.35	1.30
				Unknown	6 ³	15.82 ²	4.20	3.77
G	<i>Hemidactylus</i>	<i>Cyrtodactylus derongo</i>	MCZ R152423	Unknown	1 (bifid or 2) ²	14.4 ¹	8.80	1.64
G	<i>Hemidactylus</i>	<i>Cyrtodactylus lawderamus</i>	MCZ R3152	Unknown	1 ²	14.4 ¹	16.90	0.85

TABLE 3. Continued.

Family	Clade	Species	ID	Sensillum Location	No. of Bristles ^b	Diameter (μm)	Bristle Length (μm) ^c	Diameter : Bristles Ratio
G	<i>Hemidactylus</i>	<i>Cyrtodactylus malayanus</i>	MCZ R102031	Head	1 ²	13.86 ¹	12.46	1.12
				Head	1 ²	15.18 ²	13.11	1.16
				Head	1 (bifid) ²	11.90 ¹	12.60	0.94
G	<i>Hemidactylus</i>	<i>Cyrtodactylus mimikanus</i>	MCZ R142304	Head	1 (bifid) ²		13.44	
				Unknown	1 ²	12.92 ¹	16.15	0.80
				Snout	2 ²	16.50 ²	18.90	0.87
G	<i>Stenodactylus</i>	<i>Mediodactylus kotschy</i>	MCZ R38457	Snout	2 (bifid) ²	18.70 ²	16.50	1.13
				Unknown	3 ³	21.00 ³	7.20	2.92
				Unknown	7 ³	18.00 ²	12.00	1.50
G	<i>Uroplatus</i>	<i>Plenopus garrulus</i>	AMB 8640	Unknown	7 ³	21.10 ³	9.72	2.17
				Labial	1 ²	21.60 ³	20.25	1.07
				Dorsal	1 ²	23.0 ⁴	12.50	1.84
G	<i>Uroplatus</i>	<i>Uroplatus fimbriatus</i>	MCZ R142062	Labial	1 ²	24.6 ⁴	23.40	1.05
				Head	0 ¹	33.00 ⁵	N/A	N/A
				Labial	2 ²	18.75 ²	9.50	1.97
G	<i>Lygodactylus</i>	<i>Lygodactylus capensis</i>	MCZ R21498	Dorsal	2 ²	18.09 ²	16.20	1.12
				Unknown	2+ ²	17.82 ²	12.69	3.24
				Unknown	1 ²	12.20 ¹	15.00	0.81
G	<i>Lygodactylus</i>	<i>Lygodactylus chobiensis</i>	MCZ R163329	Unknown	3 ³	24.57 ⁴	10.80	2.28
				Unknown	4+ ³	19.92 ²	6.00	3.32
				Unknown	4+ ³	19.92 ²	3.36	5.93
G	<i>Lygodactylus</i>	<i>Lygodactylus mirabilis</i>	MCZ R67957	Unknown	4+ ³	19.65 ²	6.60	3.32
				Unknown	1 ²	13.00 ¹	19.5	0.67
				Frontal	5 ³	17.92 ²	3.52	5.09
G	<i>Calodactylodes</i>	<i>Calodactylodes aureus</i>	AMB H-8530	Unknown	1 ²	15.39 ²	21.06	0.73
				Unknown	5 ³	17.64 ²	17.64	1.00
				Unknown	4 ³	15.60 ²	14.00	1.11
G	<i>Calodactylodes</i>	<i>Calodactylodes picturatus</i>	MCZ R46801	Unknown	4 ³	14.82 ²	19.00	0.78
				Unknown	4 ³	19.08 ²	19.80	0.96
				Labial	4 ³	?	?	?
G	<i>Calodactylodes</i>	<i>Calodactylodes mirabilis</i>	AMB 5722	Labial	1 ²	24.30 ⁴	13.50	1.80
				Dorsal	4 ³	17.82 ²	5.94	3.00
				Dorsal	15+ ⁴	21.90 ⁴	11.10	1.97
G	<i>Pachydactylus</i>	<i>Pachydactylus gemmula</i>	AMB 3347	Dorsal	10 ⁴	20.70 ³	9.60	2.16
				Dorsal	4 ³			
				Labial				

TABLE 3. Continued.

Family	Clade	Species	ID	Sensillum Location	No. of Bristles ^b	Diameter (µm)	Bristle Length (µm) ^c	Diameter : Bristles Ratio
G	<i>Pachydactylus</i>	<i>Rhopropus afer</i>	MCZ R43163	Unknown	1 ²	14.40 ¹	17.28	0.83
				Unknown	1 ²	15.54 ²	23.73	0.65
				Unknown	2 ²	18.36 ²	15.12	1.21
G	<i>Pachydactylus</i>	<i>Rhopropus barnardi</i>	AMB 4074	Unknown	1 (bifid) ²	13.26 ¹	17.68	0.75
				Unknown	1 (bifid) ²	14.88 ²	12.00	1.24
G	<i>Pachydactylus</i>	<i>Rhopropus boultoni</i>	AMB 1592	Unknown	2 ²	14.74 ²	15.84	0.93
				Unknown	1 ²	15.30 ²	28.08	0.54
				Unknown	1 ²	12.76 ¹	13.64	0.94
G	<i>Pachydactylus</i>	<i>Rhopropus diporus</i>	AMB 1748	Dorsal	3+ ³	?	?	?
G	<i>Pachydactylus</i>	<i>Elasmodactylus tetensis</i>	Unknown	Unknown	1 (bifid) ²	16.38 ²	14.30	1.15
G	<i>Pachydactylus</i>	<i>Chondrodactylus angulifer</i>	MVZ 144799	Labial	1 ²	18.70 ²	19.71	?
				Labial	2 ²	14.58 ²	19.71	0.74
				Labial	1 ²	15.68 ²	22.40	0.70
				Unknown	1 (bifid) ²	10.95 ¹	31.50	0.35
G	<i>Pachydactylus</i>	<i>Chondrodactylus bibronii</i>	AMB 2072	Dorsal	1 ²	13.60 ¹	11.90	1.14
			AMB 8578	Unknown	1 ²	15.50 ²	49.50	0.31
G	<i>Pachydactylus</i>	<i>Chondrodactylus laevigatus</i>	AMB 2212	Unknown	1 ²	12.96 ¹	39.60	0.33
			MCZ R67795	Unknown	1 (bifid) ²	14.40 ¹	12.60	1.14
G	<i>Pachydactylus</i>	<i>Pachydactylus wahlbergii</i>	TM 41428	Dorsal	1 (bifid) ²	12.80 ¹	17.60	0.73
			AMB 3905	Unknown	1 ²	24.18 ⁴	23.14	1.04
G	<i>Pachydactylus</i>	<i>Pachydactylus austeni</i>	CAS 186317	Unknown	1 ²	10.80 ¹	18.90	0.57
G	<i>Pachydactylus</i>	<i>Pachydactylus caraculicus</i>	AMB 1699	Unknown	1 ²	14.08 ¹	20.68	0.68
G	<i>Pachydactylus</i>	<i>Pachydactylus scutatus</i>	AMB 4041	Unknown	2 ²	15.60 ²	15.60	1.00
G	<i>Pachydactylus</i>	<i>Pachydactylus serral</i>	AMB 2201	Unknown	1 ²	11.90 ¹	42.00	0.28
G	<i>Pachydactylus</i>	<i>Pachydactylus vansoni</i>	CAS 195506	Unknown	1 (bifid) ²	11.88 ¹	26.19	0.45
G	<i>Pachydactylus</i>	<i>Pachydactylus weberi</i>	AMB 3839	Unknown	2 (or bifid) ²	14.31 ¹	22.95	0.62
C	—	<i>Nephurus deleani</i>	AMB 046	Unknown	9 ³	24.19 ⁴	10.10	2.40
C	—	<i>Underwoodisaurus milii</i>	MCZ R130365	Unknown	3 ³	13.39 ¹	10.48	1.28
D	—	<i>Pseudothecadactylus australis</i>	MCZ R35162	Unknown	1 ²	19.22 ²	23.90	0.80
D	—	<i>Mokopirirakau granulatus</i>	AMB 451	Dorsal	1 ²	17.54 ²	19.66	0.89
S	—	<i>Aristelliger praesignis</i>	MVZ 69636	Dorsal	4 ³	14.83 ²	10.93	1.36
S	—	<i>Queденfeldtia trachyplepharus</i>	MCZ R61122	Unknown	1 ²	15.32 ²	12.24	1.25
S	—	<i>Saurodactylus mauritanicus</i>	MCZ R29937	Unknown	5 ³	11.73 ¹	11.05	1.06
S	—	<i>Sphaerodactylus townsendi</i>	MCZ R101854	Dorsal	1 (bifid) ²	11.94 ¹	16.31	0.73
Ph	—	<i>Thecadactylus rapicauda</i>	MCZ R133085	Unknown	1 ²	19.54 ²	21.21	0.92

TABLE 3. Continued.

Family	Clade	Species	ID	Sensillum Location	No. of Bristles ^b	Diameter (μm)	Bristle Length (μm) ^c	Diameter : Bristles Ratio
Ph	—	<i>Pygodactylus hasselquistii</i>	MCZ R102151	Snout	3 ³	13.35 ¹	15.74	0.85
Ph	—	<i>Tarentola americana</i>	MCZ R19566	Head	3 ³	16.86 ²	18.00	0.94
Ph	—	<i>Homonota darwini</i>	MCZ R73087	Unknown	1 ²	16.85 ²	7.74	2.18

^aAbbreviations: G, Gekkonidae; Ph, Phyllodactylidae; S, Sphaerodactylidae; E, Eublepharidae; D, Diplodactylidae; C, Carphodactylidae; Py, Pygopodidae.
^bFor the number of bristles, the following applies: ¹sensillum without bristles (a feature reported by Riedel et al. [2019] only for three species of diplodactylids); ²one or two bristles—within the range reported for diplodactylids and falling within the lower part of the range reported for carphodactylids; ³three to nine bristles—within the upper end of the carphodactylid range but exceeding the values reported for diplodactylids; ⁴exceeding the upper end of the range reported for carphodactylids.
^cFor sensillum button diameter the following applies: ¹below the lowest value reported for diplodactylids; ²within the range of diameters reported for diplodactylids; ³exceeding the maximum value reported for diplodactylids but falling below the minimal value reported for carphodactylids; ⁴falling within the range reported for carphodactylids; ⁵exceeding the maximum dimension reported for carphodactylids.

Pennsylvania, U.S.A.) and the Museum of Comparative Zoology (MCZ), Harvard University (Cambridge, Massachusetts, U.S.A.). The latter derive from a massive collection of squamate skin SEMs generated by the late Ernest E. Williams and available for study at the MCZ and were imaged following the protocol of Peterson and Williams (1981). In addition to specimens from MCZ, material was examined from the collections of the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); the California Academy of Sciences, San Francisco (CAS); Ditsong National Museum of Natural History, Pretoria, South Africa (TM); and the collections of Aaron M. Bauer (AMB) and Anthony P. Russell (APR). In addition to the 47 gekkonid species mentioned above, opportunistic sampling of carphodactylids (two genera), diplodactylids (two genera), sphaerodactylids (four genera), and phyllodactylids (four genera) was undertaken to provide a broad comparative context for our gekkonid survey (Fig. 1; Table 3) and to allow us to verify previously published statements about the morphology of sensilla (Tables 1, 2). For material examined at Villanova University samples of skin were excised from formalin-fixed, ethanol-stored museum specimens, critical point-dried or -dehydrated in hexamethyldisilazane, sputter coated with gold to a thickness of 10 nm, examined with a Hitachi 570 scanning electron microscope, and imaged on Polaroid type 52 and type 55 film. SEM images used in this paper were scanned from hard copy negatives or prints (all originally generated before 2000).

The following parameters were examined and measured: sensillum location, number of bristles borne (if any) by the sensilla, sensillum button diameter, bristle length, and ratio of bristle length to sensillum button diameter. Because some micrographs were collected by others and all were

generated long ago, we could not control the composition of the images. The sensillum in each image that provided the clearest and most orthogonal view of the bristle(s) was measured. When multiple bristles were present, only the longest were measured. For all of the bristles that were measured, the length was compiled by measuring manually from the images. Each bristle was measured three times and the average value reported. The numbers reported in Table 3 refer to values obtained from each image for a given species.

To place the data in Table 3 into comparative context, the values for setal button diameter and number of bristles per sensillum are compared (by the use of superscript numbers) to the values reported by Riedel et al. (2019) for diplodactylid and carphodactylid geckos. Riedel et al. (2019) noted that sensillum button diameter of diplodactylids ranged from 14.6 to 20.2 μm , and that of carphodactylids from 21.7 to 26.1 μm , intimating an absence of overlap of this dimension between these two clades. The range of dimensions for the button reported for carphodactylids by Riedel et al. (2019), however, is narrower than that indicated by earlier authors (Hiller, 1971; Russell and Bauer, 1987; Bauer and Russell, 1988), whose findings indicate the range to be 13–30 μm (Table 1). In our survey of gekkonid sensilla, however, we employ the value ranges reported by Riedel et al. (2019) because all such data were assembled by one team using a consistent methodology and approach and thus provide an initial baseline for comparison. Riedel et al. (2019) noted that the sensilla of diplodactylids bore zero to two bristles, whereas those of carphodactylids may greatly exceed this number and carry up to nine bristles. When we compare our findings to the diplodactylid and carphodactylid ranges for button diameter and bristle number, we explicitly refer to

the ranges reported by Riedel et al. (2019) and not to the total ranges as revealed in Table 1 (although that for bristle number does not differ between the two sources). Unfortunately, Riedel et al. (2019) did not record bristle length or diameter. Comparison of data with those assembled more opportunistically by other authors for other gekkotans, as summarized in Tables 1 and 2, is made, where appropriate, in the Results.

RESULTS

We present our findings for cutaneous receptor morphology of gekkonid geckos in a clade by clade sequence, following the order of occurrence in Figure 1.

Heteronotia clade

All sensilla diameters sampled fall within the diplodactylid range (Riedel et al., 2019) or slightly below it (Table 1). All sensilla examined bore only one bristle, this sometimes being bifid (Fig. 2A). Bristle length was always shorter than the respective sensillum diameter.

Gekko clade

Generally, the diameters of sensilla in this cluster fall within the diplodactylid range (Table 3). One sensillum on the tail of *Gekko japonicus*, however (Table 3), had a diameter (26.78 μm), greater than that of the largest value reported for carphodactylids by Riedel et al. (2019). The latter demonstrates that sensillum button diameter ranges from small to large in the *Gekko* clade and spans the range reported for both diplodactylid and carphodactylid geckos (Riedel et al., 2019; Table 3). All sensilla encountered bore only a single bristle, which may be bifid (Figs. 2B, C). Bristle length may be greater or smaller than sensillum diameter (Table 3), but only on the tail of *Gekko japonicus* (Fig. 2C) was a

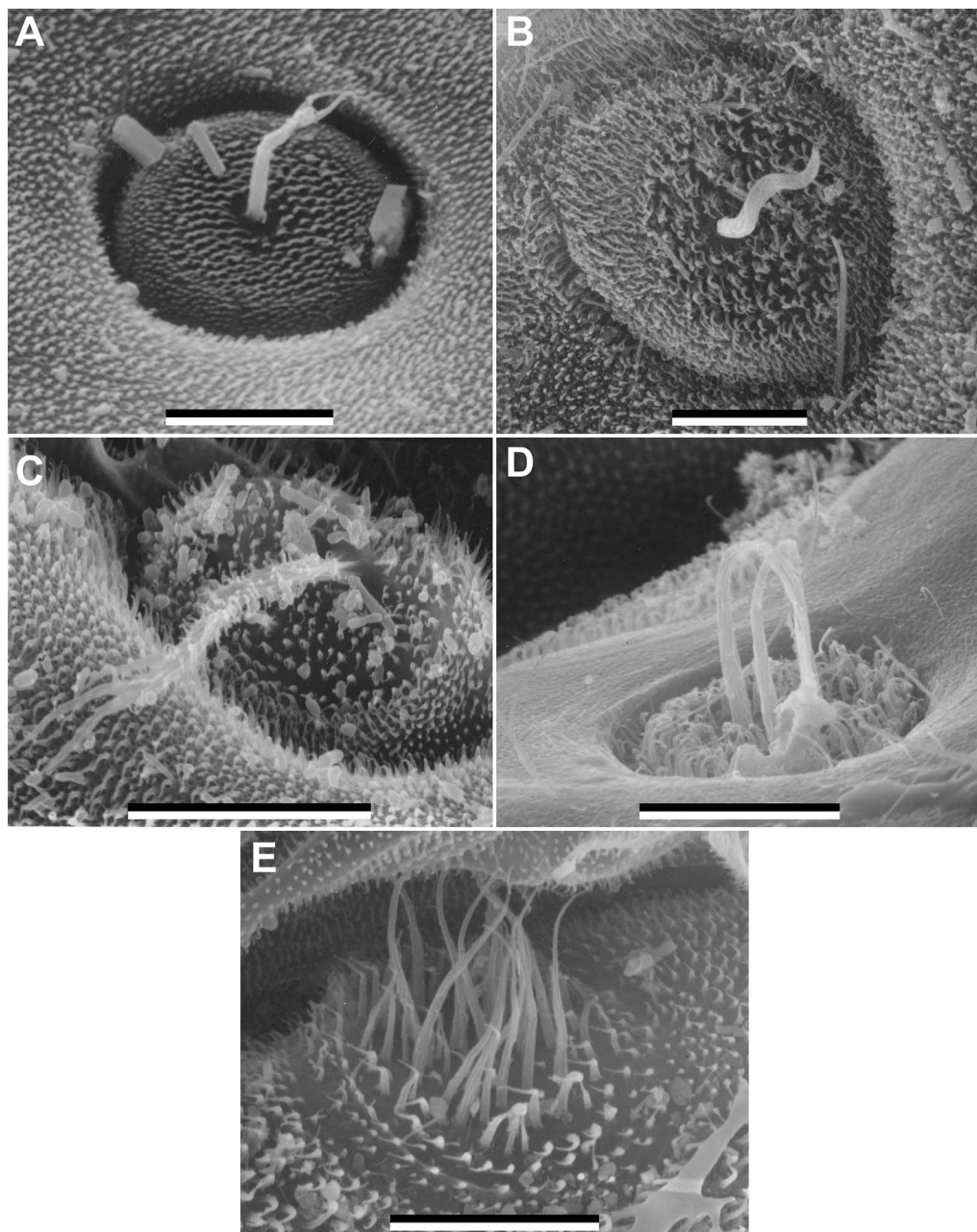


Figure 2. Cutaneous sensilla encountered in the *Heteronotia* (A), *Gekko* (B, C), and *Gehyra* (D, E) clades (see Fig. 1) of the Gekkonidae. All descriptions of size of components relate to data provided in Table 1. A, *Heteronotia spelea*: small-diameter button bearing moderately long bifid bristles; B, *Gekko japonicus*: large-diameter button with a very short bristle; C, *Gekko intermedius*: small-diameter button bearing a moderately long bifid bristle; D, *Gehyra variegata*: small-diameter button bearing multiple unbranched short bristles; E, *Gehyra variegata*: small-diameter button bearing multiple unbranched moderately long bristles. Scale bars = 10 μm .

bristle encountered that was markedly shorter than sensillum diameter, this being associated with a button of very large diameter.

Gehyra clade

Generally, the diameters of sensilla in this cluster fall either within or slightly below the diplodactylid range reported by Riedel et al. (2019) (Table 3). The sensilla of *Gehyra* all carried multiple bristles (Figs. 2D, E), some bearing a bristle complement falling within the range exhibited by carphodactylids (Table 1) and others exceeding the upper end of that range, bearing 10 or more.

Microgecko clade

All taxa examined essentially fall into the range of diameters reported for diplodactylids (Riedel et al., 2019). One value is marginally smaller and two are marginally larger, although not sufficiently so to indicate clear differences from the diplodactylid values. All species examined bear multiple bristles per sensillum, ranging from three to five (Figs. 3A, B), falling within the carphodactylid range (Table 1) and exceeding that of the diplodactylids (Riedel et al., 2019). All of the bristles are relatively short compared with the diameter of the sensillum that bears them (Table 3).

Hemidactylus clade

The diameters of the sensilla examined either fall within the range reported for diplodactylids (Riedel et al., 2019) or fall below the lowest of these values (Table 3). The smallest sensilla diameters among the taxa examined in this study ($< 11.0 \mu\text{m}$) occur in this clade. Almost all taxa examined exhibit one bristle per sensillum (Figs. 3C–E), thus falling within the range of diplodactylids (Riedel et al., 2019; Table 3). One species (*Hemidactylus mabouia*), however,

exhibited a sensillum with six bristles (Fig. 3F), thereby falling within the carphodactylid range (Riedel et al., 2019). In some instances in this clade the bristles are bifid. Bristles present singly or in pairs on a sensillum may be relatively long, subequal to, or comparatively short compared with sensillum diameter. For the case in which six bristles were observed, they were very short compared with the diameter of the sensillum (Table 3).

Stenodactylus clade

The diameters of the sensilla examined either fall within the range reported for diplodactylids (Riedel et al., 2019) or in the small hiatus between the largest values for diplodactylids and the smallest ones for carphodactylids (Riedel et al., 2019; Table 3). *Mediodactylus* has sensilla with two bristles, which are sometimes bifid (Fig. 4A), falling within the range of diplodactylids, although *Stenodactylus* bears between three and seven bristles per sensillum (Figs. 4B, C). In *Stenodactylus*, the greater the number of bristles per sensillum, the relatively shorter are the individual bristles.

Uroplatus clade

Sensilla diameters of taxa in this clade overlap with the ranges reported for the diplodactylids and carphodactylids and also occupy the hiatus of values segregating the ranges reported for these two families (Riedel et al., 2019; Table 3). *Uroplatus* exceeds the greatest button diameter reported for carphodactylids and represents the greatest gekkotan sensillar diameter ($33.0 \mu\text{m}$) yet encountered (Tables 1, 2; Fig. 4D). From zero to two bristles per sensillum (Figs. 4E, F) are encountered in this clade, thus falling below or within the range of diplodactylids. In *U. fimbriatus* the extremely large sensillum encountered lacks bristles but

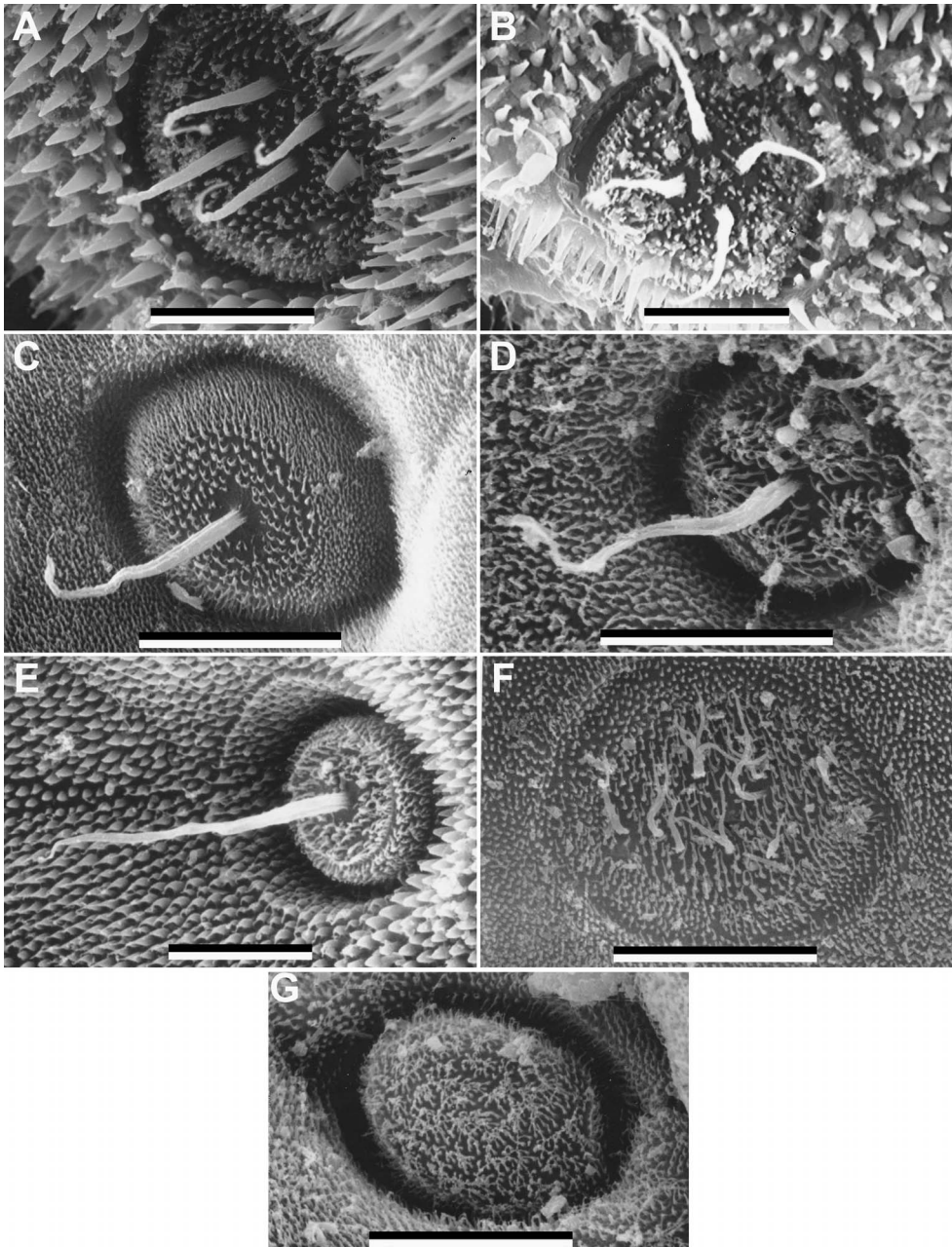


Figure 3. Cutaneous sensilla encountered in the *Microgecko* (A, B) and *Hemidactylus* (C–G) clades (see Fig. 1) of the Gekkonidae. All descriptions of size of components relate to data provided in Table 1. A, *Microgecko helenae*: small-diameter button bearing multiple unbranched short bristles; B, *Microgecko persicus*: small-diameter button with multiple unbranched moderately long bristles; C, *Cyrtodactylus malayanus*: small-diameter button with an unbranched, moderately long single bristle; D, *Hemidactylus angulatus*: small-diameter button with an unbranched moderately long bristle; E, *Hemidactylus imbricatus*: small-diameter button with a very long, unbranched bristle; F, *Hemidactylus mabouia*: small-diameter button bearing multiple unbranched short bristles; G, *Hemidactylus angulatus*: small-diameter button lacking bristles. Scale bars = 10 μ m.

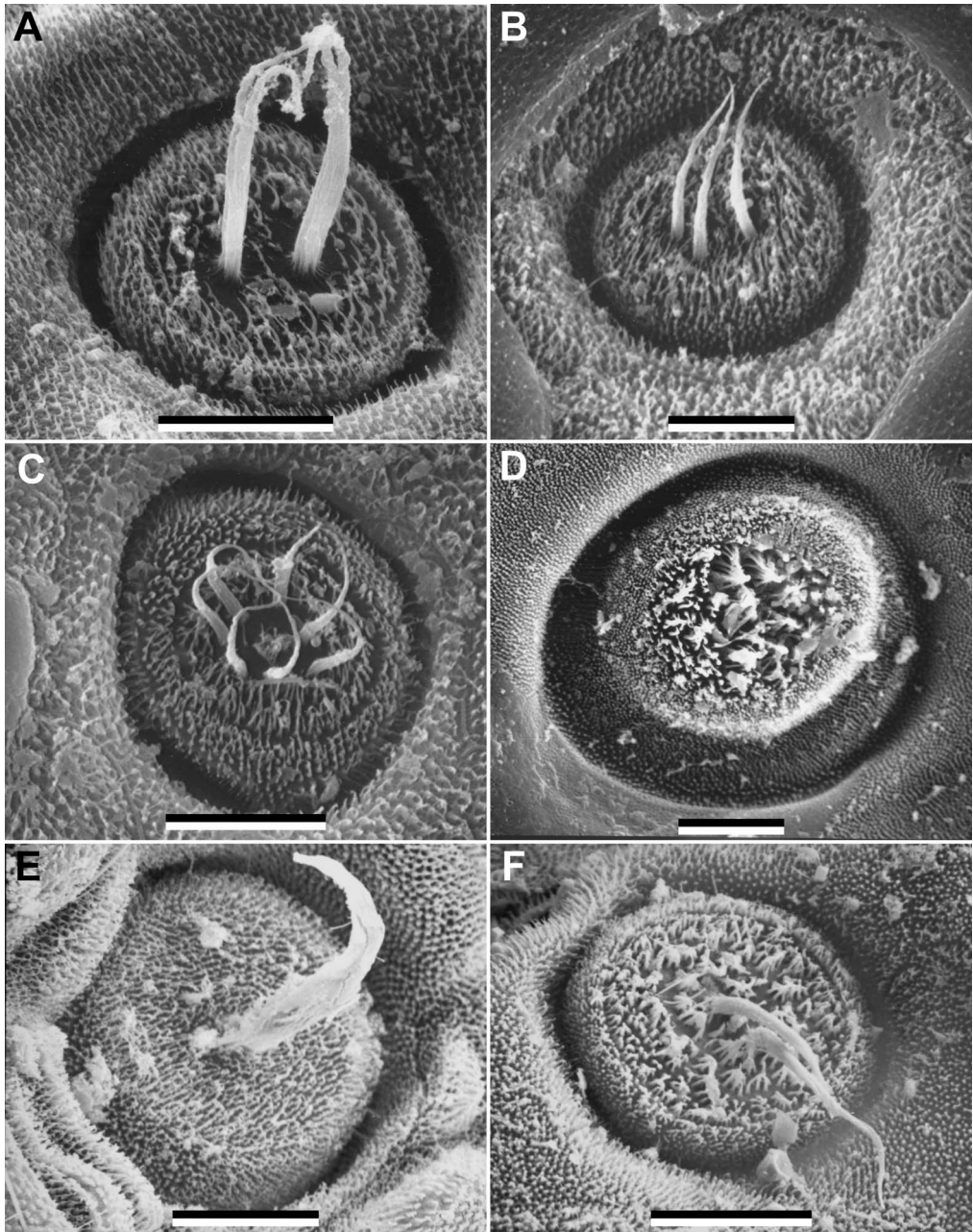


Figure 4. Cutaneous sensilla encountered in the *Stenodactylus* (A–C) and *Uroplatus* (D–F) clades (see Fig. 1) of the Gekkonidae. All descriptions of size of components relate to data provided in Table 1. A, *Mediodactylus kotschy*: small-diameter button bearing long, twinned, bifid bristles; B, *Stenodactylus doriae*: small-diameter button with multiple unbranched short bristles; C, *Stenodactylus doriae*: small-diameter button bearing multiple unbranched moderately long bristles; D, *Uroplatus fimbriatus*: large-diameter button lacking bristles; E, *Ptenopus garrulus*: large-diameter button with a moderately long bristle; F, *Ancylodactylus spinicollis*: small-diameter button bearing long, twinned, unbranched bristles. Scale bars = 10 μ m.

bears extensive micro-ornamentation on its surface (Fig. 4D), suggesting that the absence of a bristle is not artifactual. Bristle length in this clade, when present, falls short of sensillum diameter, but never extensively so.

Lygodactylus clade

Sensilla diameters in this cluster overlap with the ranges of diplodactylids and carphodactylids, as well as falling below the smallest diplodactylid values (Riedel et al., 2019; Table 3). Sensilla in this clade may bear one or two bristles (Figs. 5A, B), as per the diplodactylids, or three to five (Figs. 5C, D), overlapping the range of carphodactylids. For sensilla with one or two bristles, the latter may be longer or shorter than sensillum diameter (Table 3), but not markedly so. In instances in which sensilla bear three or more bristles, their length is considerably shorter than the diameter of the sensillum they surmount (but see Alibardi and Bonifitto, 2019). Within species the number of bristles per sensillum can vary (Figs. 5A, D).

Calodactylodes clade

Data for this clade are sparse, but available sensillum diameters fall within the diplodactylid range (Riedel et al., 2019; Table 3). Sensilla so far observed bear one, four, or five bristles (Fig. 5E), thus falling within both the diplodactylid and carphodactylid ranges (Riedel et al., 2019).

Afrogecko clade

Available sensillum diameters and number of bristles per sensillum (four) fall within the carphodactylid range (Riedel et al., 2019; Table 3; Fig. 5F). The bristles are comparatively short, although not excessively so (Table 3).

Pachydactylus clade

Sensilla diameters in this clade fall mostly within or below the range occupied by diplodactylids, but there is also some overlap with carphodactylid values (Riedel et al., 2019; Table 3). Almost all species have sensilla bearing either one or two bristles, some of which are bifid (Figs. 6, 7A–D), falling within the range of bristles per sensillum exhibited by diplodactylids. *Elasmodactylus tetensis* exhibited a sensillum with at least three bristles, transgressing into the carphodactylid range (Riedel et al., 2019; Table 3). Furthermore, *Goggia*, with 15 or more such structures adorning a single sensory receptor (Figs. 7E, F), exhibits the greatest number of bristles encountered in our sample. Bristle length may be greater than, subequal to, or smaller than sensillum diameter, and in some cases bristle length can be greater than three times sensillum diameter. In *Goggia*, the bristles tend to be two to three times shorter than the diameter of the sensillum that carries them (Table 3).

Overall observations

Our broad, but not exhaustive, sampling across clades within the Gekkonidae reveals considerable diversity of sensilla structure (Fig. 1), in accord with the previously available, although disparate, data summarized in Table 2. This diversity is greater than that currently known for any other gekkotan family (Fig. 1). Dimensions of the sensilla buttons and bristles and the number of bristles present on a sensillum (Table 3) exceed the ranges reported for the Diplodactylidae and Carphodactylidae by previous authors (Table 1; Riedel et al., 2019).

Considering button diameter, the smallest value (10.36 μm) recorded for *Hemidactylus angulatus* (Table 3) falls below the smallest value recorded for diplodactylids (14.6 μm) and that for other geckos (Table 1; 13 μm ,

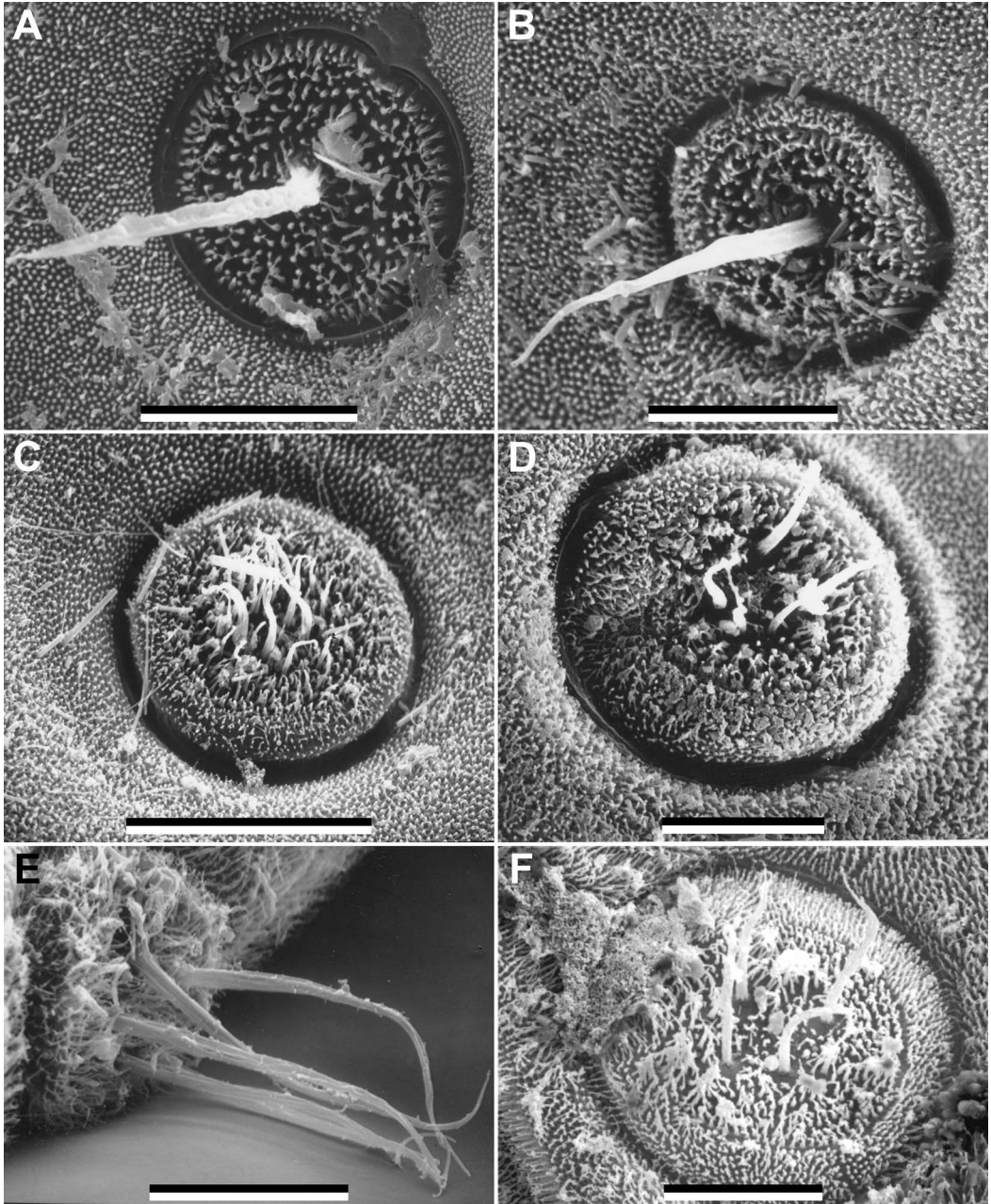


Figure 5. Cutaneous sensilla encountered in the *Lygodactylus* (A–D) *Calodactylodes* (E, F), and *Afrogecko* (F) clades (see Fig. 1) of the Gekkonidae. All descriptions of size of components relate to data provided in Table 1. A, *Lygodactylus chobiensis*: small-diameter button carrying an unbranched, moderately long single bristle; B, *Phelsuma sundbergi*: small-diameter button with an unbranched, long bristle; C, *Lygodactylus wetzeli*: small-diameter button with multiple, unbranched short bristles; D, *Lygodactylus chobiensis*: small-diameter button bearing multiple, unbranched short bristles; E, *Narudasia festiva*: small-diameter button carrying multiple, unbranched moderately long bristles; F, *Afrogecko porphyreus*: large-diameter button with multiple, unbranched moderately long bristles. Scale bars = 10 μ m.

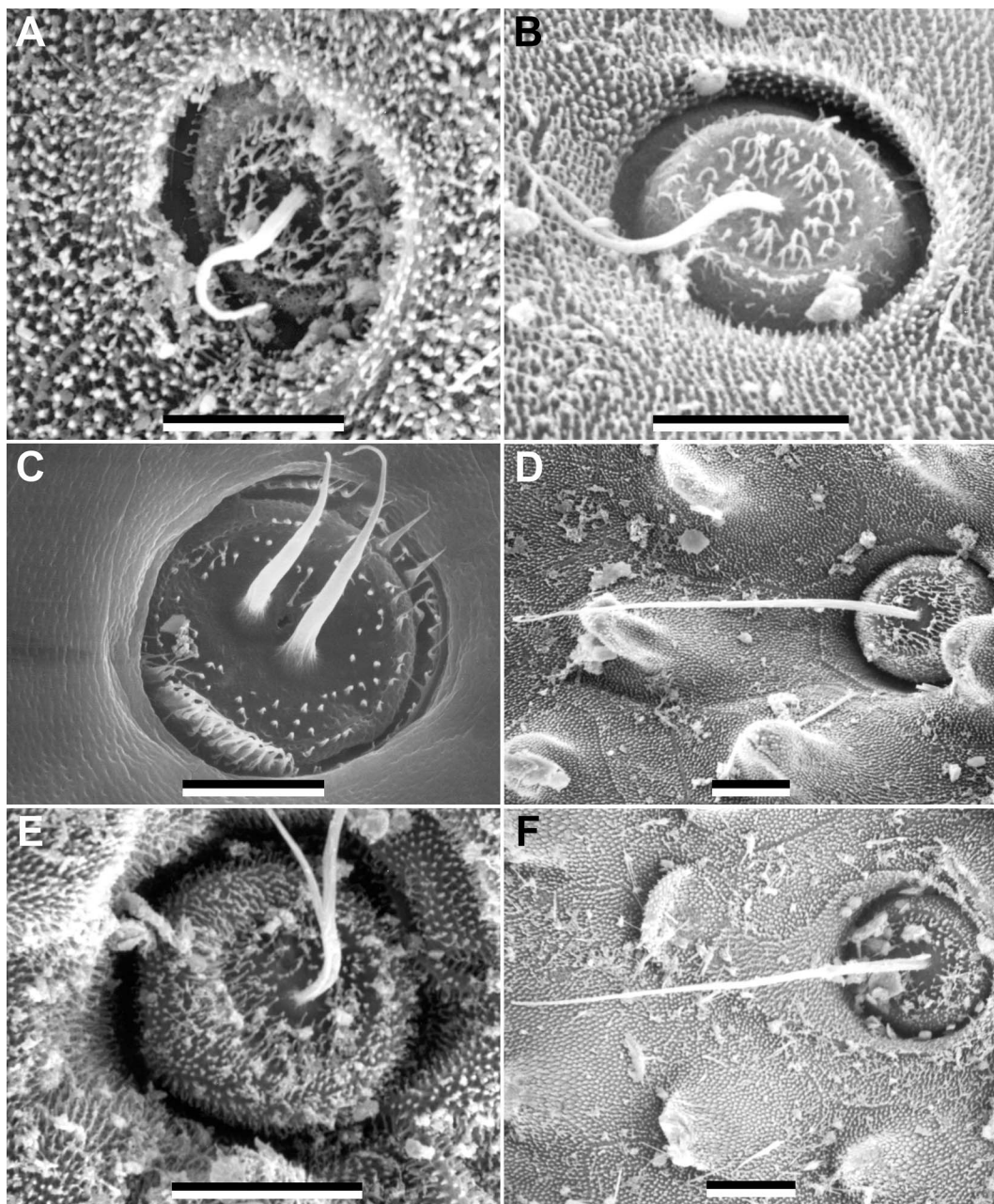


Figure 6. Cutaneous sensilla encountered in *Rhoptropus* and *Chondrodactylus* of the *Goggia* clade (see Fig. 1) of the Gekkonidae. All descriptions of size of components relate to data provided in Table 1. A, *Rhoptropus diporus*: small-diameter button with an unbranched, moderately long single bristle; B, *Rhoptropus barnardi*: small-diameter button bearing a long bifid bristle; C, *Rhoptropus afer*: small-diameter button with long, twinned, unbranched bristles; D, *Chondrodactylus bibronii*: small-diameter button bearing a very long, unbranched bristle; E, *Chondrodactylus bibronii*: small-diameter button with a moderately long, bifid bristle; F, *Chondrodactylus laevigatus*: small-diameter button with a very long, unbranched bristle. Scale bars = 10 μm .

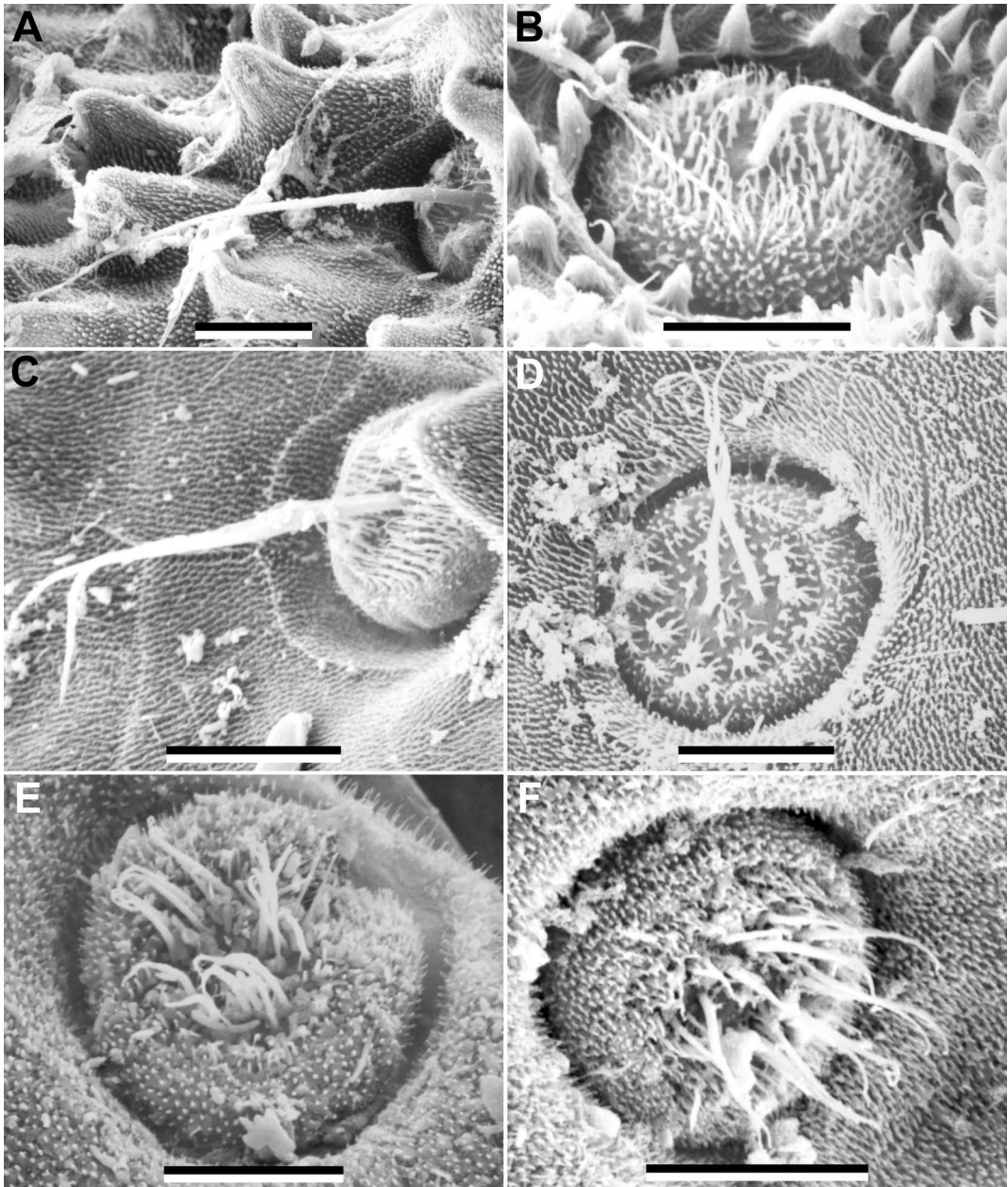


Figure 7. Cutaneous sensilla encountered in *Pachydactylus* and *Goggia* of the *Goggia* clade (see Fig. 1) of the Gekkonidae. All descriptions of size of components relate to data provided in Table 1. A, *Pachydactylus vansonii*: small-diameter button bearing a single very long, unbranched bristle; B, *Pachydactylus austeni*: large-diameter button with a moderately long bristle; C, *Pachydactylus weberi*: small-diameter button carrying a long, bifid bristle; D, *Pachydactylus serval*: small-diameter button bearing long, twinned, unbranched bristles; E, *Goggia gemmula*: small-diameter button with multiple, unbranched short bristles; F, *Goggia rupicola*: large-diameter button with multiple, unbranched moderately long bristles. Scale bars = 10 μ m.

Sphaerodactylus roosevelti and *Teratoscincus scincus*, both in the Sphaerodactylidae; Dujsebayaeva, 1995). The largest button diameter (33.0 μm for *U. fimbriatus*; Table 3) exceeds that recorded by Riedel et al. (2019) for carphodactylids (26.1 μm) and that recorded earlier (30 μm , *Phyllurus platurus*, Carphodactylidae; Hiller, 1971) for that family.

With reference to the number of bristles borne per sensillum, *H. angulatus* and *U. fimbriatus* both revealed cases in which bristles are absent (Table 3), with the button bearing a carpet of spinules. In *H. angulatus* these spinules are similar in dimensions to those of the adjacent integument (Fig. 3G). In *U. fimbriatus* the centrally located spinules are slightly longer than those covering the remainder of the button (Fig. 4D), a condition previously reported for this species by Schmidt (1913, 1920). Riedel et al. (2019) reported an absence of bristles but the presence of elongate sensillar spinules in the diplodactylid geckos *Amalosia rhombifer*, *Strophurus krisalys*, and *Strophurus taeniatatus*; Sammartano (1980) noted the same in the sphaerodactylid *E. europaea* (Table 1). At the other extreme, the greatest number of bristles borne by a sensillum in our sample of gekkonids was 15+ in *Goggia gemmula* (Table 3). This number exceeds the greatest number recorded for carphodactylids by Riedel et al. (2019) and for any other gekkotan family (Table 1) but is eclipsed by the 29 bristles reported for the gekkonid *R. ocellata* (Table 2) by Röhl (1999).

Comparing the length of bristles, the shortest recorded by us is for *Lygodactylus wetzeli* (3.36 μm ; Table 3), considerably shorter than the previously reported shortest non-pygopodid gekkotan sensillar bristle—8 μm for the sphaerodactylid *T. scincus* (Dujsebayaeva, 1995; Table 1). Very short bristle lengths (2.1–3.3 μm) have been reported for the pygopodids *Lialis jicari* and *Pygopus*

lepidopodus (Shea, 1993; Spinner et al., 2013; Table 1), but information about the structural variation of pygopodid sensilla is sparse (Dujsebayaeva et al., 2021). The shortest bristle reported previously for the Gekkonidae was 8.60 μm for *R. ocellata* (Röhl, 1999; Table 2). The longest bristle measured by us was 49.5 μm from *Chondrodactylus laevigatus* (Table 3), but this value falls well shy of the 60 μm reported for the phyllodactylid *Tarentola chazaliae* (Hiller, 1971; Table 1) and the gekkonids *G. gecko* (Hiller, 1971) and *G. polylepis* (Schmidt, 1920; Table 2).

Variability in sensillar morphology within species is evident in some of the cases included in our sample, indicating that a single morphological configuration does not necessarily characterize each species. *Hemidactylus angulatus* (*Hemidactylus* clade) exhibits sensilla with both small-diameter buttons bearing single, unbranched, long bristles (Fig. 3D) and others of similar diameter that lack bristles (Fig. 3G). *Lygodactylus chobiensis* (*Lygodactylus* clade) has both sensilla with small-diameter buttons bearing single, unbranched, moderately long bristles (Fig. 5A) and large-diameter buttons supporting multiple, unbranched, moderately long bristles (Fig. 5D).

In our sample, variation of sensilla structure within a lineage is most adequately exemplified in the *Pachydactylus* clade (Figs. 1, 6–8), the most densely sampled group in our study. Within this assemblage the majority of variation exhibited by setal dimensions, number and button dimensions for the Gekkonidae overall (Table 1) is evident. Small-diameter sensilla buttons bearing unbranched, single, moderately long (Fig. 6A; *Rhoptropus diporus*) to very long (Fig. 6F; *C. laevigatus*) bristles share these attributes with, respectively, *Cyrtodactylus malayanus* (*Hemidactylus* clade; Fig. 3C) and *Hemidactylus imbricatus* (*Hemidactylus*

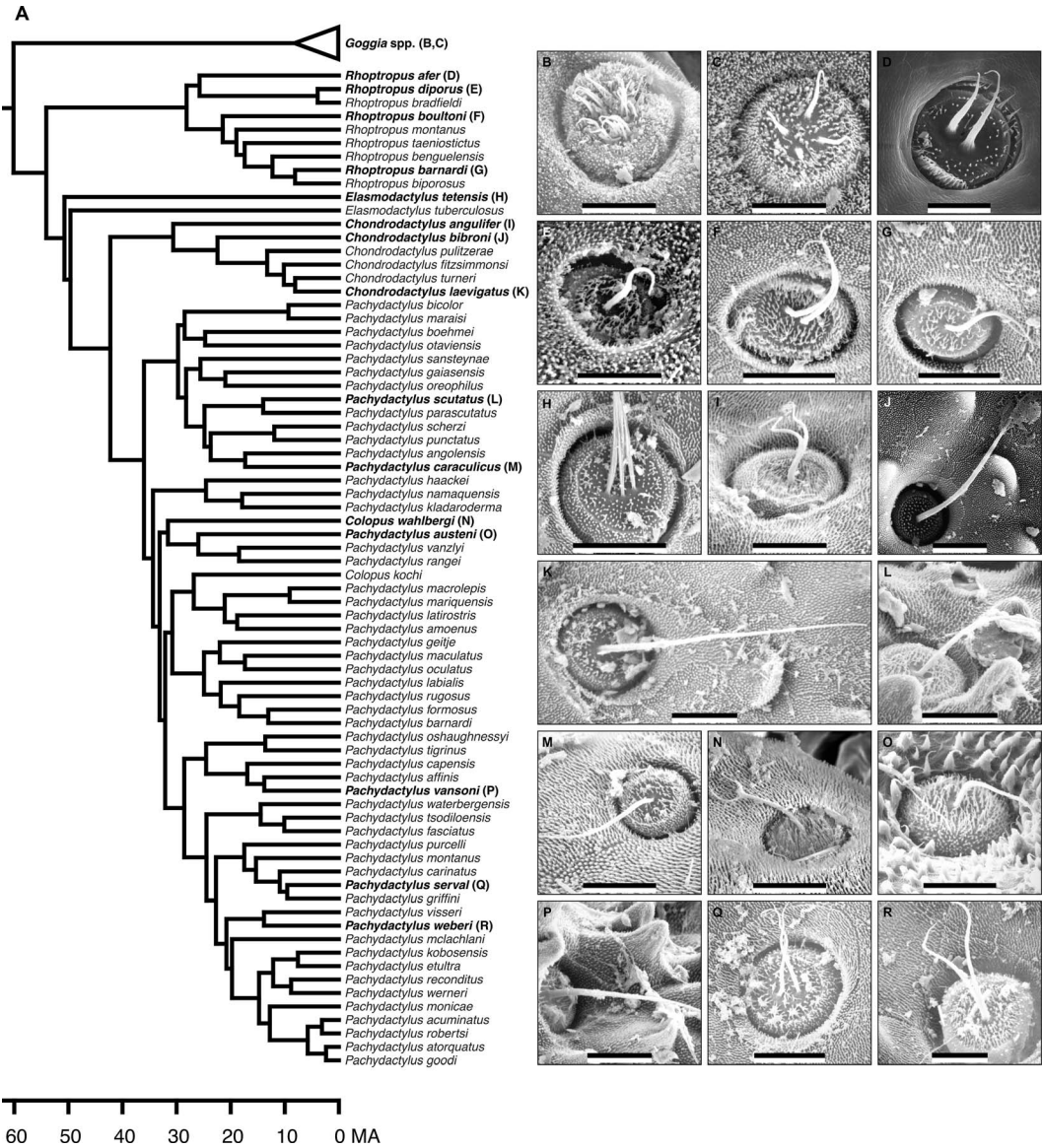


Figure 8. Phylogenetic relationships of the *Pachydactylus* + *Goggia* clade of gekkonid geckos with depiction of the diversity of the form of cutaneous sensilla revealed (by scanning electron microscopy) for this clade by our survey. A, Time-calibrated phylogeny modified from Heinicke et al. (2017). Species examined in this study are bolded. B, *Goggia gemmula*; C, *G. rupicola*; D, *Rhoptropus afer*; E, *R. diporus*; F, *Rhoptropus boultoni*; G, *R. barnardi*; H, *Elasmodactylus tetensis* (no scale data available); I, *Chondrodactylus angulifer*; J, *C. bibroni*; K, *C. laevigatus*; L, *Pachydactylus scutatus*; M, *P. caraculicus*; N, *P. wahlbergi*; O, *P. austeni*; P, *P. vansoni*; Q, *P. serval*; R, *P. weberi*. Ma, millions of years. Scale bars = 12 μm.

clade; Fig. 3E). Other patterns of unbranched bristles carried on small-diameter sensilla buttons are shared as follows: short, multiple bristles—*G. gemmula* (Fig. 3D) and *Gehyra variegata* (*Gehyra* clade; Fig. 2D); long, twinned bristles—*Pachydactylus serval* (Fig. 7D) and *Ancylodactylus spinicollis* (*Uroplatus* clade; Fig. 4F). Small-diameter sensillar buttons carrying moderately long, single bifid bristles are encountered in *Chondrodactylus bibronii* (Fig. 6E) and *Heteronotia spelea* (*Heteronotia* clade; Fig. 2A). Sensilla with large-diameter buttons bearing unbranched, long, single bristles are found in *Pachydactylus austeni* (Fig. 7B) and *Ptenopus garrulus* (*Uroplatus* clade; Fig. 6C), and those with moderately long multiple bristles are present in *Goggia rupicola* (Fig. 7F) and *Afrogecko porphyreus* (*Afrogecko* clade; Fig. 5F). Thus, across the *Pachydactylus* clade (Fig. 8) as a whole, few generalizations can be made regarding sensillar morphology, although at the level of genera there is some consistency, even within *Pachydactylus*, the genus exhibiting the greatest species richness and ecological diversity.

Opportunistic sampling outside the Gekkonidae

Sensilla morphology of the small number of non-gekkonid gekkotans we sampled is similarly diverse (Fig. 1; Table 3). *Nephurus deleani* and *Underwoodisaurus milii* (Carphodactylidae) exhibited nine and three short bristles per sensillum, respectively. Although *N. deleani* exhibits a button diameter within the known range of carphodactylids, the button diameter of *U. milii* is far below the range typical of carphodactylids, and even diplodactylids (Riedel et al., 2019). Both *Pseudothecadactylus australis* and *Mokopirirakau granulatus* (Diplodactylidae) exhibit single bristles and sensillum button diameters within the range of other diplodactylids.

The four sphaerodactylid taxa we sampled exhibit sensillum button diameters below (*Saurodactylus mauritanicus* and *Sphaerodactylus townsendi*) and within (*Aristelliger praesignis* and *Quedenfeldtia trachyblepharus*) the typical diplodactylid range (Riedel et al., 2019). Both *Q. trachyblepharus* and *S. townsendi* exhibit a single bristle per sensillum, that of the latter being bifid, but *A. praesignis* and *S. mauritanicus* exhibit four- and five-bristled sensilla, respectively. The four phyllodactylid taxa we sampled exhibit sensillum button diameters below (*Ptyodactylus hasselquistii*) and within (*Thecadactylus rapicauda*, *Tarentola americana*, and *Homonota darwini*) the typical diplodactylid range (Riedel et al., 2019). Both *T. rapicauda* and *H. darwini* exhibit a single-bristled sensillum, but *P. hasselquistii* and *T. americana* have three-bristled sensilla.

DISCUSSION

Riedel et al. (2019) provided details of a comparative study of the form and dimensions of cutaneous sensilla of the dorsal skin of carphodactylid and diplodactylid geckos. They presented data for the diameter of the sensilla and the number of bristles they carry. These two families were segregable on the basis of their data for these attributes, although earlier reports indicate that such a separation is not absolute for either button diameter or number of bristles (Table 1).

The diameters of the sensilla of gekkonids examined in our sample (Table 3) encompass and exceed the combined ranges of the diplodactylids and carphodactylids reported by Riedel et al. (2019) and other authors (Table 1). Thus, gekkonid sensilla exhibit a considerable variation in this aspect of their form, as suggested by previously reported data for this family (Table 2). Although there appears to be some consistency within genera with respect to general morphology

and size, this is not always so. There also seem to be no obvious trends in button or sensillar dimensions in relation to the body size attained by species. This is true across all gekkotans (Meiri, 2008) and is shown especially well in the *Pachydactylus* clade, our most densely sampled lineage, for which these parameters overlap substantially between the largest and smallest clade members (Heinicke et al., 2017).

Overall, the relationship between bristle length and sensillum diameter of gekkonids is highly variable. Bristle length may vary by location on the body, whether this be locally (such as labial versus rostral versus occipital scales on the head) or in relation to more broadly defined body regions (e.g., the dorsum, limbs, and tail; Table 3). The species we examined in the *Stenodactylus* clade (Fig. 1; Table 3), however, reveal potential relationships between bristle number per sensillum and bristle length (once the number of two bristles per sensillum is exceeded), with bristles becoming relatively shorter as bristle number increases. This trend is also evident in the *Hemidactylus*, *Lygodactylus*, and *Pachydactylus* clades.

Additionally, several taxa exhibit both unbranched and branched (bifid) bristles on different sensilla (Table 3). There have been occasional reports of bifid bristles (Table 2) in gekkonid genera (*Hemidactylus turcicus*—Sammartano, 1980; *C. laevigatus* and *Pachydactylus rangei*—Sammartano, 1983), taxa for which we also record this characteristic (Table 3). Lauff et al. (1993) noted the presence of sensilla with both unbranched and bifid bristles on the dorsal digital scales of *G. gecko* and reported that they showed differential and complimentary patterns of distribution, suggestive of regionally based functional differences. The actual functional role of bifid versus unbranched sensilla remains entirely unknown, however. More focused data are needed to explore the potential relationships

that may exist between bristle number, relative bristle length (in relation to sensillar diameter), and bristle form.

The potential for definitive differences in sensillar morphology between taxa was recently demonstrated by an inadvertent comparative study. El-Sayyad et al. (2009) purportedly examined a growth series of *Tropiocolotes tripolitanus* to document sensillar form through posthatching ontogeny. Although stages I and II of their assumed growth series were based on specimens of *T. tripolitanus*, the later stages (III–VII) were, unfortunately, based on specimens of *Cyrtopodion scabrum*, a member of a different gekkonid clade from *Tropiocolotes* (Fig. 1; Table 2). The change in the form of sensilla from those bearing two (stages I and II) to four (stages III–VII) bristles, attributed to an ontogenetic shift by El-Sayyad et al. (2009) was actually a reflection of interspecific (and interclade) differences. Despite numerous instances of variation within single species, in many cases it seems possible to generalize sensillar morphology at higher taxonomic levels. Thus, within the *Pachydactylus* clade, *Goggia* spp. and *Chondrodactylus* spp. are characterized by multiple short bristles and single or bifid long bristles, respectively. Not surprisingly, there is variation in sensillar parameters across the seven species of *Pachydactylus* examined, but most species are rather similar to one another (Fig. 8; Table 3) regardless of the degree of phylogenetic relatedness.

Our small sample of gekkotan outgroups further demonstrates substantial variation of sensillar anatomy. Both diplodactylids we examined exhibit the expected sensillum bristle number and button diameter (Riedel et al., 2019). Both carphodactylids we examined exhibited multiple bristles on each respective sensillum, consistent with the findings of Riedel et al. (2019). However, unlike in *N. deleani*, *U. milii* button diameter is well below the expected range for carpho-

dactylids. The remaining sphaerodactylid and phyllodactylid taxa we examined exhibit sensillum button diameters that fall either within or below the expected range for diplodactylids (Riedel et al., 2019). Bristle number is diverse in this sample, ranging from one to five per sensillum. The diversity seen in this sample warrants further investigations into sensillar microanatomy, especially in the secondmost diverse group of geckos, the sphaerodactylids.

Although a great range of form of gekkonid sensilla and the bristles that they bear is evident, whether these different morphologies are associated with functional differences is unknown. Mechanoreception has been the function most often associated with gekkotan (as well as other lizard) sensilla (Audy, 1953; Hiller, 1968, 1971; Schleich and Kästle, 1986; Bauer and Russell, 1988; Ananjeva et al., 1991; Matveyeva and Ananjeva, 1995; Nikitina and Ananjeva, 2003; Russell et al., 2014). Our increasing understanding of the morphological variation exhibited by these intriguing structures is suggestive of considerable functional versatility. Other possible functions have been suggested, such as thermoreception (Bailey, 1969; Ananjeva et al., 1991), hydroreception (Matveyeva and Ananjeva, 1995; Riedel et al., 2019), and self-cleaning of the integument (Watson et al., 2015a, 2015b; Li et al., 2016; Riedel et al., 2019), but these remain empirically untested. Carefully planned surveys of sensillum form in relation to body region, rather than the unfocused sampling typical of most studies up to now, are required to enable a more nuanced appreciation of structural differences and their potential functional differentiation. Riedel and Schwarzkopf (2022) recently conducted such a study and found variation in density but not morphology across body regions in diplodactylids and carphodactylids. No such study has yet been conducted

for the more species-rich gekkotan families, although variation across the body of a single *Lygodactylus conraui* (Bonfitto et al. 2022) has recently been assessed.

The investigation conducted by Riedel et al. (2019) for diplodactylids and carphodactylids serves as an example of a more targeted approach. They restricted their examination of sensilla to the integument of the middorsal region of the body to focus sampling on the part of the body least likely to experience mechanical stimulation of the sensilla by direct contact with the nonaerial (solid) parts of the environment. They were interested in the potential relationship between sensilla morphology and ecologically important environmental factors other than mechanoreception (e.g. thermo- and hydroreception). Such focused sampling may underrepresent overall sensillar structural diversity but may provide more clues about sensilla form in relation to particular aspects of the environment potentially monitored by these animals. Sampling consistently and repeatedly from specified regions across the entire body surface will permit determination of the extent of variation within and between species. Ontogenetic study of gekkotan sensilla is also needed (Nazarov et al., 2021) to evaluate whether bristle formation is identical for all sensilla-bearing squamates (Dujsebayaeva et al., 2021).

Such approaches can be combined with assessments of the density of sensilla, as measured by the number of these structures per scale (Dujsebayaeva et al., 2021) or within a specified area (e.g., per square millimeter) of the integument (Lauff et al., 1993; Russell et al., 2014; Riedel et al., 2019). Only by more focused approaches, such as those outlined above, can potential relationships between sensillar form, density, and function begin to be deduced. Examination of variation of such parameters within individual species can assist in the assessment of the

potential multiple functions of sensilla (Riedel et al., 2019; Bonfitto et al. 2022). Integrated approaches combining gross morphological examination (by SEM), histology (Dujsebayaeva et al., 2021), histochemistry, sensitivity testing (Bradley et al., 2021), and electrophysiologic recording (Hiller, 1978) are needed to explore the form-function relationships of the diversity of sensillar morphology more effectively.

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