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Variation in density, but not morphology, of cutaneous sensilla among body regions in nine species of Australian geckos

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Abstract

Skin sense organs, cutaneous sensilla, are a well-known feature of the integument of squamate reptiles and particularly geckos. They vary widely in morphology among species and are thought to be mechanosensitive, associated with prey capture and handling, tail autotomy and placement of the adhesive toepads in pad-bearing species. Some authors suggest that they may also sense abiotic environmental features, such as temperature or humidity. Here, we describe the morphology and distribution of cutaneous sensilla among body regions of nine Australian gecko species, in four genera. We hypothesised that if sensilla morphology was distinct, or sensilla density high, around the mouth, on the tail and on extremities, sensilla were likely used for these direct tactile functions. We found that sensilla morphology was uniform among body regions within species, but varied among species, while sensilla densities varied among species and body regions. In all species studied, sensilla density was highest on the labials and the dorsal tail scales and low on the feet, head and body, providing strong support for the hypothesis that sensilla serve tactile mechanoreceptive functions for prey capture and handling and for predator avoidance, but not for toepad placement. We suggest sensilla density may be explained by mechanoreception, whereas structure may be influenced by other factors.

KEYWORDS
Gekkota, integument, microornamentation, oberhäutchen

1 | INTRODUCTION

The integument is the main area of contact between organisms and the environment, providing protection against external agents and sensing external stimuli. To detect stimuli, the skin of most animals supports a variety of sense organs. Most commonly, skin sense organs are mechanoreceptors, supplying tactile information on immediate surroundings, either through direct contact or indirectly by detecting currents in air or water (e.g., vibrissae of mammals or neuromasts in the lateralis system of fish; Lane & Whitear, 1982; Schliemann, 2015; Yu et al., 2016), but some skin sense organs provide information on the distant surroundings, such as pit organs of pit vipers and pythons, which detect infrared radiation (Harris & Gamow, 1972). Squamate reptiles (lizards and snakes) feature particularly complex skin morphology characterised by multiple layers of α- and ß-keratin, which is completely shed, periodically (Maderson, 1966; Maderson et al., 1998). Cutaneous sensory organs are common and well documented in a large variety of squamate reptiles, including Agamidae and Iguanidae (e.g., Ananjeva et al., 1991; Ananjeva et al., 2001), Cordylidae and Gerrosauridae (Harvey & Gutberlet Jr, 1995), Gekkota

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(e.g., Bauer & Russell, 1988), Phrynosomatidae (Sherbrooke & Nagle, 1996), Varanidae (e.g., Bucklitsch et al., 2012), Xenosauridae (Harvey, 1993) and snakes (e.g., Crowe-Riddell et al., 2016; Crowe-Riddell, Williams, et al., 2019; Jackson & Sharawy, 1980). Most clades feature one of two basic types of skin sense organs: cutaneous sensilla (sometimes called 'oberhäutchen hairy sensory organs'), which are round flat discs with one or more small hair-like bristles in the centre or lenticular sense organs lacking bristles (Ananjeva et al., 1991; Dujsebayeva et al., 2021; Landmann, 1975). Geckos are a particularly speciose and diverse clade of squamates, which have relatively thin and soft skin compared to other reptiles (Boulenger, 1885, p. 5), typically covered with cutaneous sensilla (Bauer & Russell, 1988; Hiller, 1976) and occasionally lenticular sense organs in some species (Riedel et al., 2019). Despite the uniformity of internal structures, cutaneous sensilla in geckos vary considerably in their surface morphology, especially the bristles (Hiller, 1971; Lauff et al., 1993; Riedel et al., 2019; Schleich & Kästle, 1982; Schmidt, 1912).

Cutaneous sensilla are mechanoreceptive (Hiller, 1978), and although the bristles are not innervated themselves, bristle movement triggers a neural reaction through the innervated dermal papilla (Hiller, 1978; von Düring & Miller, 1979). For example, the cutaneous sensilla on the fringes of the adhesive toepads of *Tarentola* geckos were associated with the placement of the toepads during locomotion (Hiller, 1976) and there are different sensilla morphologies (unbristled, bristled with an unbranched bristle and bristles with a split tip) on different regions of the dorsal manus and pes of Tokay Geckos (*Gekko gecko*), another species with adhesive toepads, suggesting that the sensilla may play a role in toepad placement in this species as well (Lauff et al., 1993). In contrast, the sensilla of a padless leopard gecko (*Eublepharis macularius*) were uniform across all body regions except for the labials (Russell et al., 2014). Similarly, associations between density and distribution of cutaneous sensilla on the tail and particularly above the autotomy planes (the locations for tail autotomy), of *E. macularius* suggest that cutaneous sensilla mediate the location of tail breakage and the movement of the tail after breaking (Russell et al., 2014). Most squamates, including geckos, show relatively high numbers of cutaneous sensilla on the head and particularly the labial scales. This has repeatedly been associated with a diversity of functions including locomotion (e.g., burrowing), sensing the environment in complex habitats with low visibility (e.g., murky water), or feeding (e.g., prey capture and handling; Jackson, 1977; Matveyeva & Ananjeva, 1995; Povel & Van Der Kooij, 1996; Sherbrooke & Nagle, 1996). But, except for the latter associations, most studies have examined single species, so sampling and comparing additional species is required to increase the generalizability of these results.

Skin sense organs, like cutaneous sensilla, may be variable in their morphology both among and within different taxa (Bauer & Russell, 1988; Hiller, 1971). This variation could be purely phylogenetic in nature and indeed, sensilla morphology has been used to corroborate phylogenetic hypotheses in some clades (Ananjeva et al., 2000; Ananjeva & Matveyeva-Dujsebayeva, 1996). However, some authors have suggested that high variation in sensilla morphology, as well as their positions, indicate that they could have functions other than providing direct tactile information, for example, they may sense humidity or temperature (Ananjeva et al., 1991; Matveyeva & Ananjeva, 1995). None of these functions has been tested with neurobiological or physiological techniques so far, but cutaneous sensilla on the tail of some sea snakes are phototactic, in addition to their mechanoreceptive function (Crowe-Riddell, Simões, et al., 2019) supporting the possibility of the polyfunctionality of squamate cutaneous sensilla. Additionally, if sensilla detect temperature or humidity, sensilla density, distribution or morphology might be associated with ecology, and indeed, Riedel et al. (2019) found associations between sensilla morphology and microhabitat use and habitat humidity in Australian geckos. In particular, terrestrial and arid-dwelling species tended to have sensilla with relatively smaller diameters and more bristles. Sensilla and bristle density were also higher in terrestrial species compared to scansorial (climbing) species. However, Riedel et al. (2019) only assessed sensilla morphology on the dorsal side of the trunk. Higher sensilla density or differences in sensilla morphology among body regions could further suggest possible roles for cutaneous sensilla in these species. For example, different morphologies or higher densities of cutaneous sensilla on the manus and pes of pad-bearing species, on the tail and on the labials would corroborate and increase the generalizability of previous results from other species, related to toe placement, tail autotomy and the general importance of the sensory field of the rostrum for diverse functions, including feeding.

Here, we examine the morphology, number and distribution of the sensilla on different body regions of seven diplodactylid and two carphodactylid geckos, all but one of which we examined previously to describe dorsal sensilla morphology (Riedel et al., 2019). Here, we quantify sensilla morphology, number and distribution on different body regions. We determine if sensilla morphology is uniform across body regions. We expect that, consistent with some other species (Bauer & Russell, 1988; Lauff et al., 1993), sensilla morphology may differ among the tail, head and feet of geckos. Next, we quantify sensilla number and distribution among body regions and species. We predict that, as with some other species (Matveyeva & Ananjeva, 1995; Russell et al., 2014), we will see relatively high numbers on the labials, the tail and the extremities.

2 | MATERIAL AND METHODS

2.1 | Study species

For this study, we sampled specimens from three different genera of the Diplodactylidae and two species of the carphodactylid genus *Nephrurus* Günther, 1876 (Data S1). All specimens except for *Nephrurus amyae* (see below) were captured by hand at night. Broad sampling locations are provided in Table S1, further details on sampling location and method are provided elsewhere (Pillai et al., 2020; Riedel et al., 2020). We sampled three species of the genus *Oedura* Grey, 1842, a mid-sized genus widely distributed across continental Australia, whose members generally occupy a scansorial niche (Cogger, 2018; Hoskin, 2019; Oliver et al., 2012): *Oedura castelnaui*

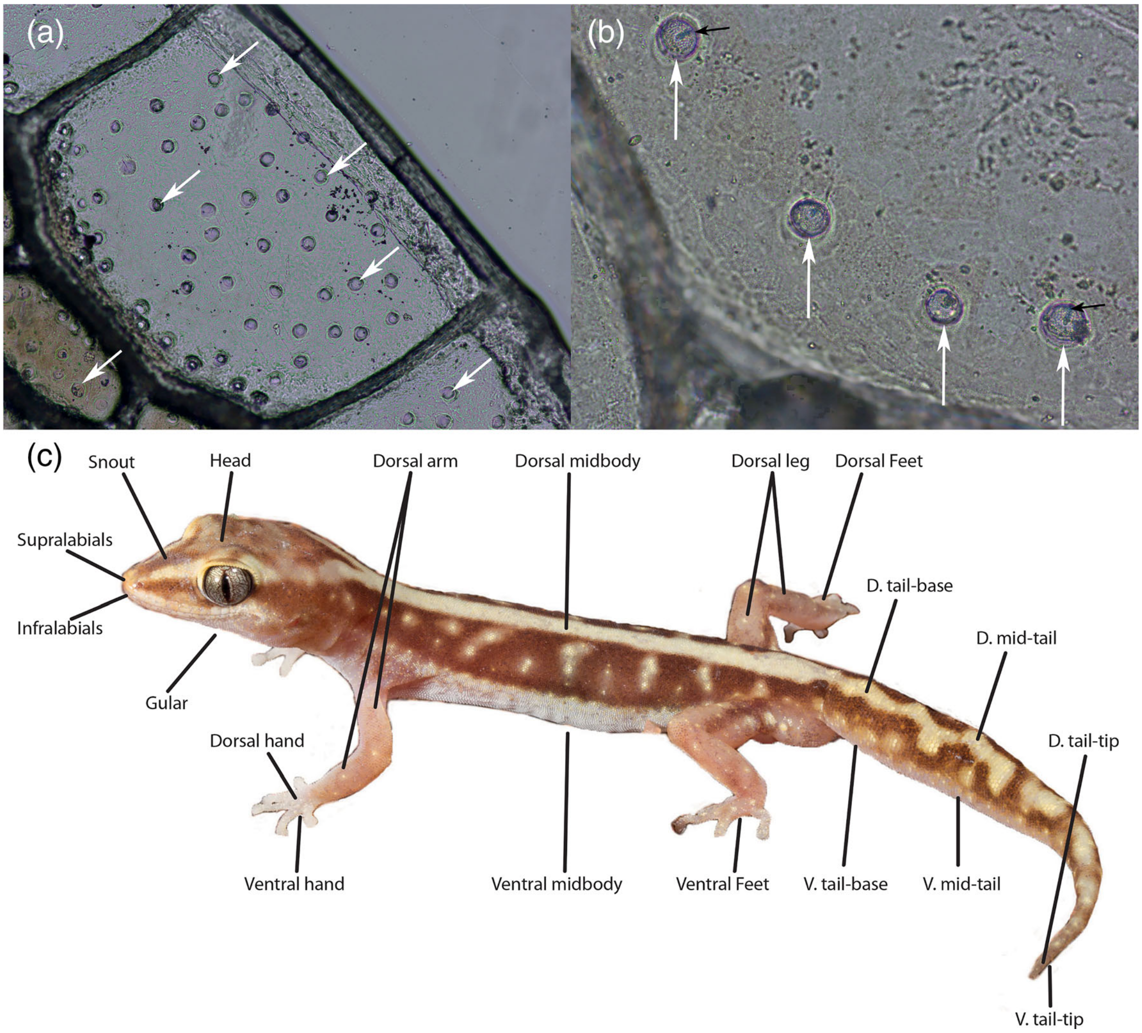

FIGURE 1 Cutaneous sensilla, sampling locations and examples. (a) A labial scale of *L. immaculatum*. The edges of the adjacent scales are also visible. Cutaneous sensilla are visible as small dots or circles on the scales, some of which are highlighted with white arrows. Light microscope (LM), magnification ×100. (b) Four cutaneous sensilla (white arrows) are visible on the edge of a scale bordering the labials (labial scale not visible) of *O. coggeri*. At this magnification (×1000), bristles are visible as faint lines in some sensilla (smaller black arrows). (c) Locations from which skin samples were taken are shown on a *L. immaculatum* (© S. Zozaya), except for 'above labials' and 'below labials' which could not be depicted at this magnification

(Thominot, 1889) ($n = 4$) an arboreal species, *Oedura coggeri* Bustard 1966 ($n = 3$) a saxicoline species found on granite boulders or rocky outcrops and *Oedura monilis* De Vies 1888 ($n = 2$), a generalist species using both rocks and trees as microhabitats (Hagey et al., 2017; Pillai et al., 2020). The three species occur and partially co-occur, in woodland habitats in north-east Queensland (QLD), with *O. monilis* extending southwards into New South Wales (NSW) (Cogger, 2018; Hoskin, 2019; Riedel et al., 2020). We also sampled two species of the primarily twig- or shrub-dwelling genus *Strophurus* Fitzinger, 1843 (Brown et al., 2012; Melville et al., 2004; Nielsen et al., 2016; Riedel et al., 2020): *Strophurus williamsi* (Kluge, 1963) ($n = 3$), which is widely distributed across eastern QLD and northern NSW, and *Strophurus krisalys* Sadlier et al., 2005 ($n = 2$), occupying central QLD. We also sampled two species of the terrestrial genus *Lucasium* Wermuth 1965 (Oliver et al., 2007; Vanderduys et al., 2020): *Lucasium steindachneri* (Boulenger, 1885) ($n = 2$) and *Lucasium immaculatum* (Storr, 1988) ($n = 3$), partially co-occurring in north QLD (Cogger, 2018; Riedel et al., 2020). Of the genus *Nephrurus*, we sampled *Nephrurus asper* Günther, 1876 ($n = 1$) and *Nephrurus amyae* Couper & Gregson, 1994 ($n = 1$), two large-bodied terrestrial species (Oliver & Bauer, 2011). The former is widely distributed across north QLD, whereas the second occurs in the southern parts of the Northern Territory (Cogger, 2018). Because general scale surface structure and at least some microstructure dimensions are known to scale ontogenetically in some species (Baeckens et al., 2019; Webster et al., 2009), we used only adult specimens. Intraspecific variation in squamate skin sense organ number was relatively low for those few clades examined (Kalyabina et al., 1998; Orejas-Miranda et al., 1977, both as cited in Dujsebayeva et al., 2021; Sherbrooke & Nagle, 1996), thus we expected that our limited sample size should not hamper our results. All specimens were transported to the housing facilities at James Cook University, Townsville, Australia. Specimens were checked regularly for shedding, and sheds were collected and used for all further analysis. *N. amyae* skin sheds were generously provided by Matt Summerville (Hartley's Crocodile Adventures). This study was approved by the JCU Animal Ethics commission (A2409), and field work was conducted under the Queensland Department of Environment and Heritage Protection (DEH) permit WA0005590.

2.2 | Sample preparation for morphology

The scales of most geckos are non-imbricated. Granular scales are surrounded by smaller intergranules devoid of sensilla, and some geckos, including species from the genera *Nephrurus* and *Strophurus*, also have larger tubercle scales scattered across all body regions in the former and across the dorsum in the latter (Riedel et al., 2019). All measurements and counts in this study were taken from granules for consistency.

To assess detailed sensilla morphology, skin samples were mounted on stubs using conductive tape, sputter-coated with titanium in a JEOL JUC-5000 sputter-coater (JEOL, Tokyo, Japan), and examined in a Hitachi SU5000 FE-scanning electron microscope (SEM) (Hitachi, Tokyo, Japan) operating at an acceleration voltage of 3 kV and a working distance of 5.5–6.5 mm. We used the established terminology (Bauer & Russell, 1988; Landmann, 1975; Riedel et al., 2019) to describe the sensilla morphology on the different body regions of all species, except for *N. amyae*, for which SEM images could not be obtained.

To quantify sensilla numbers and distribution, shed skin was dissected, mounted on a glass slide with a cover slip and examined using a Axioscope 5 Materials Stand light microscope with an Axiocam 105 mounted camera (Carl Zeiss, Jena, Germany). Cutaneous sensilla are visible as small dark dots or circles (Figure 1a,b). We defined 23 body regions following Russell et al. (2014) on which we counted the number of sensilla per scale (Figure 1c). On the dorsal side of the head, these were the supralabials, the first three scale rows above the supralabials (termed 'above labials' hereafter), the snout and the centre of the head between the eyes (termed 'head'). For the ventral side of the head, these were the infralabials, the first three scale rows bordering the infralabials (termed 'below labials') and the gular region directly below the eyes. For the body (counted separately for dorsum

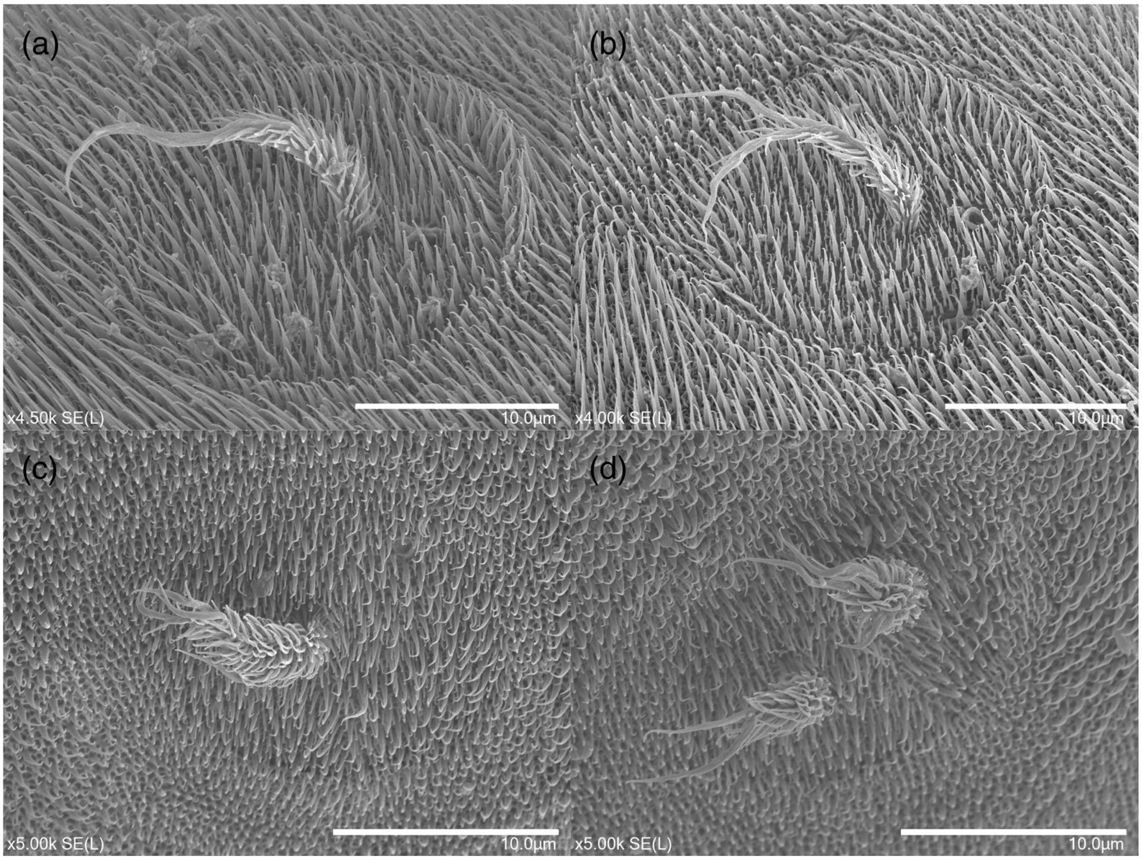

FIGURE 2 SEM images showing the variation in cutaneous sensilla (CS) morphology in the genus Lucasium. Scalebar: 10 μm. (a) Cutaneous sensillum on the dorsal side of the manus of *L. immaculatum* with a single bristle in the centre, partially covered with setules. No 'moat' is present (compare Figure 3), but the border of the sensillum can be seen as a ring bordering the slightly longer, denser spinules of the main scale area. (b) CS on the ventral side of the lower arm of *L. immaculatum*, similar in morphology to that depicted in a, except that the bristle is split distally. (c) CS on the dorsal midbody region of *L. steindachneri*. The border of the sensillum is less clear than in *L. immaculatum*. The single bristle is strongly covered with setules until shortly to the distal tip, which is split into three branches. (d) another CS from the dorsal midbody region of *L. steindachneri*. One of the occasionally occurring sensilla with two bristles

and ventrum) these were hands, feet, arms, legs, the midbody region and the upper, middle and lower parts of the tail. The regions 'arms' and 'legs' were combined from the upper and lower part of the extremities, because in preliminary examinations we found no differences between these, either dorsally or ventrally. Sensilla were counted on 10 randomly selected scales of each region for each specimen. Unfortunately, we could not count sensilla numbers on all body regions for all specimens, thus ending up with a total of 4108 counted scales (Data S2). To account for differences in scale size we also measured scale area (in μm^2) for 10 randomly selected scales and calculated mean area values per species per body region. Of the 23 body regions, 18 were included in the statistical analysis (partially summed) due to their importance for the hypothesis we tested.

2.3 | Data analysis

All analyses were conducted in R v.4.0.3 (R Core Team, 2020). Scale area was log transformed prior to analysis to improve normality, while cutaneous sensilla counts were log ($x + 1$) transformed to prevent negative values caused by zeros. We assessed the fit between our data and the distributions implemented in the models using *fitdistrplus* (Delignette-Muller & Dutang, 2015). We used standard linear models for all analysis using the 'lmer' function of the R package *lme4* (Bates et al., 2015) because we did not have the statistical power to reliably apply phylogenetically informed methods. We inspected the distribution of Pearson residuals for each of the predictor variables of each model to ensure they were normally distributed and centred around zero. Initially, we ruled out that cutaneous sensilla density differed between original and regenerated tails in our species (Data S3). To test if species had more sensilla around the mouth, on the tail, on the feet, or on the dorsum of the head or body, we used a linear model (M1) with scale area, body region and species as fixed effects, and specimen ID as a random effect, and analysed it applying type II ANOVA followed by *Tukey's* post hoc comparisons using the 'emmeans' function from the R package *emmeans* for significant categorial fixed effects (Russell, 2018). The data set for M1 included both regenerated and original tails, and we combined the three dorsal and the three ventral tail regions into the two categories 'tail dorsal', and 'tail ventral' as we found no significant differences between these categories in the preliminary analysis (Data S3). We furthermore summarised upper and lower labials as they should contribute equally to prey capture and handling, and excluded the body regions 'above labials', 'below labials', 'snout', 'gular' and 'body ventral' from the analysis, because these body regions were not relevant to the specific questions we were examining.

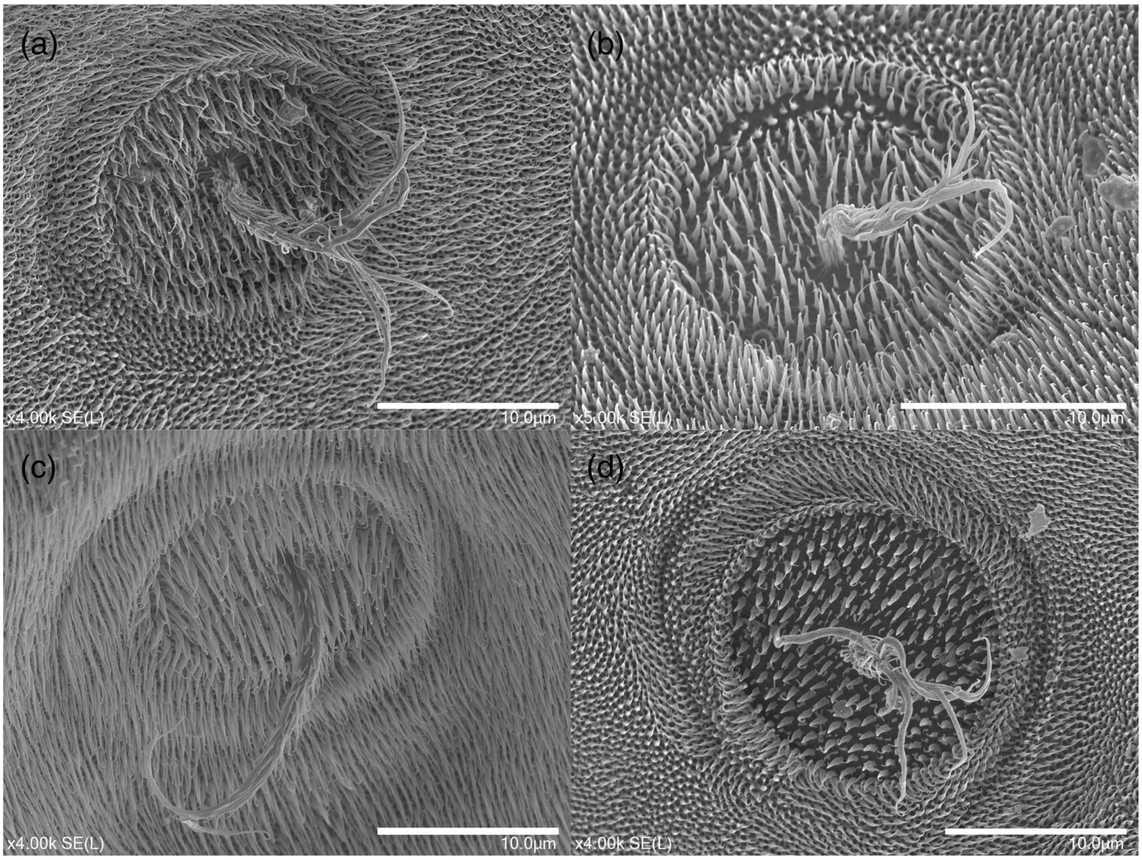

FIGURE 3 SEM images of the cutaneous sensilla (CS) in the genus Oedura. Scalebar: 10 μm. (a) CS on the dorsal midbody of *O. castelnaui*, with a clearly visible moat and a single bristle that is covered with setules on its lower half, and split multiple times on the upper half. (b) CS on the ventral side of the arm of *O. castelnaui*. (c) CS on the dorsal side of the tail of *O. castelnaui*. (d) CS on the dorsal midbody region of *O. coggeri*

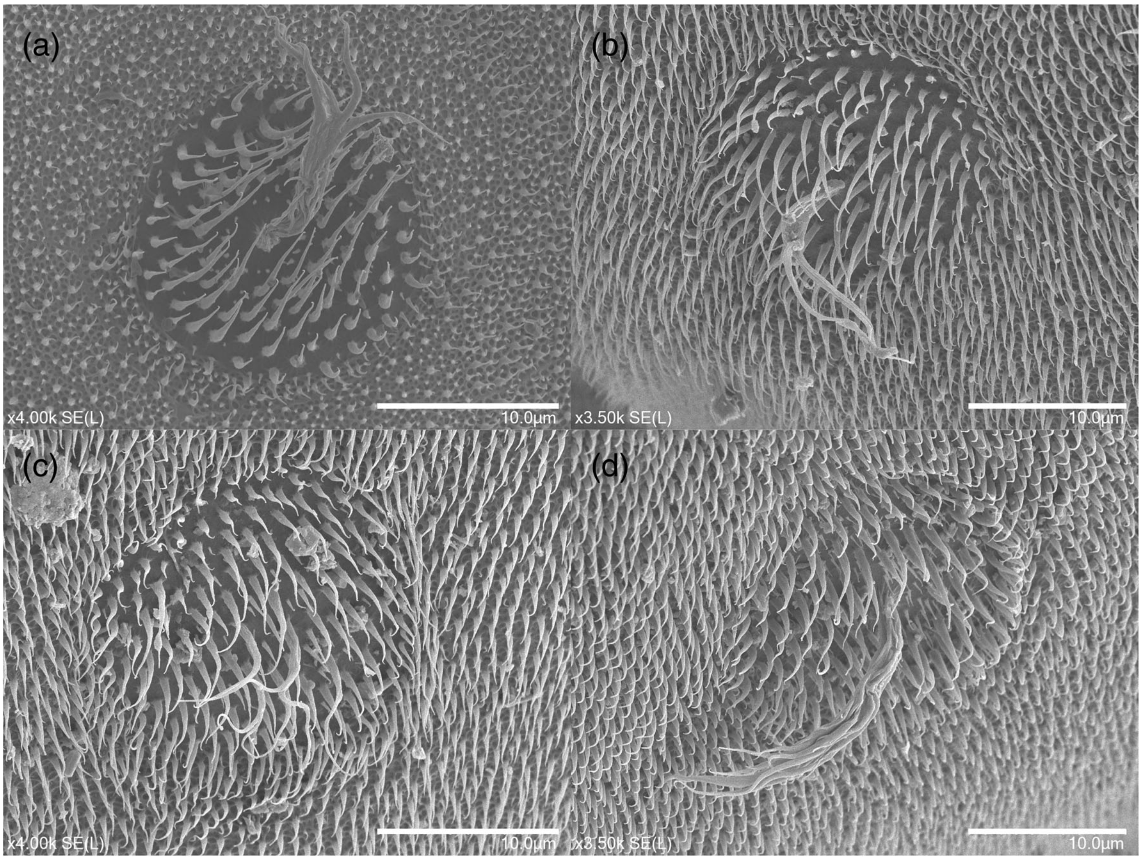

FIGURE 4 SEM images of cutaneous sensilla (CS) in the genus Strophurus. Scalebar: 10 μm. (a) Typical CS of *S. krisalys* on the dorsal midbody region, covered with spinules longer than the spinules on the surrounding scale surface. The single bristle branches four times and has only few setules. (b) CS on the ventral midbody region of *S. williamsi*. Spinules are only slightly longer but are less dense than those on the surrounding scale surface. The bristle is relatively thin and split only once, with only few setules present. (c) CS on the ventral midbody region of *S. williamsi* without a bristle. Instead, there are a few longer, thicker spinules in the central area of the sensillum. (d) CS from the ventral side of the tail of *S. williamsi* with a single bristle in the centre, splitting multiple times and with only a few setules

Based on the results from M1, we constructed a second model, M2, to explore interacting differences among the body regions relevant for our hypothesis and among species. For M2, we excluded the arms and legs (both dorsal and ventral) from the data set to focus on toe placement relative to overall locomotion. And, we summarised, respectively, both extremities (dorsal and ventral side of manus and pes), dorsal and ventral side of the tail and the dorsal head and midbody region each into one functional category. Furthermore, we summarise the species by genera, as there were no significant differences among species within each genus (see results). M2 included scale area, body region and genus as fixed effects and an interaction between body region and genus. ID was again included as a random factor, and M2 was analysed as described for M1.

3 | RESULTS

3.1 | Descriptive morphology

Variation in sensilla morphology among body regions within species was low, and did not show any detectable pattern, so we concluded that, for our group of species, cutaneous sensilla morphology was essentially uniform across body regions within species, and genera. Apart from differences in the number of sensilla (see below), the only regular differences across body regions, in all diplodactylid species examined, were in the position of the sensilla on each scale. Whereas sensilla were found only on the posterior margins of the scales on the head, body, and tail, sensilla were distributed all over the scales on the labials, and the scales directly bordering the labials, as well as on the snout. On the extremities, cutaneous sensilla were found on the distal margins of the scales. In contrast, in both *Nephrurus* species, sensilla were distributed all over the scales on all body regions. In all diplodactylid species examined, sensilla normally had one, or occasionally no bristle, whereas multiple bristles per sensillum were the rule for *N. asper*. Exemptions or variations in these patterns are reported in the following description of sensilla morphology for each genus.

3.1.1 | Lucasium

Cutaneous sensilla of both *Lucasium* species examined were uniform across all body regions and uniformly covered with spinules of

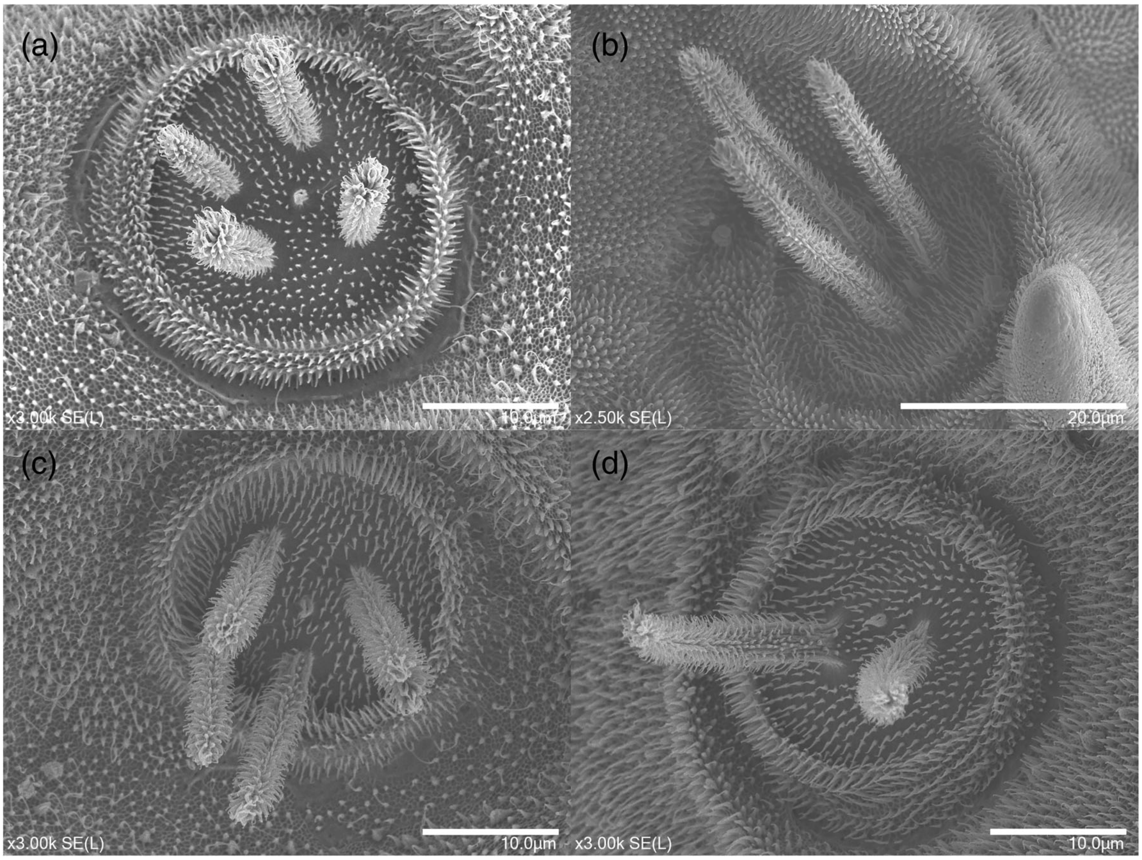

FIGURE 5 SEM images of the cutaneous sensilla (CS) of *N. asper*. Scalebar: 10 μm unless notes otherwise. (a) CS on the dorsal side of the arm, with four bristles covered with setules and thus resembling a bottle-brush. The opening in the Centre may represent the opening for the nerve enervating the CS, on the shed skin from the previous shedding cycle (compare von Düring & Miller, 1979). (b) CS with three bottle-brush-like bristles on the ventral side of the distal part of a digit. Scalebar: 20 μm. (c) CS on the dorsal side of the distal tip of the tail. (d) CS on the ventral side of the tail base, with only two bristles

comparable length to that of the surrounding scale surface (Figure 2). These sensilla had a single bristle, which can either be unbranched (Figure 2a,c) or split at the distal third (Figure 2b,d). Roughly, the lower two-thirds of the bristle were covered with setules. Occasionally, multi-bristled sensilla occurred (Figure 2d) and they appeared to occur slightly more frequently in *L. steindachneri* than in *L. immaculatum*, but not on any particular body region in either species.

3.1.2 | Oedura

The cutaneous sensilla of the genus *Oedura* are also uniform across body regions and superficially similar to those of the genus *Lucasium*. They differ from the latter in that sensilla were separated from the surrounding scale area by a visible moat (Figure 3). The surface of the sensilla is covered with spinules that appear to be of similar length, but lower density compared to the surrounding spinules. Spinules on the sensilla of *O. coggeri* are visibly broader, thicker and less dense than in the other two species (Figure 3d). Each sensillum carried a single bristle, which is normally split distally, often multiple times (Figure 3). The lower part of the bristle below the split is covered with setules (Figure 3a–c). A few multiple-bristled sensilla were present in *O. monilis*, but not in the other two species.

3.1.3 | Strophurus

The cutaneous sensilla of *S. krisalys* are slightly recessed into the scale but are not surrounded by a moat (Figure 4a). The spinules on the sensillum are visibly longer, broader, but less dense compared to spinules on the surrounding scale surface. Each sensillum has a single bristle (with rare multi-bristled sensilla), which splits multiple times toward its distal half but is mostly devoid of setules (Figure 4a). Cutaneous sensilla in *S. williamsi* showed overall more variation than the other species, but again no detectable pattern of variation across body regions existed. The general sensilla morphology was similar to that of *S. krisalys* (Figure 4d), but multi-bristled sensilla occurred more frequently than in *S. krisalys*, and in some sensilla the bristles branched only once or not at all. Bristles with few or no branches were often relatively short and thin, whereas the spinules were very long and think, so that the bristle(s) were hardly discernible from spinules (Figure 4b), while some sensilla lacked bristles altogether (Figure 4c).

TABLE 1 Number of cutaneous sensilla per scale for each species and body region.

	Dorsal											
Species	**Supralabials**	**Above labials**	**Snout**	**Head**	**Arms**	**Hands**	**Midbody**	**Legs**	**Feet**	**Tail-base**	**Mid-tail**	**Tail-tip**
L. immaculatum	40.75 ± 14.92	10.3 ± 1.98	7.3 ± 2.26	1.45 ± 0.64	1.60	0.60	1.1 ± 0	1.5 ± 0.14	2.40	6.70 ± 2.96	6.90 ± 2.91	4.29 ± 2.03
L. steindachneri	61.60	19.70	3.2 ± 1.56	1.65 ± 0.07	1.95 ± 0.92	1.2 ± 0.71	1.9 ± 0.43	0.95 ± 0.21	1.4 ± 0.85	2.5 ± 0.14	4.1 ± 1.41	2.75 ± 0.64
S. krisalys	22 ± 2.55	10.15 ± 3.32	6.65 ± 0.64	1.85 ± 0.35	3.3 ± 0.57	1.8 ± 0.71	3.15 ± 0.07	2.55 ± 1.48	2 ± 1.13	3.75 ± 1.34	4.95 ± 0.49	4.3 ± 0.57
S. williamsi	16.05 ± 1.49	4.15 ± 0.35	1.8 ± 0	1.2 ± 0.15	1.25 ± 0.50	0.95 ± 0.78	2.55 ± 1.49	1.3 ± 0.71	1.15 ± 0.35	2.5 ± 1.28	2.6 ± 0.28	2.25 ± 0.7
O. castelnaui	87 ± 35.94	27.83 ± 5.99	9.63 ± 2.57	4.23 ± 1.46	3.60 ± 1.74	1.63 ± 1.79	3.73 ± 2.56	5.63 ± 2.44	1.53 ± 0.21	8.97 ± 2.57	14.10 ± 5.70	20.33 ± 3.15
O. coggeri	80.47 ± 10.04	20.03 ± 3.17	9.73 ± 1.22	3.56 ± 1.60	4.47 ± 0.81	2.00 ± 1.06	3.80 ± 1.40	5.45 ± 2.62	3.85 ± 0.07	10.17 ± 5.16	13.00 ± 5.44	13.50 ± 2.89
O. monilis	71.18 ± 3.56	22.00 ± 15.84	6.00 ± 2.69	3.45 ± 0.92	3.45 ± 2.76	2.3 ± 0.71	5.25 ± 2.76	7.50 ± 2.55	2.95 ± 1.06	12.00 ± 1.41	11.05 ± 2.33	9.85 ± 1.91
N. amyae	66.00	35.70	25.00	43.60	15.30	4.00	12.90	17.50	9.70	13.50	17.30	11.20
N. asper	83.00	38.40	4.40	1.80	3.30	2.80	0.80	11.60	9.90	3.20	2.00	4.20

	Ventral										
	Infralabials	**Below labials**	**Gular**	**Arms**	**Hands**	**Midbody**	**Legs**	**Feet**	**Tail-base**	**Mid-tail**	**Tail-tip**
L. immaculatum	53.3 ± 10.32	8.6 ± 014	1.55 ± 0.78	1.40	0.60	1.27 ± 0.39	1.30	1.50	5.88 ± 3.29	4.89 ± 2.70	3.76 ± 2.46
L. steindachneri	38.64 ± 0.51	12.75 ± 1.63	0.7 ± 0.14	0.6 ± 0.28	0.6 ± 0.14	0.65 ± 0.35	1.15 0.63	0.8 ± 0	1.95 ± 1.2	1.05 ± 0.07	1 ± 0
S. krisalys	23.05 ± 1.49	10.15 ± 0.50	0.85 ± 0.64	2.25 1.91	1.6 ± 0.14	1.35 ± 0.21	2.7 ± 1.13	2.35 ± 0.50	2.95 ± 0.78	2.5 ± 0.42	1.35 ± 0.07
S. williamsi	17.75 ± 3.18	4.35 ± 1.77	1.75 ± 0.21	1.7 ± 0.57	0.7 ± 0.42	3 ± 1.70	1.3 ± 0.14	1.55 ± 0.64	1.85 ± 1.20	1.55 ± 0.92	1.3 ± 0.42
O. castelnaui	85.25 ± 8.54	13.03 ± 2.02	1.80 ± 0.53	2.40 ± 0.50	2.60 ± 2.97	3.23 ± 1.99	1.50 ± 0.36	1.53 ± 0.65	10.30 ± 1.31	12.50 ± 3.99	13.30 ± 2.69
O. coggeri	71.27 ± 8.32	10.93 ± 3.82	1.00 ± 0.20	3.00 ± 2.25	1.07 ± 0.70	2.47 ± 1.56	2.7 ± 2.12	1.75 ± 0.78	7.75 ± 4.17	8.85 ± 1.91	8.00 ± 0.28
O. monilis	61.00 ± 3.39	15.60 ± 1.27	3.80 ± 4.10	2.35 ± 1.63	1.05 ± 0.50	1.10 ± 0.99	2.25 ± 1.34	1.60	9.60 ± 8.63	10.60 ± 6.65	7.85 ± 1.77
N. amyae	83.10	36.20	15.30	3.20	2.10	7.20	10.20	11.80	21.00	13.80	9.00
N. asper	80.50	24.06 ± 14.22	24.11	1.90	0.90	1.90	9.90	11.20	3.00	2.30	3.40

Note: Mean value ± standard deviation.

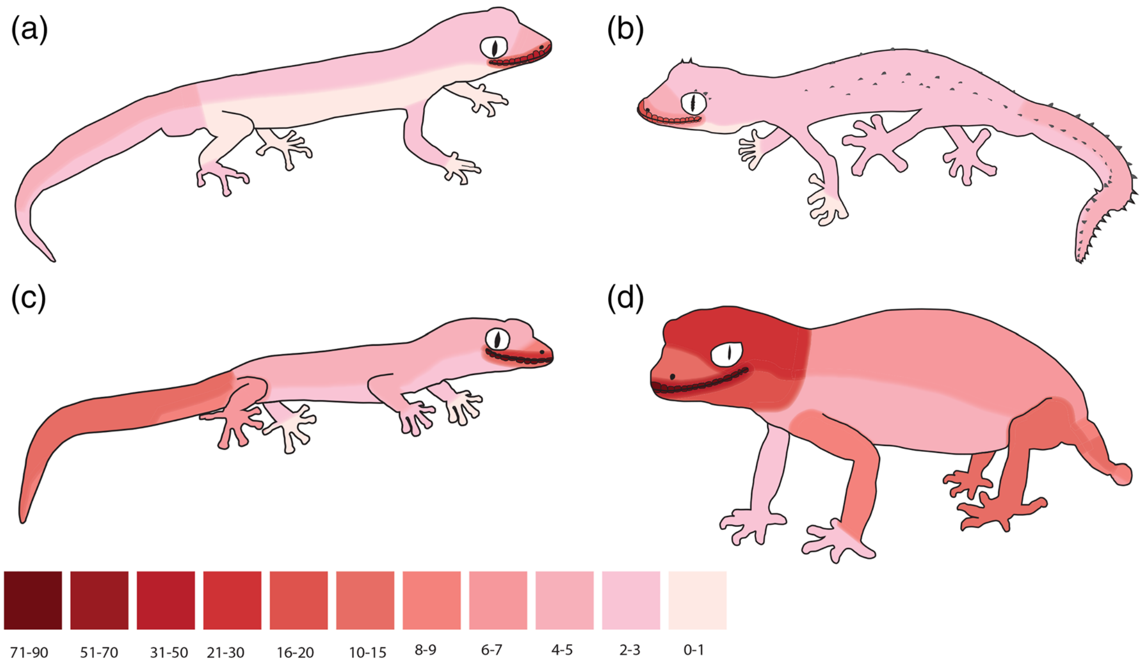

FIGURE 6 Heat map illustrating the numbers of cutaneous sensilla per scale on different body regions. Shown are mean values for each genus examined, with the extremities facing toward the viewers depicting values for the dorsal side whereas the extremities in the background depicting the ventral side. (a) Lucasium. (b) Strophurus. (c) Oedura. (d) Nephrurus. Gecko drawings are based on images from S. Zozaya (a, b), R. Rillai (c), and E. Budd (d)

3.1.4 | Nephrurus asper

Cutaneous sensilla of *N. asper* were slightly recessed and surrounded by a moat with a wall-like structure forming a ring at the edge, elevated slightly above the level of the remaining sensillum. Spinules are mostly absent in the moat, and of equal length and density on the ring compared to the surrounding scale surface, but shorter and sparser on the remaining surface of the sensillum (Figure 5). Each sensillum normally had 3–6 but occasionally only one or two bristles. Bristles were broad and did not split at their end. They were covered with thick, dense setules along the whole length, giving them a bottle-brush-like shape (Figure 5a).

3.2 | Distribution of sensilla among body regions

In contrast to the relative uniformity of sensilla morphology on each species, cutaneous sensilla distribution across the different body regions differed considerably, and in a relatively consistent pattern across species. High numbers of sensilla were found on the labial scales, on the scales bordering the labials and on the scales of the tail, although the latter trend was more pronounced in *Oedura* and *Lucasium* than in *Strophurus* or *Nephrurus* (Table 1, Figure 6). A similar pattern was found for sensilla density (cutaneous sensilla per mm^2) calculated from mean scale size per species and body region (Table 2). While sensilla numbers per scale on the labials drastically exceeded sensilla numbers per scale on all other body regions, sensilla density was roughly equal on the labials and the scales bordering the labials and then gradually declined toward the gular region (dorsal and ventral). From there, both sensilla number and density were roughly constant across body regions but increased again on the tail (Tables 1 and 2; Figure 6). Both *Nephrurus* species had particularly high numbers of sensilla, both in absolute terms and per scale area (Tables 1 and 2; Figure 6). In some species, sensilla numbers were higher on the legs and feet than on the arms and hands, whereas they were relatively similar in others (Table 1, Figure 6).

3.3 | Statistical analysis

We found a significant positive relationship in the first model (M1) between scale size and sensilla number ($F_{1,1} = 272.54$, $p < 0.001$), and significant differences among body regions ($F_{1,12} = 88.10$, $p < 0.001$) and among species ($F_{1,8} = 4.18$, $p = 0.011$) in terms of sensilla density (CS number after accounting for scale size in the model). Among species, *N. amyae* had significantly higher numbers of CS than both *Strophurus* species and *O. castelnaui*, while all other species overlapped (*Tukey's* post hoc tests, Figure S4a). Among body regions, we found the highest number of CS on the labials, which were significantly higher than the number of CS on any other body region (*Tukey's* post hoc tests, Figure S4b). Scales on the dorsal side of the tail had significantly fewer CS than the labials, but significantly more than all other regions. The ventral side of the hands had significantly fewer CS than all other body regions. Sensilla

TABLE 2 Mean number of cutaneous sensilla per mm^2 for each species and body region.

	Dorsal											
Species	**Supralabials**	**Above labials**	**Snout**	**Head**	**Arms**	**Hands**	**Midbody**	**Legs**	**Feet**	**Tail-base**	**Mid-tail**	**Tail-tip**
L. immaculatum	88.68 ± 32.47	180.29 ± 34.66	174 ± 54.02	72.07 ± 31.63	76.78	17.90	46.85 ± 0.16	63.73 ± 6.00	101.49	207.62 ± 162.98	112.50 ± 77.46	141.97 ± 108.00
L. steindachneri	119.95	175.20	112.07 ± 54.48	56.14 ± 2.41	96.36 ± 45.43	63.12 ± 37.19	74.35 ± 16.60	49.76 ± 11.11	57.80 ± 35.03	49.87 ± 2.82	56.78 ± 19.59	201.67 ± 46.67
S. krisalys	44.93 ± 5.19	84.59 ± 27.70	42.05 ± 4.02	14.33 ± 2.73	53.19 ± 9.12	31.41 ± 12.34	29.21 ± 0.66	43.15 ± 25.12	31.85 ± 18.02	32.95 ± 11.81	53.66 ± 5.37	62.88 ± 8.28
S. williamsi	30.67 ± 2.84	77.25 ± 6.58	38.15 ± 0	27.82 ± 3.28	27.43 ± 10.86	49.11 ± 40.21	44.54 ± 25.94	31.09 ± 16.91	48.53 ± 14.92	44.49 ± 22.65	42.30 ± 4.60	35.36 ± 1.11
O. castelnaui	47.88 ± 19.78	83.47 ± 17.97	35.05 ± 9.35	18.61 ± 6.41	24.84 ± 11.97	12.59 ± 13.81	17.50 ± 11.99	24.94 ± 10.79	14.00 ± 1.90	21.34 ± 8.62	17.47 ± 7.06	30.89 ± 4.79
O. coggeri	56.55 ± 7.05	74.58 ± 11.79	41.08 ± 5.16	14.13 ± 6.32	24.55 ± 4.48	25.34 ± 13.41	14.90 ± 5.49	40.94 ± 19.66	38.90 ± 0.72	37.54 ± 20.37	34.88 ± 14.59	63.69 ± 13.65
O. monilis	43.39 ± 2.17	70.43 ± 50.71	20.57 ± 9.21	17.55 ± 4.68	23.05 ± 18.43	19.40 ± 5.97	19.58 ± 10.29	47.14 ± 16.00	59.05 ± 21.23	37.11 ± 4.37	24.24 ± 5.12	44.20 ± 8.57
N. amyae	69.62	175.03	202.69	265.15	199.51	72.47	235.66	233.16	115.06	176.50	174.40	165.29
N. asper	93.49	233.17	65.71	21.53	78.77	65.61	18.24	244.04	194.72	149.54	85.47	132.41
	Ventral											
	Infralabials	**Below labials**	**Gular**	**Arms**	**Hands**	**Midbody**	**Legs**	**Feet**	**Tail-base**	**Mid-tail**	**Tail-tip**	
L. immaculatum	60.86 ± 11.78	222.90 ± 3.67	93.57 ± 46.96	44.51	18.06	71.53 ± 21.99	58.59	87.47	34.35 ± 20.57	39.81 ± 28.45	87.51 ± 102.53	
L. steindachneri	36.36 ± 0.46	32.72 ± 4.17	55.24 ± 11.16	26.73 ± 12.60	18.54 ± 4.37	16.93 ± 9.21	73.17 ± 40.50	28.38 ± 0	39.93 ± 24.61	76.21 ± 5.13	85.66 ± 0	
S. krisalys	36.44 ± 2.25	45.29 ± 2.21	24.37 ± 18.25	18.57 ± 15.75	36.70 ± 2.35	18.61 ± 2.92	38.94 ± 16.31	45.57 ± 9.60	29.89 ± 7.88	21.40 ± 3.63	17.17 ± 0.90	
S. williamsi	23.11 ± 4.14	68.24 ± 27.73	74.54 ± 9.04	39.92 ± 13.28	19.38 ± 11.74	85.49 ± 48.36	36.13 ± 3.93	44.98 ± 18.47	21.00 ± 13.65	19.81 ± 11.75	17.37 ± 11.17	
O. castelnaui	36.91 ± 3.70	48.96 ± 7.60	20.64 ± 6.07	17.80 ± 3.72	23.23 ± 26.55	19.55 ± 12.00	4.45 ± 1.07	11.77 ± 4.99	20.75 ± 2.64	15.75 ± 5.03	19.55 ± 12.01	
O. coggeri	39.66 ± 4.63	34.01 ± 11.89	10.08 ± 2.02	14.91 ± 11.20	9.96 ± 6.56	9.57 ± 6.07	38.84 ± 30.52	10.80 ± 4.80	19.36 ± 10.42	18.89 ± 4.08	27.83 ± 0.98	
O. monilis	32.66 ± 1.82	46.90 ± 3.83	19.67 ± 21.23	13.93 ± 9.64	8.61 ± 4.06	5.18 ± 4.66	5.47 ± 3.27	8.02	29.69 ± 26.68	25.26 ± 15.84	35.27 ± 7.94	
N. amyae	94.17	108.69	351.26	57.06	102.36	82.47	76.14	139.97	146.03	95.77	72.54	
N. asper	103.09	171.47 ± 101.37	419.21	57.84	25.29	42.28	173.20	135.55	63.72	88.58	74.48	

Note: Mean value ± standard deviation. (mean scale size data is listed in Data S2).

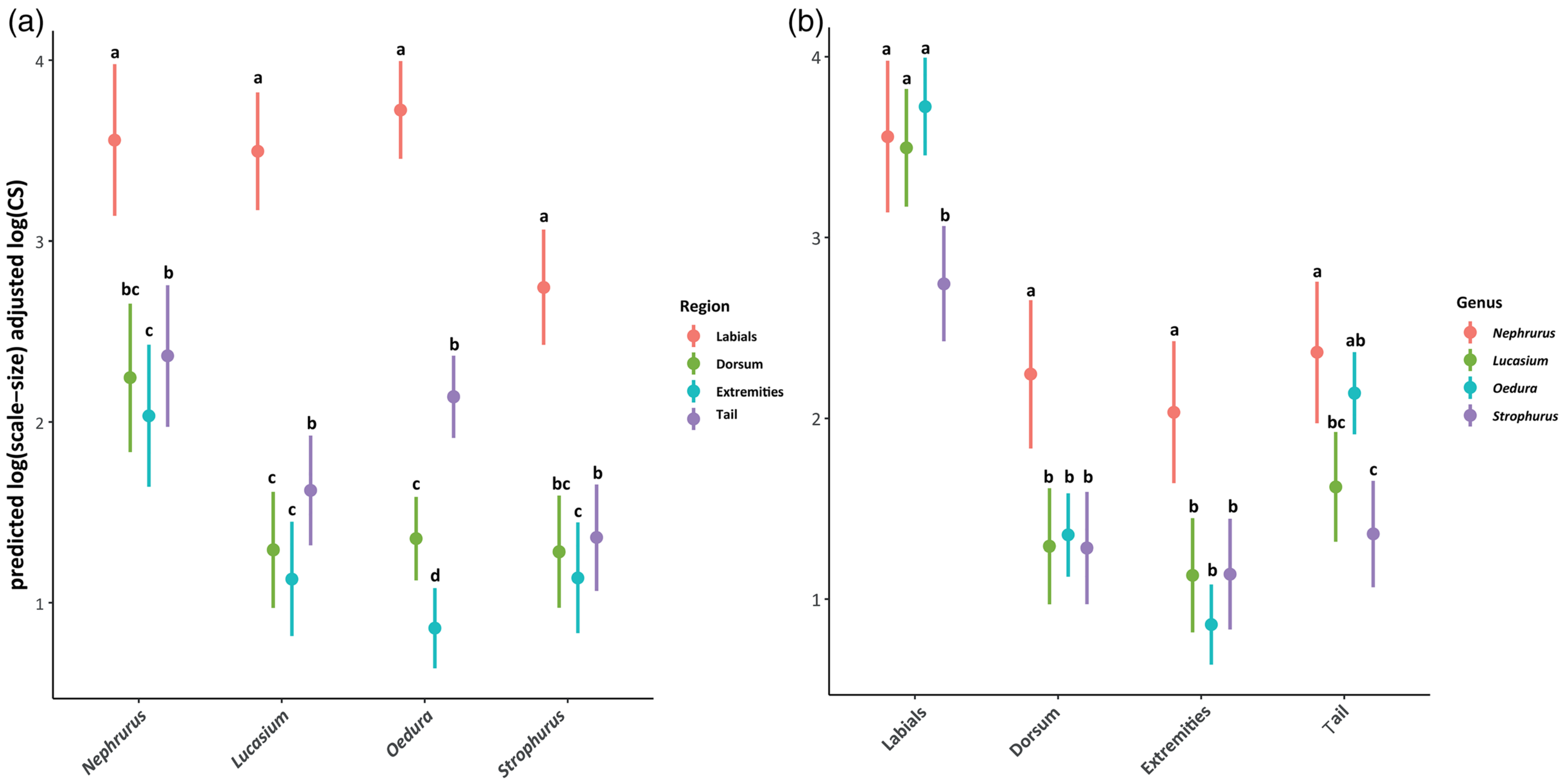

FIGURE 7 Cutaneous sensilla (CS) predicted mean values and 95% confidence interval from M2 accounting for scale size. Significant differences (a–c) are shown (a) among body region for each genus, and (b) among genera for each body region. Tukey adjustment of p-values for multiple comparisons

numbers on the arms, legs, dorsal midbody and the head partially overlapped, showing a gradual reduction toward the distal and ventral parts of the extremities (Figures S4b and S5).

There was a significant positive relationship between scale size and sensilla number ($F_{1,1} = 50.03$, $p < 0.001$) in model 2 (M2). The interaction between the body region and genus was significant ($F_{1,9} = 43.01$, $p < 0.001$), indicating that different genera differed in their relative sensilla density among different body regions, although the labials were always highest. Both fixed effects, body region ($F_{1,3} = 226.36$, $p < 0.001$) and genus ($F_{1,3} = 5.68$, $p < 0.005$), were significantly different as well. Post hoc comparisons for the region by genus (Figure 7a) showed that the labials had the highest numbers of CS in all genera, whereas the extremities and dorsum were at the lower end and overlapped in all genera except *Oedura*, where the extremities had significantly lower numbers of CS than the dorsum. Cutaneous sensilla densities on the tail were significantly higher than on both, the dorsum and the extremities, in *Oedura* and *Lucasium* but overlapped with the dorsum in *Strophurus* and *Nephrurus*. Post hoc comparison for genus by region (Figure 7b) revealed *Nephrurus* had significantly higher sensilla numbers than all other genera on the dorsum and the extremities, while *Strophurus* had significantly lower sensilla numbers on the labials compared to the other genera. On the tail, the sensilla numbers increased from *Strophurus* over *Lucasium*, *Oedura* toward *Nephrurus*.

4 | DISCUSSION

We present detailed data on the diversity, density and distribution of cutaneous sensilla among seven diplodactylid and two carphodactylid geckos. We expected that sensilla morphology would vary among body regions within species, and among species. We did observe variation among species, but little within species among body regions, such that each species had similar sensilla morphology on their whole body, regardless of position. Numbers of cutaneous sensilla varied among species, with high numbers in *Nephrurus* and low numbers in *Strophurus*. We expected to find high sensilla densities in locations where well-developed tactile sensory abilities might be required, that is, around the mouth, on the tail and around the hands and feet (Hiller, 1976; Lauff et al., 1993; Russell et al., 2014). Consistent with these predictions, in all species sensilla densities were highest on the labial scales (and the scales surrounding the labials), followed by the scales on the dorsal side of the tail. In contrast to our predictions, we found only moderate densities of sensilla on the manus and pes, and the lowest sensilla densities were found on the ventral side of the manus. Thus, our first prediction, that sensilla morphology would vary among body regions, was not supported, instead, sensilla morphology was the same on all regions of each species. Our second prediction, that sensilla density would vary consistently with proposed functions, that is, high densities on the labials and associated regions, probably for diverse functions, including prey capture, and on the tail, probably for autotomy (Russell et al., 2014), was supported. We did not find evidence that sensilla density was increased on the manus and pes, ostensibly for toepad placement (Lauff et al., 1993), even though many of the species we examined had adhesive toepads.

4.1 | Comparative morphology of cutaneous sensilla

Nephrurus asper had multiple-bristled sensilla completely covered by setules, giving them a bottlebrush-like appearance, whereas the cutaneous sensilla of the diplodactylid species were normally single-bristled, only covered with setules basally, and were often split distally. This basic distinction is consistent with previous studies (Bauer & Russell, 1988; Riedel et al., 2019). Bauer and Russell (1988) also describe unbranched, setule-covered bristles for at least some body regions of all Carphodactylidae examined. We also described similar, bottle-brush type sensilla for *Nephrurus laevis* and *Nephrurus levissimus*, but noted bristles with a broadened mace-like end for *N. asper* (Figure 5d in Riedel et al., 2019). The difference between this study and our previous work could be due either to within-species variation in sensilla morphology, or to preparation differences. Riedel et al. (2019) used moulds made from dental imprint material negatives of the skin (Vucko et al., 2008) while our present study examined original shed skin. Bauer and Russell (1988), using ethanol-preserved museum specimens, reported bristle-less sensilla on 'glabrous' subdigital scales and on 'glabrous' scales on the knob of the tail tip of *N. asper* (and *Nephrurus levis*), whereas we found uniformly multi-bristled sensilla across all body regions. The mesos layer of the squamate integument, which separates the outer microornamentation-bearing ß-layer from the inner α-layer, is rich in lipids (Alibardi & Maderson, 2003; Landmann, 1975; Maderson et al., 1998). When specimens are stored in ethanol over extended periods, as is typical for older specimens in museum collections, sometimes the outer microornamentation-bearing ß-layer gets partially removed from the skin's surface, probably because the lipids are dissolved by the ethanol (Barthlott et al., 2016; Dujsebayeva et al., 2021; Irish et al., 1988). This may explain the lack of bristles on the sensilla and spinules on the remaining scale surface reported by Bauer and Russell (1988). Further studies with larger sample sizes, comparing different preparation methods, will prove highly informative to determine causes of apparent, within-species differences in morphology, not corroborated in this study.

Cutaneous sensilla morphology of the Diplodactylidae in our study is largely consistent with Riedel et al. (2019), who reported that all species had single-bristled sensilla, densely covered with setules basally in *L. immaculatum* and *L. steindachneri*, and normally split at least once distally in *Oedura*. However, in the present study, we found setules on the basal parts of the bristles in the genus *Oedura*. In *Strophurus*, our earlier study found bristle-less sensilla in *S. krisalys* and single-bristled sensilla in *S. willamsi*. This time, we found bristle-less sensilla were more prevalent in *S. willamsi* than in *S. krisalys*. Overall *Strophurus* (and particularly *S. williamsi*) showed the largest variation in sensilla morphology among our sampled species. Single-bristled sensilla have been described for other diplodactylid species and seem to be the norm in that family (Bauer & Russell, 1988; Hiller, 1971), while multi-bristled sensilla could be prevalent in the Carphodactylidae and in their sister clade the Pygopodidae (Dujsebayeva et al., 2021; Riedel et al., 2019; Skipwith et al., 2019; Spinner et al., 2013). In the Gekkonidae, Eublepharidae and Phyllodactylidae, both single-bristled and multi-bristled sensilla occur, although the former seem to be more prevalent (Darwish, 2012; Hiller, 1972; Koppetsch et al., 2020; Nikitina & Ananjeva, 2003; Röll, 1995; Yonis et al., 2009).

Differences in sensilla density among species will primarily be discussed in terms of their functional implications below, but the higher sensilla density on most body regions in the genus *Nephrurus*, compared to the diplodactylids, could be at least partially phylogenetic. High numbers of cutaneous sensilla have been proposed as plesiomorphic for Pygopodidae (Dujsebayeva et al., 2021). Thus, high sensilla densities might be pleomorphic for both families. Notably, sensilla density in pygopods is particularly high on the head, and may be related to the borrowing lifestyle of many species (Dujsebayeva et al., 2021).

Overall, our results indicate that sensilla morphology might be more consistent within species than previously thought, and that previously detected, within-species differences (Bauer & Russell, 1988) might occur because preserved material is missing the uppermost corneous layers (ß- and oberhäutchen layer; Barthlott et al., 2016; Dujsebayeva et al., 2021; Irish et al., 1988). We, therefore, encourage researchers working on microornamentation with preserved specimens to carefully examine the material for loose or missing skin layers. The uniform patterns of sensilla morphology among species and among families, which are consistent with previous studies (Bauer & Russell, 1988; Riedel et al., 2019; Spinner et al., 2013) corroborate previous suggestions that differences among species might be primarily phylogenetic and useful for taxonomy (Ananjeva et al., 2000; Landmann, 1975). However, this does not rule out functional differences, because cutaneous sensilla could be suitable for multiple tasks even in the absence of distinct morphologies or higher densities, as functional and phylogenetic drivers of morphology are not necessarily mutually exclusive (Dujsebayeva et al., 2021).

4.2 | Functional implications

Our results, that sensilla numbers are particularly high on the labials and the scales bordering the labials, are consistent with previous studies, further corroborating the proposed importance of the sensory field surrounding the rostrum (e.g., Ananjeva et al., 1991; Jackson, 1977; Matveyeva & Ananjeva, 1995; Povel & Van Der Kooij, 1996). As nocturnal predators, geckos might particularly benefit from this well-developed sensory field for prey capture and handling, and for orientation in complex habitats at night. High sensilla numbers were also present on the dorsal (and to a lesser degree on the ventral) side of the tail, consistent with the results of Russell et al. (2014) for leopard geckos (*E. macularius*), indicating that cutaneous sensilla may play an important role in inducing tail autotomy and control of tail movement post-autotomy. Our results deviated from the latter study in that we found no differences between original and regenerated tails (Data S3). This could be due to differences in the importance of the regenerated tail for predatory evasion or locomotor abilities among species. However, a recent study by Bradley et al. (2021) indicates that tactile sensitivity is effectively restored in regenerated tails of leopard geckos. Behavioural experiments, comparing the use of regenerated and original tails, and further neurobiological studies on more species would be highly informative. Interestingly, both *Nephrurus* species examined in this study also have high sensilla density on the tail, despite having lost the ability to autotomize it (Bauer & Russell, 1988). This could be plesiomorphic for *Nephrurus*, as discussed above. Alternatively, or additionally, the sensilla on the tail of *Nephrurus* may fulfil functions associated with monitoring the environment (Russell & Bauer, 1987), for example, *N. asper* uses the knob on their tail tip for a 'probing behaviour' (repeatedly touching the tail to the substrate) with which they may collect information about their surroundings, for which they could benefit from high sensilla density on the tail (Budd, 2018).

Previous studies on Gekkonidae have indicated that cutaneous sensilla may allow correct placement of the adhesive toepads (Hiller, 1968; Lauff et al., 1993). This hypothesis was recently corroborated for *Anolis sagrei* and *Anolis carolinensis*, two species of anoline lizards also possessing adhesive toepads (Russell et al., 2021). However, we found relatively low sensilla densities, and no evidence for distinct morphologies on the hands and feet of any species examined, thus do not support this hypothesis for Diplodactylidae. Of the species we sampled, members of the genera *Oedura* and *Strophurus* have adhesive toepads and are scansorial, *Lucasium* species are secondarily terrestrial and have reduced pads, while Carphodactylidae are primarily pad less and terrestrial (Gamble et al., 2012; Riedel et al., 2020; Russell & Gamble, 2019). All species had uniform sensilla morphology across the manus and pes, and the scansorial and pad-bearing species did not have higher sensilla density on the extremities compared to pad-less or pad-reduced terrestrial species. For sensilla density, these differing results may be partially due to more detailed categorisation and examination of different areas of the extremities (Lauff et al., 1993; Russell et al., 2021), while we summarised each extremity as one category due to the broader focus of our study. More detailed examinations and behavioural or neurobiological experiments could be useful to further examine the role of cutaneous sensilla on toe placement in Diplodactylidae.

In Riedel et al. (2019), cutaneous sensilla diameter and the number of bristles per sensillum were the important features of the sensilla morphology separating ecological groups (arboreal, saxicoline, terrestrial and xeric, mesic and hydric) and neither of these characteristics were examined in this study. Riedel et al. (2019) also found that cutaneous sensilla density was higher on the dorsal midbody region of terrestrial species compared to climbing species. In this study, only the terrestrial carphodactylid genus *Nephrurus* had significantly higher sensilla density than the remaining diplodactylid genera, including the terrestrial genus *Lucasium*. Thus, it appears that within the Diplodactylidae, terrestrial species might have overall higher sensilla densities, but consistent patterns among body regions, compared to climbing species, whereas members of the genus *Nephrurus* also have relatively more sensilla on the dorsum. Increased sensilla numbers on the dorsal surface might be associated with differences in life-history traits. For example, *Lucasium* species often hide in spider holes during the day, while *N. asper* often hide in spinifex grass during the day (Budd, 2018; Wilson & Swan, 2017). Thus, *Nephrurus* species might be more exposed while resting, compared to *Lucasium*. Increased dorsal sensilla numbers may provide the information required while resting (on predator approach, increased temperatures or decreased humidity) allowing a faster response from a more exposed animal. Overall, the differences between this study and our previous study warrant further examination, ideally including neurobiological approaches and behavioural experiments.

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AUTHOR CONTRIBUTIONS

Jendrian Riedel: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (equal); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Lin Schwarzkopf:** Conceptualization (equal); formal analysis (supporting); investigation (equal); methodology (equal); resources (lead); supervision (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/jmor.21462.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are in Table S2. The SEM and LM images are available from the corresponding author upon request. Skin samples are stored at JCU, Townsville, Australia

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