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Investigating mechanoreceptor variability and morphometric proxies in Rhesus Macaques: Implications for primate precision touch studies

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Abstract

The origin of primates has long been associated with an increased emphasis on manual grasping and touch. Precision touch, facilitated by specialized mechanoreceptors in glabrous skin, provides critical sensory feedback for grasping-related tasks and perception of ecologically-relevant stimuli. Despite its importance, studies of mechanoreceptors in primate hands are limited, in part due to challenges of sample availability and histological methods. Dermatoglyphs have been proposed as alternative proxies of mechanoreceptor density. We investigated the relationships between mechanoreceptors (Meissner and Pacinian corpuscles), dermatoglyphs, and demography in the apical finger pads of 15 juvenile to adult rhesus macaques (*Macaca mulatta*) from a free-ranging population at Cayo Santiago Primate Field Station (Puerto Rico). Our results indicate substantial interindividual variation in mechanoreceptor density (Meissner corpuscles: 11.9–43.3 corpuscles/mm^2; Pacinian corpuscles: 0–4.5 corpuscles/mm^2). While sex and digit were generally not associated with variation, there was strong evidence of a developmental effect. Specifically, apical pad length, Meissner corpuscle size, and Pacinian corpuscle depth increased while mechanoreceptor densities decreased throughout juvenescence, suggesting that primate mechanoreceptors change as fingers

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grow during adolescence and then stabilize at physical maturity. We also found Meissner corpuscle density was significantly associated with dermatoglyph ridge width and spacing, such that density predicted by a dermatoglyph model was strongly correlated with observed values. Dermatoglyphs thus offer a useful proxy of relative Meissner corpuscle density in primates, which opens exciting avenues of noninvasive research. Finally, our results underscore the importance of considering demographic factors and methodology in comparative studies of primate touch.

KEYWORDS

glabrous skin innervation, growth, *Macaca*, Meissner corpuscle, non-human primate, Pacinian corpuscle, sensory system, somatosensation

1 | INTRODUCTION

The origin of primates is characterized by two major shifts in sensory function—an increased emphasis on vision and an increased emphasis on touch and manual grasping (Cartmill, 1992; Martin, 1990). While primate visual specializations have been well explored (Dominy & Melin, 2020; Kirk & Kay, 2004; Veilleux et al., 2022), similar comparative work on primate touch is lacking. A number of studies have investigated the anatomy and biomechanics of primate manual grasping, finding that primates are characterized by several derived features, including prehensile digits, tactile apical pads, and specialized brain regions, that improve grasping and object manipulation relative to most mammals (e.g., Heffner & Masterton, 1975; Marzke, 2013; Napier, 1980; Patel & Maiolino, 2016). Manual grasping is dependent on sensory feedback provided by the sense of precision (or discriminative) touch, which permits detection of an object's texture, shape, size, vibration, and movement (Zimmerman et al., 2014). Several ecological factors have been hypothesized to select for sensitive manual precision touch, including frugivory, arboreality, and tool use (Dominy et al., 2016; Hoffmann et al., 2004). However, quantitative comparative studies evaluating these hypotheses are currently limited (Veilleux et al., 2022).

The sensation of precision touch is achieved via specialized mechanosensory end organs (e.g., mechanoreceptors) in the skin that respond to different types of tactile stimuli. Although hair-covered skin contains mechanoreceptors, the most acute precision touch organ is nonhairy "glabrous" skin found in the hand, foot, face, and genitals (Zimmerman et al., 2014). Four types of mechanoreceptors are found in glabrous skin: Meissner corpuscles, Pacinian corpuscles, Ruffini corpuscles, and Merkel cells (also known in non-eponymous terms as tactile corpuscles, lamellar corpuscles, bulbous corpuscles, and tactile epithelial cells, respectively). In glabrous skin, Merkel cells are involved in high acuity resolution of texture and object shape, while Meissner corpuscles and Pacinian corpuscles respond to vibrations and object movement (Zimmerman et al., 2014). These mechanoreceptors provide critical sensory feedback for grasping and dexterity-related tasks in the glabrous hand (Dominy et al., 2016; Zimmerman et al., 2014). Ruffini corpuscles, which respond to stretch, are also found in joint capsules and ligaments and are only rarely observed in primate glabrous skin (Paré et al., 2002, 2003). In humans, variation in the density of mechanoreceptors across different regions is associated with differences in tactile acuity and sensitivity. Fingertips, for example, have high densities (≥100 mechanoreceptors/cm^2) of Meissner corpuscles, Pacinian corpuscles, and Merkel cells, corresponding to their very high tactile acuity in two-point discrimination tests (Corniani & Saal, 2020; Johansson & Vallbo, 1979; Mancini et al., 2014). By contrast, the hairy skin of the dorsal hand, which is rarely involved in haptic exploration, can exhibit less than 10 corpuscles/cm^2 and is impoverished in Meissner and Pacinian corpuscles (Edin & Abbs, 1991; Johnson, 2001). Because of these functional relationships, variation in mechanoreceptor densities may be a useful measure for comparing relative reliance on precision touch across species.

There are currently only a handful of studies quantifying mechanoreceptor density using histology in primate manual glabrous skin (Table 1). These studies have almost exclusively focused on Meissner corpuscles, which is not surprising given their critical role in reflex grip control (Zimmerman et al., 2014) and the relative ease of identifying them histologically in skin sections. Hoffmann et al. (2004) conducted the first comparative study of Meissner corpuscle density across primates fingers. They combined previous density estimates from

TABLE 1 Summary of previous studies investigating mechanoreceptor densities in primate digits.

Study	Histological approach	Mechanoreceptor type	Species	Density	Digits	Sample demographics
Paré et al. 2002	Sections perpendicular to skin surface (14 μm); immunofluorescence	Meissner corpuscles	*Macaca fascicularis*	47.25–60.4	I,II,V	2 Unkn
		Pacinian corpuscles		1.15–1.99	I,II,V	2 Unkn
Güclü et al. 2003	Longitudinal sections parallel to skin surface (60 μm), immunohistochemistry	Meissner corpuscles	*Aotus* spp.	33–46.2	II,III,V	1 F
			Papio spp.	7.2	I	1 M
			Macaca mulatta	21–37.4	I-V	1 M, 1 F (6 year)
			Macaca radiata	27.5–31.2	I,II,V	1 F (12 year)
			Homo sapiens	23.3	III	1 M (32 year)
Bolanowski & Pawson, 2003	Longitudinal sections (60 μm) for immunohistochemistry, cross sections (12–18 μm) H&E staining	Meissner corpuscles	*Macaca mulatta*	48.7		5 unkn adults
			Aotus spp.	40.3		1 unkn adult
			Papio spp.	20.4		2 unkn adults
			Homo sapiens	28.1		not listed (ages 44–90 year)
Hoffmann et al. 2004	4–5 sections in transverse or sagittal plane (4 μm), trichrome staining	Meissner corpuscles	*Hylobates lar*	45.8	II	1 adult M
			Gorilla gorilla	11.3	II	1 adult M
			Pongo pygmaeus	14.3	II	1 adult F
			Pilocolobus badius	16.7	II	1 adult F
			Theropithecus gelada	10.2	II	1 adult M
			Trachypithecus cristatus	11.7	II	1 adult F
Verendeev et al. 2015	3–4 transverse sections (5 μm) in distal-proximal gradient, H&E staining	Meissner corpuscles	*Callithrix jacchus*	34.7–44.7	I,II,IV	4 Ms. (2–5 year)
			Papio anubis	28.5–38.7	I,II,IV	1 F (9 year), 1 M (7 year)
			Macaca mulatta	46.5–67.3	I,II,IV	1 F (13 year), 1 M (20 year), 1 Unkn
			Pan spp.	28.6–36.3	I,II,IV	4 Fs (25–57 year)
			Homo sapiens	44.6–54.7	I,II,IV	4 F (78–89 year., 2 unk), 4 M (89–91 year., 2 unkn)
Crowley et al. 2019	8 transverse sections (4 μm) every 100 μm, H&E staining	Meissner corpuscles	*Macaca fascicularis*	27–43.6	I-V	11 Ms. (3–5 year)
García-Piqueras et al., 2019	6 sections (7 μm) perpendicular to skin surface every 200 μm; immunohistochemistry	Meissner corpuscles	*Homo sapiens*	27.7 ± 6.8	I,II	20–39 years: 3 Ms., 3 Fs
				12.5 ± 2.7	I,II	40–59 year: 5 Ms., 2 Fs
				7.12 ± 2.3	I,II	60+ year: 7 Ms., 2 Fs

Note: Density in receptors/mm^2.

Abbreviations: F, female; H&E, hematoxylin & eosin; M, male; Unkn, unknown.

four taxa and new estimates from six taxa with diverse diets to explore the relationship between precision touch and frugivory. The authors found a positive relationship between corpuscle density and time spent feeding on fruit, consistent with the "fruit texture hypothesis" (i.e., more frugivorous primates rely on precision touch to detect ripeness; Hoffmann et al., 2004). A subsequent study by Verendeev et al. (2015) measured Meissner corpuscle density and size in five taxa (including humans) and found no relationship with dietary frugivory or manual dexterity, although they acknowledge the small size and lack of dietary and taxonomic diversity among their sample.

The available data also indicate substantial variation in Meissner corpuscle density estimates within species and between studies. A number of factors may be contributing to this variation. In humans, mechanoreceptor density has been found to vary significantly with part of the digit sampled, digit size, and individual age (Ciano & Beatty, 2022; García-Piqueras et al., 2019; Peters et al., 2009). Several studies, for example, have observed significant reductions in Meissner corpuscle density across the lifespan, both between adolescence and adulthood, and between young, middle, and old adulthood (Bhat et al., 2014; Bolton et al., 1966; García-Piqueras et al., 2019). For nonhuman primates, sexual dimorphism in finger size may also impact density estimates, and many of the species currently sampled exhibit high levels of body size sexual dimorphism. Crowley et al. (2019) additionally found significant variation in Meissner corpuscle density between digits in long-tailed macaques (*Macaca fascicularis*), with the highest densities in the first and second digits. Moreover, studies vary in their histological approaches (Table 1), as well as in the details of the criteria used to count Meissner corpuscles and how density was quantified. Some studies, for example, calculate density as corpuscle count over the volar area of the sections sampled or the number of corpuscles within a defined area (Bolanowski & Pawson, 2003; Güçlü et al., 2003; Hoffmann et al., 2004), while others use Abercrombie's (1946) formula to account for effects of histological sectioning (Crowley et al., 2019; García-Piqueras et al., 2019; Verendeev et al., 2015). These types of methodological differences could contribute to observed intraspecific and interspecific variation between studies. Estimates by Verendeev et al. (2015), for example, generally appear higher than those reported for the same taxa in other studies (Table 1). This is most apparent in their estimates for humans, where they found densities of 44.6–54.7 corpuscles/mm^2 in a sample of elderly individuals (>75 years). By contrast, other studies of similarly aged participants have found Meissner corpuscle density to be much lower due to age-related deterioration (2.8–14.4: corpuscles/mm^2: Bolton et al., 1966; 7.1 corpuscles/mm^2: García-Piqueras et al., 2019). Thus, we need a clearer understanding of how sampling (digit sampled, age, and sex) and methodology impact intraspecific variation in mechanoreceptor densities in a controlled primate sample before engaging in broader-scale comparative meta-analyses of precision touch.

Additionally, histological analysis is labor-intensive and access to glabrous skin tissues from diverse primate species (particularly highly endangered species) is limited. There is a need for more easily assessed proxies of precision touch in primate glabrous skin. Growing evidence suggests that dermatoglyph (fingerprint) papillary ridges are intimately connected to precision touch and serve as the "basic computational unit of glabrous skin", meaning that the arrangement and structure of these ridges are central for detecting and processing tactile stimuli (Jarocka et al., 2021; Tymms et al., 2018). In primates, dermatoglyph ridges are often lined by regularly-spaced Meissner corpuscles and clusters of Merkel cells (Bolanowski & Pawson, 2003; Güçlü et al., 2003; Paré et al., 2002). Consequently, ridge width and spacing have been negatively correlated with Meissner corpuscle abundance, proxies of Merkel cell density, and psychophysical measures of tactile acuity and sensitivity (Dillon et al., 2001; Jarocka et al., 2021; Peters et al., 2009; Tymms et al., 2018).

In this study, we investigate the relationships between mechanoreceptors, dermatoglyph features, and demographic variables (age, sex) in a population of free-ranging rhesus macaques (*Macaca mulatta*). Macaques are semi-terrestrial quadrupeds with highly dexterous hands (Feix et al., 2015; Heffner & Masterton, 1975; Macfarlane & Graziano, 2009; Vanhoof & Vereecke, 2020) and are emerging as an important model of human health and aging (Chiou et al., 2020). This species has been included in three previous studies of Meissner corpuscles, but samples were limited to 2–5 individuals (Table 1). Here, we collected dermatoglyphs and histological data on Meissner and Pacinian corpuscles for the first and second digits of 15 individuals (12 male, 3 female) spanning juvenile to young adult age classes (2.3–7.4 years old). We explore how digit, age, and sex influence variation in the density and size of Meissner and Pacinian corpuscles, as well as in dermatoglyph features (e.g., papillary ridge width, between-ridge spacing). We then test whether dermatoglyph features are useful proxies for Meissner corpuscles. Specifically, we predicted that more dense ridges (e.g., narrower widths and spacing) would be associated with higher Meissner corpuscle densities, and that ridge width would positively correlate with Meissner corpuscle size.

2 | MATERIALS AND METHODS

2.1 | Study population and sample collection

Tissue samples and dermatoglyphs were collected from individuals at the Cayo Santiago Primate Field Station in Puerto Rico, which is home to a large population of free-ranging macaques. The Cayo Santiago population was founded in 1938 using wild born monkeys from northern India (Widdig et al., 2016) and is maintained by the Caribbean Primate Research Center at the University of Puerto Rico. The population lives in naturally formed social groups and are subject to minimal intervention. While they are provisioned with water and commercial monkey chow, they also spend time foraging on wild vegetation (Marriott et al., 1989; Widdig et al., 2016). Because of the lack of natural predators, population control is necessary to maintain the long-term viability of the population (Hernandez-Pacheco et al., 2016). In 2016, the Cayo Biobank Research Unit (CBRU) began collecting postmortem samples (including tissue samples and soft tissue measurements) from individuals removed from the island as part of population control (Newman et al., 2023). For the present study, CRBU opportunistically collected postmortem dermatoglyphs and skin samples from the apical pads of the first (D1) and second (D2) digits of the right hand of 15 individuals (12 males, 3 females) between 2021 and 2023. We focused on D1 and D2 apical pads because Crowley et al. (2019) previously found those digits to have the highest Meissner corpuscle density in *M. fascicularis*. The individuals sampled range in age from 2.3 to 7.4 years with known body mass data (Table S1). Because macaque lifespans are ~3–4 times faster than humans (Chiou et al., 2020), these individuals span both juvenile (1–4 years) and adult (>5 years) age classes (Munds et al., 2022). Additionally, we collected a second independent dermatoglyph dataset from the first and second digits from 58 other individuals (37 females, 49 males) ranging in age from 2.1 to 8.1 years.

For each individual, CRBU collected dermatoglyphs from the distal apical pads of D1 and D2 of the right hand during necropsy using carbon paper, cellophane tape, and cardstock (O'Leary et al., 1986). Next, the skin of the right hand was removed and preserved in 10% formalin until shipped. The dermatoglyphs and samples were then shipped to Midwestern University (MWU) where the dermatoglyphs were digitized at 4800 dpi resolution (CanoScan LiDE 400, Canon USA, Inc., One Canon Park Melville, NY) and the skin samples were then stored in 70% ethanol until the tissue was processed.

2.2 | Histological preparation

We collected the glabrous skin from the distal apical pads of D1 and D2 for each of the 15 individuals. Samples included either the entire pad (six individuals) or the pad was halved vertically (Figure S1) and the lateral half was used (nine individuals). All samples were processed for routine embedding in paraffin wax at MWU's Histology Core. We collected 6–7 transverse sections (5 μm thick) every 100 μm starting mid-pad and working distally, similar to other recent studies (Table 1). Sections were mounted on microscope slides and stained with hematoxylin and eosin (H&E).

2.3 | Microscopy and data collection

We visualized sections at 20× objective lens magnification using a IX73 microscope coupled to a U-TV0.63XB camera adapter (Olympus, Shinjuku, Japan), which provides a stitched image at 12.6× magnification. We used cellSens processing software (Olympus, Shinjuku, Japan) to stitch the image, which is equipped with an embedded scale with a conversion factor of 1 pixel = 0.5081 μm. This embedded scale facilitated measurements in micrometers, ensuring accurate and precise quantification of mechanoreceptor characteristics. We performed all subsequent data collection using Fiji processing software (version 2.15.0; Schindelin et al., 2012). For each section, we collected data on the section length, Meissner corpuscle count and average width, and Pacinian corpuscle count, average width, and depth. We focused on Meissner and Pacinian corpuscles because Merkel cells can only be accurately assessed with an immunohistochemistry approach. Data were collected by two observers. Section length is defined as the length of the section over which we collected data, and was measured using Fiji's segment line tool to create segments extending from each epidermal ridge atop the stratum spinosum (Figure S1). We only collected data over skin with dermatoglyph ridges visible in the stratum corneum layer of the epidermis because we wanted to focus on the part of the apical pad most used in precision touch.

Our inclusion criteria for counting Meissner corpuscles focused on an ovoid/elliptical shape with either clear terminal glial cells or a defined capsule (Figure 1) located within the dermal pegs protruding into the epidermis. We measured the cross-sectional width of each Meissner corpuscle counted at its widest point, with the width measured perpendicular to the long axis of the corpuscle. We then calculated the average width across all Meissner corpuscles within a section, and then across all sections for a given sample. Pacinian corpuscles were identified

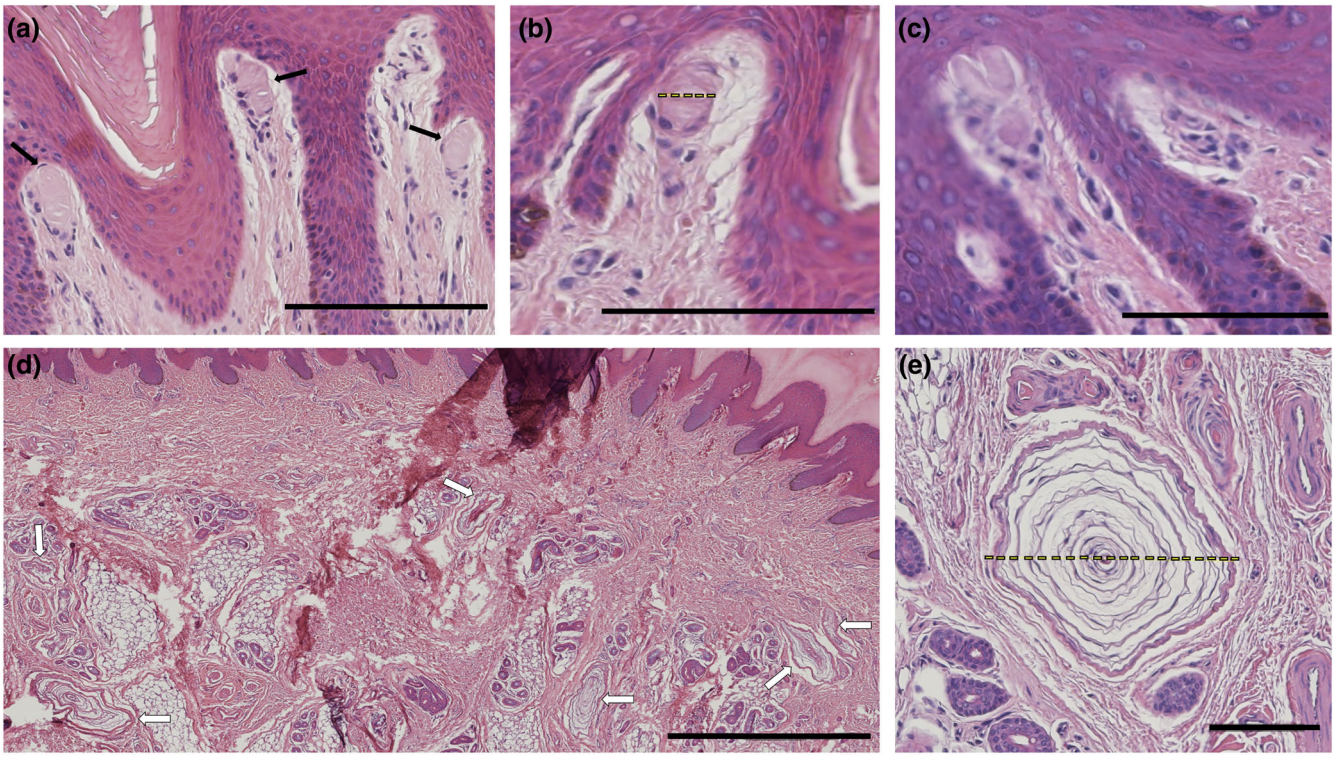

FIGURE 1 Identification and measurement of Meissner and Pacinian corpuscles. Meissner corpuscles (black arrows) were recognized by their stacked terminal glial cells (a) or ovoid capsular shape (b, c) and dermal peg location. (b) Example measurement of cross-sectional width (dashed line) for a Meissner corpuscle. (c) Two Meissner corpuscles were occasionally observed in a single dermal peg. (d, e) Pacinian corpuscles (white arrows) were identified by concentric onion-like layers and were located in either the dermis or hypodermis. (d) While most sections contained a single Pacinian corpuscle, a few sections had more than five like this one. (e) Example width measurement (dashed line) of Pacinian corpuscle. Scale bars represent 100 μm for panels (a–c, and e), and 1000 μm for (d).

by their circular or elongated shape and concentric "onion-like" layers, and location in the dermis or hypodermis (Figure 1). For each Pacinian corpuscle, we measured width as its widest dimension parallel to the skin surface and its depth from its center to the closest dermal–epidermal junction. We calculated the average width across all Pacinian corpuscles in a section, and then across all sections for a given sample. We measured Pacinian corpuscle depth from the closest epidermal peg and calculated an average depth across all Pacinian corpuscles in a given digit. In contrast to other data, depth was collected by one observer.

2.4 | Quantifying corpuscle density

The use of a microtome for cell counting introduces an inherent challenge, as some cells may not be entirely encompassed within the microtome section. Cell fragmentation further complicates matters, leading to instances where cells span neighboring sections, which makes it challenging to differentiate between fragmented and whole cells. To address this limitation, we followed other recent Meissner corpuscle studies (Crowley et al., 2019; García-Piqueras et al., 2019; Verendeev et al., 2015) and applied Abercrombie's (1946) formula, which corrects for cells that do not entirely lie within sampled microtome sections. Abercrombie's formula is expressed as: $N = n\,[T/(T+H)]$, where n represents the average corpuscle count per section across all sampled sections, T is the section thickness (5 μm), H is the average cross-sectional diameter of the corpuscle type, and N is the corrected count of corpuscles per section. For H, we used the average Meissner corpuscle and Pacinian corpuscle widths calculated for a given sample across all of the sections of that sample. Next, we calculated the surface area (mm^2) we sampled across as the average section length for a sample in mm times section thickness (0.005 mm). Finally, to calculate total corpuscle density/mm^2, we divided the corrected cell count N by the sampled surface area (see interactive Cell Density Calculator in Supporting Information). We used this approach to calculate Meissner corpuscle and Pacinian corpuscle densities for each individual and digit.

2.5 | Dermatoglyphs

We collected dermatoglyph data for each individual and digit using the Fiji processing software. First, we established absolute measurements by scaling pixels to the 19.05 mm-wide cellophane tape containing each dermatoglyph print. We next collected 20 unique measures of dermatoglyph ridge width, adapting the method described by Peters et al. (2009), with width measured as perpendicular to the long axis of the ridge (Figure 2). We similarly collected 20 unique measures of ridge spacing, defined as the space between dermatoglyph ridges, following the same approach. For each digit, we then calculated an average ridge width and average ridge spacing. Additionally, we used Fiji to measure the length of the apical pad print as a rough approximation of apical pad length. While this measurement lacks precision due to a variety of factors (including variation in the degree of pressure applied when fingerprinting which can distort the shape of the print), in some sampling situations, precise measures of body size (e.g., body mass, digit length) may not be readily available for scaling. We wanted to investigate whether apical pad dermatoglyphs offer a useful size-proxy for precision touch analyses in these sampling situations. Specifically, we assessed the suitability of apical pad print length as a size-proxy in individuals with known size measurements. Length was measured along the longitudinal midline of the print (Figure 2). The print for one digit (m22.11 D1) only covered a partial pad, so it was excluded from the pad length analysis. Body mass (kg) was available for all individuals. We collected lengths of the first and second digits for six individuals (11 digits) from necropsy photographs of the hands, with length measurements of D1 and D2 averaged between left and right hands.

2.6 | Statistical analyses

We first assessed interobserver reliability in density estimates using intraclass correlation coefficients (ICC) implemented in the *icc* package in R (Wolak et al., 2012) using average-rating, two-way mixed-effects models for absolute agreement and consistency. In this approach, ICC estimates reliability between observers as poor (<0.50), moderate (0.5 < ICC <0.75), good (0.75 < ICC <0.90), or excellent (>0.90; Koo & Li, 2016). We found good to excellent reliability in Meissner corpuscle density ($ICC_{Agreement} = 0.89$, $ICC_{Consistency} = 0.93$) and size ($ICC_{Agreement} = 0.79$, $ICC_{Consistency} = 0.78$) estimates and excellent reliability in Pacinian corpuscle density estimates ($ICC_{Agreement} = 0.92$, $ICC_{Consistency} = 0.93$), but only moderate reliability in Pacinian corpuscle size ($ICC_{Agreement} = 0.57$, $ICC_{Consistency} = 0.71$). Consequently, we averaged Meissner corpuscle and Pacinian corpuscle density estimates and Meissner corpuscle size estimates across both observers to calculate final values for subsequent analyses, but did not include Pacinian corpuscle size in analyses due to the relatively lower reliability than the other values.

We used linear mixed effects models (LMMs) to evaluate effects of digit, age, and sex on corpuscle densities, Meissner corpuscle size, Pacinian corpuscle depth, and dermatoglyph features (apical pad print length, ridge width, ridge spacing). LMMs included individual identity as a random effect, thus allowing us to control the inherent variability between individuals and manage

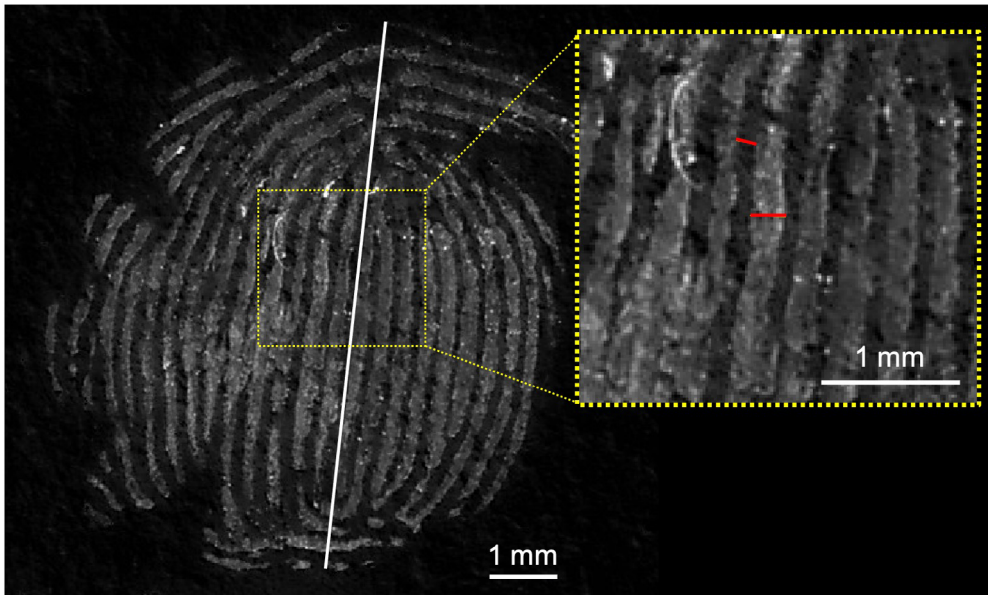

FIGURE 2 Methods of dermatoglyph measurements. Ridge width and between-ridge spacing (red lines) were measured for 20 unique ridges and spaces in each dermatoglyph. Each measurement was marked by a permanent line in Fiji to prevent measuring duplicate ridges/spaces (red line as example). Print length (white line) was measured along the longitudinal midline of the print.

the nonindependence of repeated measures from the same individual. For each metric, we performed an LMM including the response variable and fixed effects of digit (D1/D2), age (in years) and sex (female/male), with individual identity as a random effect. To parse out potential developmental effects on these response variables, we repeated each LMM using only mature adults (>6 years). When performing some models, we encountered "singular fit" warnings in lme4 due to a random effect exhibiting zero variance. Following recent recommendations (Oberpriller et al., 2022), we dropped the random effect and changed to a fixed effect multiple linear regression for that variable. All LMMs were implemented in *R* (version 4.3.3) using the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) packages. Additionally, we performed Pearson's correlations to evaluate relationships between mechanoreceptor metrics.

We also investigated relationships between dermatoglyph features (ridge width, ridge spacing) and Meissner corpuscle density and size to evaluate the effectiveness of dermatoglyphs as proxies of Meissner corpuscles for comparative studies. For these analyses, we used linear regression rather than more complex LMMs in order to specifically test direct functional relationships between dermatoglyphs and Meissner corpuscles. For each metric, we performed stepwise linear regression using the "stepAIC" function (direction = "both") in the *MASS* package in *R* (Venables & Ripley, 2002) to identify the most important predictors of that metric. In this approach, we began with a model including all predictors, then as predictors were iteratively removed and added model fit was assessed using the Akaike Information Criterion (AIC). Our starting model included dermatoglyph ridge width, ridge spacing, and an interaction between width and spacing to approximate the patterning of Meissner corpuscles. For Meissner corpuscle density, we then used the best linear model to calculate a predicted corpuscle density metric ("rMC density") based on ridge width and ridge spacing of each digit. We compared these dimensionless rMC density values to the observed Meissner corpuscle density for each individual with a Pearson's correlation. Finally, we calculated rMC density using the independent dermatoglyph dataset from an additional 58 macaques and performed LMMs to explore effects of age, sex, and digit on rMC density.

3 | RESULTS

3.1 | Variation in Meissner corpuscles

The density of Meissner corpuscles varied dramatically across sampled individuals and digits (11.9–43.3 corpuscles/mm^2; Figure 3a). The average density calculated across digits was 22.9 ± 7.8 corpuscles/mm^2. Average cross-sectional diameter, however, was fairly constrained, with a mean of 22.2 ± 1.9 μm (range = 18.2–25.0 μm) across all digits. LMM results found no significant effects of sex or digit on Meissner corpuscle density, but there was a significant effect of age (Table 2). Specifically, corpuscle density decreased with increasing age in our sample (Figure 3a, Figure S2). The fixed predictors in the model alone accounted for 65% of the variance in density across samples, and the whole model explained 81% of the variance, suggesting that 16% was driven by individual differences. When we reran this model only including adult individuals (n = 20 digits), the age effect disappeared and there were no significant effects (Table S2), suggesting that Meissner corpuscle density stabilizes once individuals reach maturity (at least in young adulthood). Instead, individual differences were responsible for 49% of the variability in corpuscle density among adult macaques.

Interestingly, both age and digit were significant predictors in Meissner corpuscle size (Table 2, Figure S2). According to the LMM, cross-sectional diameter increased with increasing age and was significantly smaller in the D2 relative to D1. Still, the fixed effects only accounted for 28% of the variance in corpuscle size, and individual identity accounted for only another 25% of the variance, leaving 47% unaccounted for by the model. With the adults-only data, we found that the age effect on corpuscle size disappeared, although the difference between digits remained (Table S2).

3.2 | Variation in Pacinian corpuscles

Consistent with previous reports (García-Piqueras et al., 2019), we found that Pacinian corpuscles occur sporadically across the fingertips. Their depth in the skin was also highly variable, spanning dermis and hypodermis and ranging from 267.4 to 2540.4 μm from the nearest epidermal peg. Not surprisingly, density varied across all digits sampled (Figure 3b) with a mean of 1.0 ± 1.0 corpuscles/mm^2 across all digits, but with a range of 0–4.5 corpuscles/mm^2. In contrast to the results for Meissner corpuscles, individual identity did not contribute to the variance in the density of Pacinian corpuscles, again consistent with the irregular distribution of these sensory corpuscles. However, there was a significant negative effect of age, which was retained when we reran the model as a fixed effects-only model (Table 3, Figure S3). The models suggest that corpuscle density declines as macaques grow to adulthood, although the low R^2 of the model (0.14) suggests that age contributes only a minor contribution to the variance in corpuscle density overall. Consistent with this observation, we found no significant

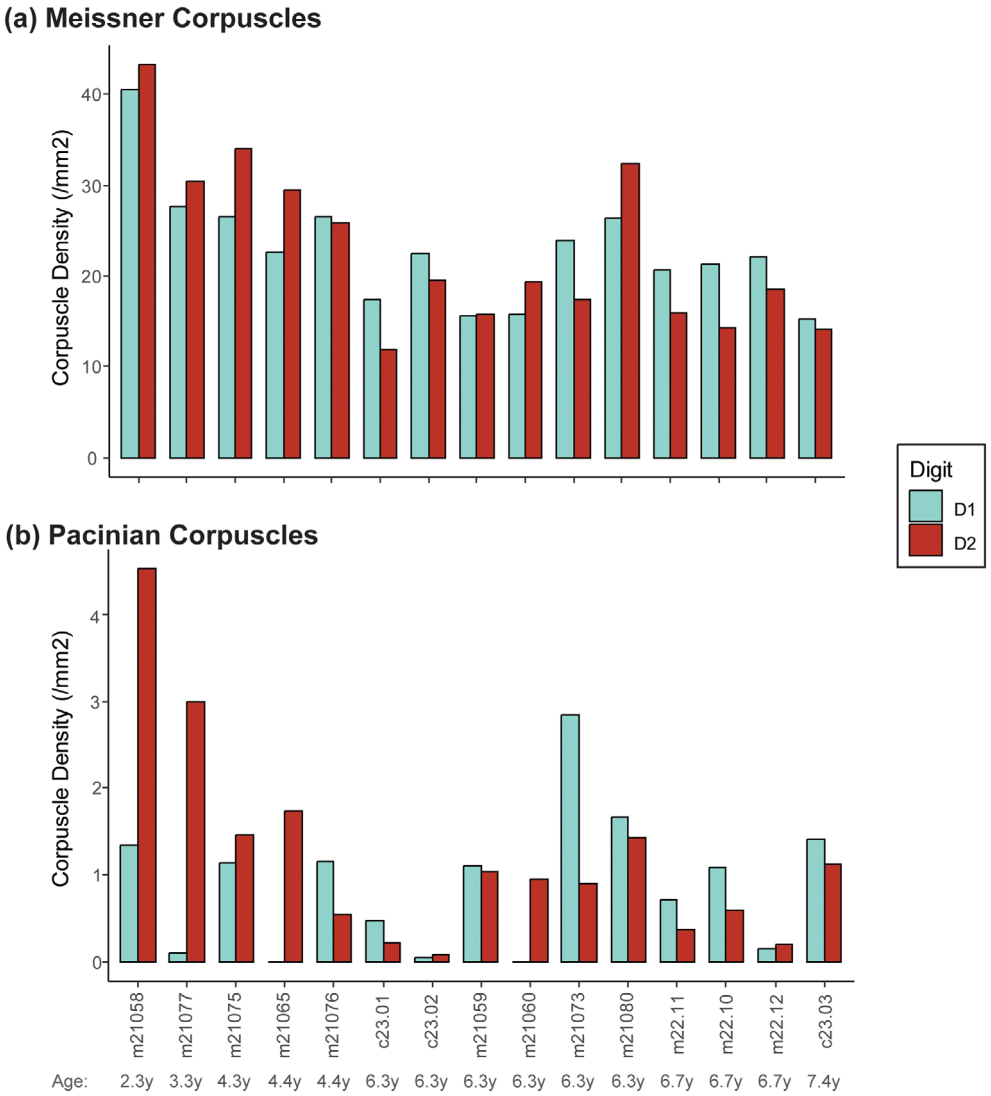

FIGURE 3 Meissner and Pacinian corpuscle density estimates for each individual and digit. Individuals are ordered by ascending age.

TABLE 2 Model parameters for Meissner corpuscle density and size across all macaques.

	Meissner corpuscle density			Meissner corpuscle size		
Predictors[a]	**Estimates**	**CI**	***p***	**Estimates**	**CI**	***p***
(Intercept)	49.44	37.51–61.37	**<0.001**	18.79	14.65–22.93	**<0.001**
Age	−4.55	−6.16 to −2.93	**<0.001**	0.60	0.04–1.16	**0.048**
Digit [D2]	−0.16	−2.77 to 2.44	0.899	−1.37	−2.39 to −0.34	**0.016**
Sex [male]	−1.23	−7.01 to 4.56	0.669	0.97	−1.03 to 2.97	0.336
Random Effects				Random effects		
σ^2	11.93	$\tau_{00\ Individual}$	10.02	σ^2	1.86	$\tau_{00\ Individual}$ 0.99
ICC[b]	0.46			ICC[b]	0.35	
Marginal R^2	0.65			Marginal R^2	0.28	
Conditional R^2	0.81			Conditional R^2	0.53	

Note: Data from 15 individuals (30 digits). Marginal R^2 is the proportion of variability explained by the fixed effects and conditional R^2 is the total proportion of variability explained by the model (including random effects). CI = confidence interval of estimate. Bolded values should be $p < 0.05$.

[a]For categorical predictors, reference categories are D1 (Digit) and female (Sex).

[b]Proportion of variance explained by individual identity after taking into account fixed effects.

TABLE 3 Model parameters for Pacinian corpuscle density and depth across all macaques.

	Pacinian corpuscle density[a]			Pacinian corpuscle depth			
Predictors	**Estimates**	**CI**	***p***	**Estimates**	**CI**	***p***	
(Intercept)	2.18	0.20–4.15	**0.032**	−12.5	−834.66–809.65	0.975	
Age	−0.27	−0.54 to −0.01	**0.045**	155.27	43.51–267.03	**0.015**	
Digit [D2]	0.33	−0.37 to 1.03	0.341	−185.91	−406.16 to 34.34	0.103	
Sex [male]	0.28	−0.67 to 1.23	0.545	167.68	−231.14 to 566.50	0.400	
				Random Effects			
				σ2	71792.33	$\tau_{00\ Individual}$	36661.46
				ICC	0.34		
Adjusted R^2	0.14			Marginal R^2	0.33		
				Conditional R^2	0.56		

Note: Data from 15 individuals (30 digits for density, 27 digits for depth). See Table 2 for definitions, abbreviations, and reference categories for categorical variables.

[a]Model for corpuscle density is a fixed-effects only model.

effects on corpuscle density when we restricted analyses to mature adults (Table S3). There was, however, substantial variance in density among adult digits explained by individual identity (45%).

We also detected a significant effect of age (but not digit or sex) on Pacinian corpuscle depth (Table 3, Figure S3), with corpuscle depth increasing with increasing age in the LMM. However, the model only explained 56% of variability in corpuscle depth, with the random effect of individual identity accounting for 23%, and the fixed effects accounting for only 33%. As with the other analyses, the significant age effect disappeared when we only included adult digits.

3.3 | Variation in apical pad size and dermatoglyphs

We next used the dermatoglyph data to explore whether the size of macaque digital apical pads (as approximated by pad print length) and dermatoglyph features were affected by age, sex, and digit. As would be expected, pad print length was significantly positively correlated with body mass (Pearson's correlation: $r = 0.80$, $p < 0.0001$, $n = 30$), suggesting that larger-bodied individuals have longer apical pad prints (Figure S4). Similarly, despite a limited sample size, pad print length was significantly correlated with digit length ($r = 0.69$, $p = 0.0272$, $n = 10$), indicating that longer digits are also associated with longer pad prints (Figure S4). The LMM for pad print length identified significant effects of age, sex, and digit (Table 4), with these fixed effects explaining 53% alone of the variance in length. When individual identity was included, the model explained 89% of the variance. As would be expected with developmental growth, pad print length increased with age (Figure 4). Additionally, the data suggest sexual dimorphism in pad length, with males having larger apical pads than females. Further, the pad print for D2 was significantly longer than that of D1. These results suggest that despite its lack of precision, the length of the apical pad print offers a potentially useful measure of body size when more precise options are not available. When we restricted the data to only mature adults (Table S4), the age effect on pad print length disappeared ($p = 0.723$) but the digit and sex effects remained ($p < 0.001$ and $p = 0.033$, respectively). These results suggest that apical pads continue to grow until the macaques reach maturity.

We similarly observed significant effects of age, sex, and digit on the width of dermatoglyph ridges across all sampled individuals. Overall, ridge width increased with age, and was higher in males and in D1 (Table 4). When the analysis was restricted to mature adults (Table S4), only the sex effect remained significant ($p = 0.025$). For ridge spacing, however, there were no significant effects of sex ($p = 0.280$) or digit ($p = 0.217$) and only a near-significant trend for wider spacing with increasing age across all sampled individuals ($p = 0.051$; Table S5). There were no significant effects on ridge spacing when only adults were considered.

3.4 | Dermatoglyphs as proxies of Meissner corpuscle density and size?

We used stepwise linear regressions to identify the best anatomical predictors of Meissner corpuscle density and size. For density, the best fit model according to AIC

TABLE 4 Model parameters for apical pad length and ridge widths.

	Apical pad length			Dermatoglyph ridge width			
Predictors	**Estimates**	**CI**	**p**	**Estimates**	**CI**	**p**	
(Intercept)	3.29	−0.09 to 6.66	0.066	0.11	0.02–0.20	**0.032**	
Age	0.78	0.33–1.24	**0.004**	0.02	0.00–0.03	**0.017**	
Digit [D2]	0.97	0.53–1.42	**<0.001**	−0.03	−0.05 to −0.01	**0.003**	
Sex [male]	2.53	0.87–4.19	**0.008**	0.07	0.03–0.12	**0.006**	
Random effects				Random effects			
σ^2	0.33	$\tau_{00\ Individual}$	1.10	σ2	0.00052	$\tau_{00\ Individual}$	0.0007
ICC	0.77			ICC	0.58		
Marginal R^2	0.53			Marginal R^2	0.48		
Conditional R^2	0.89			Conditional R^2	0.78		

Note: Data for all individuals includes 15 individuals (29 digits for length, 30 digits for ridge width). See Table 2 for definitions, abbreviations, and reference categories for categorical variables.

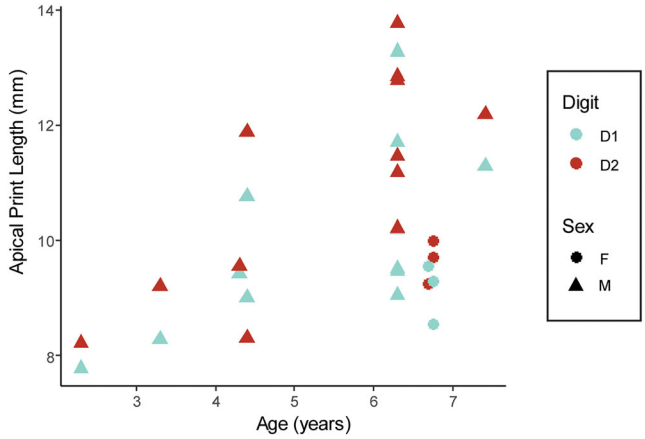

FIGURE 4 The relationship between apical pad length and age. Apical pad length was approximated by the length of the dermatoglyph from the distal apical pad of each individual for D1 (light blue) and D2 (red). Note that females (circles) are only represented in the mature adults (e.g., >6 years old). Apical pad size increases with age up to maturity, then does not appear to increase after 6 years old.

included all possible predictors (Table 5). The model suggests an important interaction between dermatoglyph ridge width and spacing that while not quite reaching significance ($p = 0.074$), was important for model fit. Plotting this modeled interaction (Figure 5a,b) suggests some interesting functional relationships. When ridges were narrow and closely spaced, Meissner corpuscle density was high. Meanwhile, at wider spacing between ridges, density was lower in narrower ridges compared to wider ones (that theoretically contain more corpuscles; Figure 5a). Interestingly, if we included individual sex into the stepwise regression model, sex was retained as a significant predictor ($p = 0.006$) with the anatomical predictors, and the adjusted R^2 increased to 0.44 (Table S6). This result suggests that sexual dimorphism in apical pad size may be influencing the relationship between dermatoglyphs and corpuscle densities. The best fit model for Meissner corpuscle size only included dermatoglyph ridge width (Table 5). Including sex in this stepwise regression did not change the result, indicating that sexual dimorphism does not impact the size of Meissner corpuscles.

3.5 | Predicting relative Meissner corpuscle density from Dermatoglyphs

We used the best fit regression to develop a predictive model for a relative measure of corpuscle density: *rMC* Density $= 1/((\text{width} * \text{spacing} + \text{width} + \text{spacing}) * \text{size})$. We included a size scaling factor in the predictive model to help account for potential differences with body or apical pad size. We then evaluated the performance of models using different scaling factors with Pearson's correlations between observed Meissner corpuscle density and predicted densities. Overall, we found that rMC density for all conditions exhibited strong significant positive correlations with observed density (Table 6). However, results from models including a size scaling factor were stronger than when no size scaling factor was included. Given the significant sex effect in the relationship between dermatoglyphs and corpuscle density, we repeated the correlation with only males (the number of female observations, six digits, was too low for statistical analysis). With the male-only data, we similarly found stronger positive correlations when either pad print length ($r = 0.84$) or body mass ($r = 0.83$) were included as

TABLE 5 Parameters of best fit model of dermatoglyph predictors of Meissner corpuscles.

Meissner corpuscle density				Meissner corpuscle size			
Predictors	**Estimates**	**CI**	***p***	**Predictors**	**Estimates**	**CI**	***p***
(Intercept)	91.2	37.88–144.53	**0.002**	(Intercept)	17.16	13.76–20.55	<0.001
Spacing	−450.77	−865.32 to −36.21	**0.034**	Width	20.71	7.07–34.36	0.004
Width	−228.72	−438.79 to −18.64	**0.034**				
Spacing × Width	1419.32	−150.59 to 2989.22	0.074				
Adjusted R^2	0.27			Adjusted R^2	0.23		

Note: Data for all individuals (15 individuals and 30 digits).

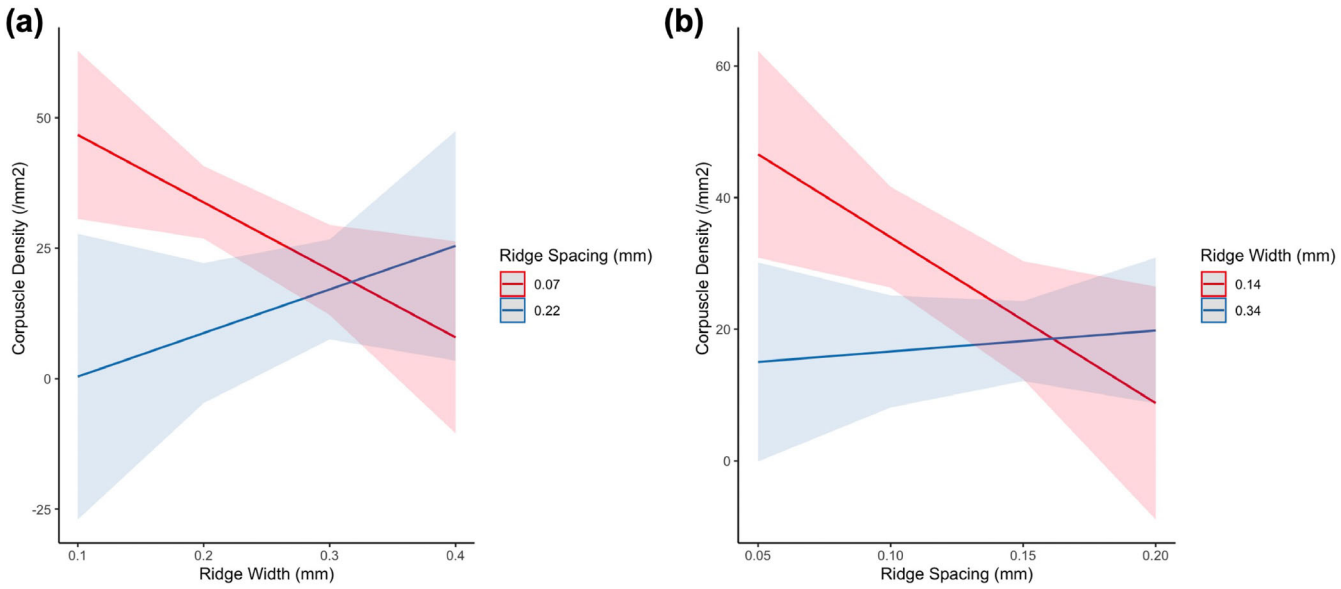

FIGURE 5 Effects of ridge width and spacing interaction on modeled Meissner corpuscle density. Line graphs depicting how the interaction between ridge width and spacing in the best fit multiple regression model is predicted to influence corpuscle density (Y-axis). (a) Lines reflect modeled corpuscle density for the narrowest ridge spacing in the data (red) compared to the widest spacing (blue) across the observed distribution of ridge widths. (b) Lines reflect modeled corpuscle density for the narrowest ridge width (red) compared to the widest ridge width (blue) across the observed distribution of ridge spacing. Shaded bars reflect 95% confidence intervals of the estimated marginal effects of the interaction. Plot generated in sjPlot R package (Lüdecke, 2018).

scaling factors compared to no scaling factor ($r = 0.72$). Comparing the plots of age and rMC density versus observed corpuscle density, the rMC density of the females (circles) is much higher than the 6.3 year old males (Figure 6a), whereas the observed corpuscle density in females overlaps that of those males (Figure 6b). We suggest that the predictive model appears to overestimate corpuscle density in females due to their smaller fingers and narrower ridges relative to males, given the significant sex effects for both ridge width and apical pad print length (e.g., Table 4, Table S4).

Finally, we explored the suitability of rMC density as a proxy of Meissner corpuscle density in a large additional dataset of dermatoglyphs from an independent sample of macaques ($n = 58$ individuals, 86 digits), using body mass as the size scaling factor (Figure 7). This sample included juveniles to young adults (2.1–8.1 years). An LMM including age, sex, and digit for these individuals found that rMC density declined with age ($p < 0.0001$), and was significantly higher in females ($p = 0.0002$), as expected by how the model overestimates female corpuscle density. It also found higher rMC densities in D2 ($p = 0.0005$). When we restricted the data to mature adults ($n = 13$ individuals, 20 digits), only sex remained significant in the LMM ($p = 0.0003$) while age and digit were not significant ($p = 0.338$ and $p = 0.286$, respectively). The loss of the age effect when using a mature adult dataset mirrors the LMM results for observed Meissner corpuscle density in our original sample.

TABLE 6 Performance of different size scaling factors in predictive model of Meissner corpuscle density.

	All individuals		Males only	
Scaling factor	n_{digits}	**Correlation statistics**	n_{digits}	**Correlation statistics**
none	30	$r = 0.57$, $p = 0.0009$	24	$r = 0.72$, $p < 0.0001$
Pad Print Length (mm)	29	$r = 0.70$, $p < 0.0001$	24	$r = 0.84$, $p < 0.0001$
Body Mass (kg)	30	$r = 0.76$, $p < 0.0001$	24	$r = 0.83$, $p < 0.0001$

Note: Pearson's correlations between rMC density estimates calculated using different size scaling factors and observed Meissner corpuscle density. Number of digits varies between scaling factors, as pad print length was not available for 1 digit.

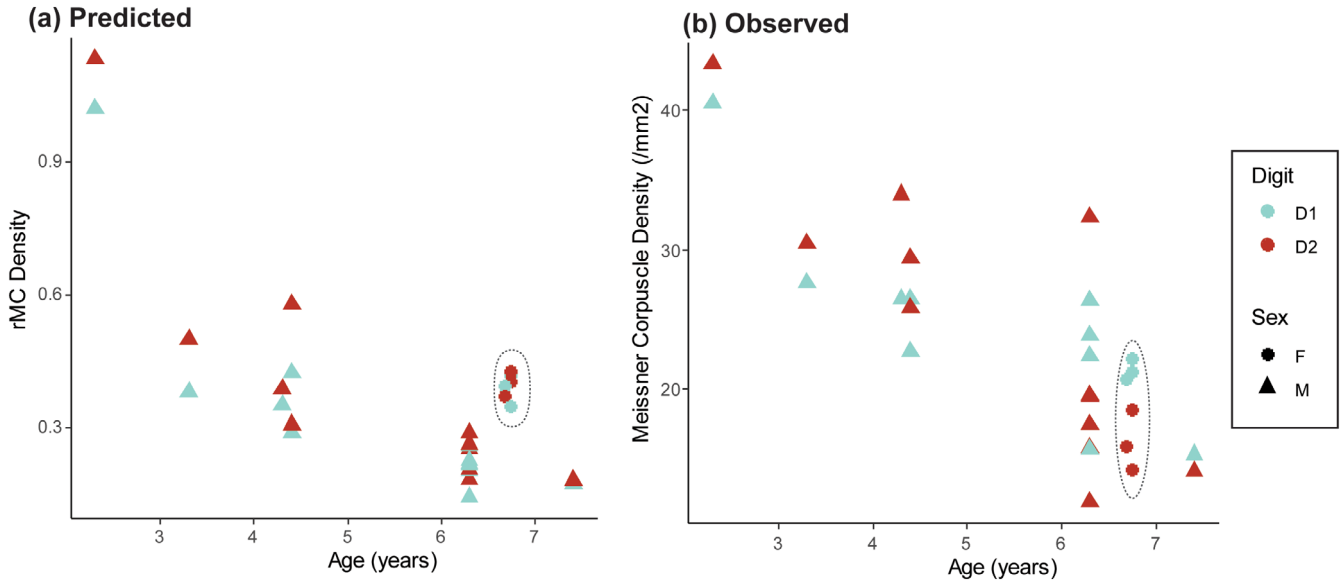

FIGURE 6 Predicted relative Meissner corpuscle density (rMC density) and observed Meissner corpuscle density. The rMC density values are based on body mass as the size scaling factor. Note how rMC density overestimates values for females (in dashed oval) relative to males compared to observed corpuscle density.

4 | DISCUSSION

4.1 | Development of primate touch

In this study, we explored variation in the anatomy of precision touch (Meissner and Pacinian corpuscles) in a sample of male and female rhesus macaques spanning juvenility to young adulthood. We found age to be the strongest factor driving variation in all mechanoreceptor metrics we examined. However, this effect was only significant when we sampled across the adolescence period; no significant age effects were found for any metric when only mature adults were included, suggesting many aspects of sensory corpuscles in the skin stabilize at adulthood. These results suggest that developmental changes associated with growth impact precision touch anatomy. Specifically, as fingers increase in size during adolescence (as measured by the increasing finger pad length), Meissner corpuscles

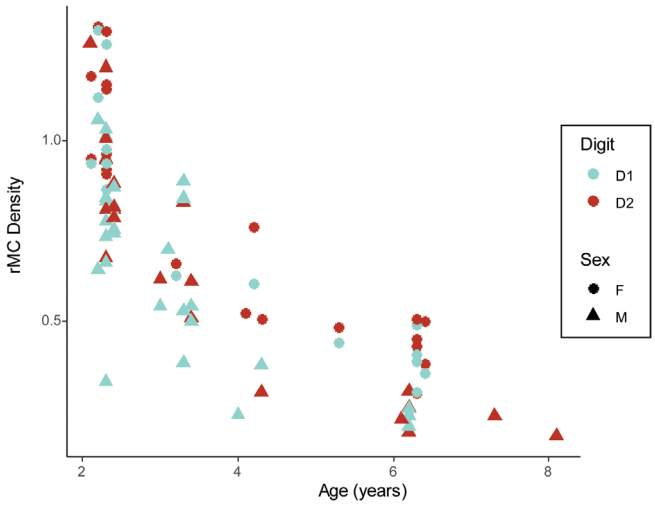

FIGURE 7 Age and rMC density for an independent macaque dermatoglyph dataset. The rMC density values were calculated for 58 additional individuals (86 digits) and are based on body mass as the size scaling factor.

appear to get larger, Pacinian corpuscles migrate deeper into the skin, and both sensory corpuscles decrease in density. We also observed concomitant growth-related changes in dermatoglyph ridge width and spacing.

Previous studies have reported similar developmental effects for at least some mechanoreceptors in humans. Bolton et al. (1966), for example, noted much higher Meissner corpuscle densities among children in both their own work and other studies from the 1930s and 1940s. They propose that the total number of Meissner corpuscles is likely unchanged throughout growth. Instead, they suggest density changes are the result of changes in digit size. Moreover, these density changes may be associated with psychophysical changes in touch sensitivity—vibration detection thresholds have been found to increase between the ages of 10 and 20 for the low frequencies (<40 Hz) that stimulate Meissner corpuscles (Verrillo, 1980), indicating reduced sensitivity to those vibrations. While vibration detection thresholds for the high frequencies stimulating Pacinian corpuscles (160–250 Hz) also increased during adolescence, the increase was not as dramatic as that observed at low frequencies (Verrillo, 1980). Pacinian corpuscles are described as declining gradually in number during postnatal life in humans (Cauna, 1965), consistent with the relatively minor age effect on Pacinian corpuscle density that we observed in macaques.

More recently, Peters and Goldreich (2013) reached similar conclusions in their study of tactile acuity and anatomy in children. They found that fingertip surface area exhibited a significant positive relationship with age during development, while sweat pore density, a proposed proxy of Merkel cells, declined with age. They also found that spacing between sweat pores on adjacent ridges increased with age, suggesting growth-related changes in ridge width and/or spacing in human fingers comparable to those we observed in macaques. Interestingly, in contrast to the results for vibration detection (Verrillo, 1980), Peters and Goldreich observed no significant functional differences in estimated tactile acuity. The authors propose that any decrease in tactile acuity associated with decreasing Merkel cell density may be offset by the maturation of the central nervous system occurring at the same time. Additionally, while studies in humans have found that mechanoreceptors (particularly Meissner corpuscles and Merkel cells) decline in density and deteriorate in older adults (Bolton et al., 1966; García-Piqueras et al., 2019), the adults in our study were all in young adulthood. Future work should explore whether macaques exhibit similar declines in aged individuals.

4.2 | Other sources of variation in primate mechanoreceptors: Sex and digit

Factors in addition to age have been linked to variation in mechanoreceptor density in humans and other primates. Sexual dimorphism in finger size, for example, is thought to be responsible for sex differences in behavioral estimates of tactile acuity in humans (Peters et al., 2009; Wong et al., 2011). Smaller fingers (which typically characterize women) have higher densities of sweat pores and presumably, Merkel cells (Peters et al., 2009). Bolton et al. (1966) similarly report higher densities of Meissner corpuscles in human female fingers. In our study, we did not detect any significant sex differences in corpuscle densities, Meissner corpuscle size, or Pacinian corpuscle depth. However, our sample of macaques was highly biased toward males (80%) due to limited sampling opportunities. It is very possible that sex does impact mechanoreceptor anatomy and density in macaques and we lacked the sample size to detect it. Interestingly, we did find that despite a limited sample size, females had significantly smaller apical pads and narrower dermatoglyph ridges, consistent with results in humans (Peters et al., 2009). Future work should include less sex-biased sampling when possible to investigate sex effects on primate mechanoreceptor density.

Some authors have also suggested differences in mechanoreceptor densities between digits due to different roles in grasping and manual manipulation. Although several studies in humans and nonhuman primates have not found significant differences in Meissner corpuscle density between digits (Ciano & Beatty, 2022; Paré et al., 2002; Verendeev et al., 2015), a study of 13 long-tailed macaques (*M. fascicularis*) found that Meissner corpuscle density was significantly higher in D1 relative to other digits and D2 relative to digits 3–5 (Crowley et al., 2019). The authors propose that higher densities in D1 and D2 are associated with manual tasks involved in D1/D2 grips, including grooming and foraging. Meissner corpuscles are involved in detecting object slippage, textures, and reflex grip control (Zimmerman et al., 2014), which are important for precision grips. In humans, tactile acuity declines from D2 to D4, which may be similarly related to a need for higher acuity in D1/D2 precision grips (Tymms et al., 2018; Vega-Bermudez & Johnson, 2001). Pacinian corpuscles, meanwhile, exhibit a different pattern of variation with digit, possibly reflecting their different functional roles in grasping tasks compared to Meissner corpuscles. Because of their tuning for high frequency vibrations, Pacinian corpuscles may be particularly useful in detecting vibrations within held objects (Zimmerman et al., 2014). Work in both humans (Stark et al., 1998) and Japanese

macaques (*Macaca fuscata*; Kumamoto et al., 1993) suggests that Pacinian corpuscles are more common in the middle three digits (D2–D4) relative to D1, although Paré et al. (2002) found the highest Pacinian corpuscle density in D1in long-tailed macaques (*M. fascicularis*). Thus, for both Meissner and Pacinian corpuscles, there is substantial conflict in the literature over whether digits vary in corpuscle densities, what the pattern of that variation is, and whether it can vary between species. Future work should compare mechanoreceptors across all five digits and the palm to better understand the extent of regional variation in the densities of different receptors in the hand and how this variation may contribute to different manual grasping tasks.

4.3 | Functional implications and physiological constraints

Our results confirm those of previous studies suggesting functional relationships between dermatoglyph ridges and mechanoreceptors (Dillon et al., 2001; Jarocka et al., 2021; Peters et al., 2009; Tymms et al., 2018). Specifically, Meissner corpuscle density was highest in digits with narrow closely-spaced ridges. However, there also was an interaction between ridge width and spacing; for more widely-spaced ridges, density was higher in wider ridges relative to narrow ones, suggesting that overall ridge surface area may be functionally important for corpuscle density. Moreover, we found that including both ridge width and spacing (and their interaction) performed surprisingly well in a predictive model for Meissner corpuscle density (rMC density) in our sample. Including some type of size scaling factor generally improved the predictive model's performance (e.g., pad print length, body mass). We believe that more precise applicable size scaling factors like digit length may perform even better, and encourage researchers to collect these metrics along with dermatoglyphs. Additionally, we found a positive relationship between dermatoglyph ridge width and Meissner corpuscle cross sectional diameter. This makes functional sense, as corpuscles are located within ridges, so larger ridges would permit larger corpuscles. We consider it notable that we were still able to identify these significant relationships between dermatolgyphs collected from fresh tissue and Meissner corpuscles in histological tissues, despite the shrinkage of tissue that occurs during formalin fixation and histological processing.

Thus, dermatoglyphs may be useful noninvasive proxies for comparative studies of Meissner corpuscle density and precision touch, with a few important caveats. First, we found that the predictive model overestimated corpuscle density in females, likely due to sexual dimorphism in apical pad size. Future analyses should be careful to either analyze sexes separately or include sex as a factor in linear models. Second, dermatoglyphs may reflect peak Meissner corpuscle density and might not be accurate measures after individuals reach mature body size. In humans, Meissner corpuscles deteriorate and density declines with increasing age (García-Piqueras et al., 2019). While the patterns of dermatoglyph ridges and spaces do not appear to change with age, ridges do tend to flatten, reducing the visibility of their edges (Maceo, 2011). Consequently, the number of visible ridges in a dermatoglyph decreases with age (Silva et al., 2016), but it is not clear if the rate of decrease in the number of ridges mirrors that of Meissner corpuscle density or if it is reflected in average dermatoglyph ridge width and spacing.

A third caveat of using dermatoglyphs as a proxy of Meissner corpuscle density is that we do not currently know whether these functional relationships extend to other species, particularly smaller species. However, there is evidence of constraints on Meissner corpuscle size across taxa. The average cross-sectional diameter observed in our study (22.2 μm, range 18.2–25.0 μm) overlapped that of other primates and nonprimate mammals across a range of body sizes (Table 7). These data suggest Meissner corpuscles maintain a similar size across a 1900-fold difference in body mass! We hypothesize that this indicates physiological constraints on Meissner corpuscle function preventing smaller corpuscle sizes. These physiological constraints may limit the presence and size of dermatoglyph ridges, and even limit Meissner corpuscle density, in other taxa. For example, because of these physiological constraints and the relationship between ridge width and corpuscle size, species with very small fingers can only decrease ridge width so much before ridges are too narrow for Meissner corpuscles. We thus predict that there is a threshold digit size for which dermatoglyph ridges are beneficial for precision touch, and that species below this size will lack dermatoglyphs. Moreover, the constrained Meissner corpuscle size also suggests that, for species with digits above this size threshold, we would expect dermatoglyphs to exhibit a relationship with Meissner corpuscle density consistent to that observed in this study. Future work should investigate dermatoglyphs as proxies for mechanoreceptors in primates over a range of body sizes to explore these predictions.

4.4 | Comparisons with other studies and methodologies

Previous studies of primate Meissner and Pacinian corpuscle densities have employed a variety of approaches

TABLE 7 Interspecific comparisons of tactile corpuscle cross-sectional diameter.

Species[a]	Body Mass (kg)[b]	Meissner corpuscle diameter	Source
Rhesus macaque	8.3	18.2–25.0 μm	This study
Long-tailed macaque	4.5	20–30 μm	(Paré et al., 2002)
Human	60.2	20-40 μm	(Vega et al., 2012)
Mouse	0.03	10-30 μm	(Wai et al., 2021)
Domestic cat	3.9	19.95 μm[c]	(Bolanowski & Pawson, 2003)
Wistar rat	0.18	16.1 μm[c]	(Kobayashi et al., 2001)

[a]Species names: *Macaca mulatta, Macaca fascicularis, Homo sapiens, Mus musculus, Felis catus, Rattus norvegicus*.
[b]Average body mass from either Meissner corpuscle study, Smith and Jungers (1997) for long-tailed macaque and human, and Cuff et al. (2015) for cat.
[c]Diameter estimated from published figures in source using Fiji.

(Table 1), differing in whether sections were collected perpendicular versus parallel to the skin surface, the size and number of sections examined, the types of stains and antibodies used, and the methods of identifying and calculating corpuscle density. They also have differed in the sex and age of individuals included and digit sampled, which is potentially concerning considering the growth signal detected in this study and the potential effects of age, sex (humans: Bolton et al., 1966), and digit (long-tailed macaques: Crowley et al., 2019) reported in previous work. Given the diversity of approaches, it is encouraging that our Meissner corpuscle results (11.9–43.3 corpuscles/mm^2) overlapped the values found in a previous rhesus macaque study that sectioned parallel to the skin surface and used immunohistochemistry (21–37.4 Meissner corpuscles/mm^2; Güçlü et al., 2003) in contrast to our approach. This similarity suggests that histological approach does not necessarily impact Meissner corpuscle density estimates in primate glabrous skin. While Pacinian corpuscle density has not been previously reported for rhesus macaques, our results (1.0 ± 1.0/mm^2) are also comparable to the density reported for long-tailed macaques (1.15–1.99 corpuscles/mm^2; Paré et al., 2002).

However, our Meissner corpuscle density estimates were lower than those observed in two other rhesus macaque studies. Bolanowski and Pawson (2003) reported an average of 48.7 corpuscles/mm^2 in five adult macaques (sex and exact ages not provided, but between 6 and 14 years), while Verendeeev and colleagues (2015) found estimates of 46.5–67.3 corpuscles/mm^2 across the digits of a 13-year-old female, a 20-year-old male, and an individual of unknown sex and age. The lack of details on individual variation and demographics makes it challenging to compare our results with Bolanowski and Pawson's. The values found by Verendeev and colleagues, meanwhile, are relatively high given the advanced ages of two of the three macaques sampled. We would predict that Meissner corpuscle density declines in aged macaques (>15 years) as has been observed in middle-aged and elderly humans (Table 1; Bolton et al., 1966; García-Piqueras et al., 2019). Instead, Verendeev et al.'s values were 7%–55% higher than our highest estimate (from a 2.3 year old juvenile), and 291%–465% higher than our lowest estimate (6.3 year old adult male). This high estimate for older macaques mirrors Verendeev's high estimates for elderly humans (Table 1) and for *Papio* (28.5–38.7 corpuscles/mm^2) relative to a previous estimate (7.2 corpuscles/mm^2: Hoffmann et al., 2004).

We suspect that differences in the criteria used for identifying Meissner corpuscles may drive some of the variation in estimates across studies. Studies are often vague or do not describe the inclusion criteria employed (but see Crowley et al., 2019 for an example of providing criteria). Hoffmann et al. (2004), for example, counted "whole and partial" Meissner corpuscles without defining what features qualified as a "partial" Meissner corpuscle. Differences in the strictness of inclusion criteria can lead to substantial variation in Meissner corpuscle density estimates for the same digit. This difference would likely be magnified if the study employed Abercrombie's (1946) formula, which was designed to account for the fact that some corpuscles may not be identifiably present within a single microtome section. Abercrombie thus required that the cell capsule be visible for a cell to be counted, and including structures that do not contain a visible cell capsule could lead to overestimates of corpuscle density. This may explain the high density values estimated by Verendeev et al. (2015)—at least one of the structures included in their figures (Figure 2f) would not have been counted as a Meissner corpuscle according to the criteria used by our study as it lacks a visible ovoid capsule and/or stacked terminal glial cells.

5 | CONCLUSIONS

Evaluating the histomorphology of precision touch can be challenging, and researchers must cope with confounding variables such as tissue preservation and collection methodologies (e.g., fresh vs. frozen) that can significantly alter tissue quality and therefore, influence sectioning ability and subsequent interpretation. These issues are particularly pressing when working with wild and endangered species like primates where access and preservation methods are often even more restricted. Previous comparative studies of mechanoreceptors in primate glabrous skin have laid a solid foundation for exploring ecological determinants of precision touch (e.g., Hoffmann et al., 2004; Verendeev et al., 2015). Nevertheless, our results raise concerns regarding indiscriminately pooling published mechanoreceptor data in comparative analyses, which can overlook potential confounding effects of demographic variation, sampling, and methodology. We found substantial variation in mechanoreceptor density between individuals, as well as evidence of a growth effect for individuals sampled prior to physical maturity. Our results also suggest that study differences in mechanoreceptor inclusion criteria can dramatically affect density estimates. One possible approach for future comparative work investigating precision could be to include sample metadata (e.g., sex, age, and digit) and study identity as factors in statistical models. Such an approach, for example, could potentially account for study-level differences in the criteria used in Meissner corpuscle identification. Additionally, we propose that, moving forward, research on the anatomy of primate precision touch follows a standardized data collection framework, including explicit inclusion criteria for sensory corpuscle identification as employed here (and as used by Crowley et al., 2019 for *M. fascicularis*). To facilitate this, we have provided a Cell Density Calculator (see Supporting Information) that can assist other researchers in applying Abercrombie's (1946) formula in density estimates.

Perhaps more importantly, we have also developed a potentially new comparative tool for studying primate precision touch using easily collected and noninvasive dermatoglyphs. Although this tool has currently only been tested in rhesus macaques, it may be useful for assessing tactile acuity in both wild and captive primate populations, and allow researchers to collect data from ecologically and taxonomically diverse species. We plan to evaluate the validity of this dermatoglyph approach in additional primate and nonprimate mammals in the future. Moreover, we focused on Meissner and Pacinian corpuscles in this study because they are easily visualized using standard H&E histology. Future work will expand our approach to Merkel cells, which are critical for tactile acuity (Zimmerman et al., 2014), but need an immunohistochemical approach for accurate identification and quantification.

AUTHOR CONTRIBUTIONS

Brandon Vera Covarrubias: Data curation; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Jordan M. Kamminga:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; visualization; writing – original draft; writing – review and editing. **M. N. Muchlinski:** Conceptualization; data curation; funding acquisition; investigation; methodology; supervision; validation; writing – original draft; writing – review and editing. **R. A. Munds:** Data curation; investigation; writing – review and editing. **V. Villero Núñez:** Data curation; investigation; methodology. **S. Bauman Surratt:** Funding acquisition; investigation; resources. **Cayo Biobank Research Unit:** Data curation; funding acquisition; resources. **M. I. Martinez:** Funding acquisition; resources; writing – review and editing. **M. J. Montague:** Data curation; funding acquisition; resources. **J. P. Higham:** Funding acquisition; resources; writing – review and editing. **A. D. Melin:** Conceptualization; funding acquisition; project administration; resources; supervision; writing – review and editing. **C. C. Veilleux:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; resources; supervision; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R code used in this analysis (e.g., receptor densities, sizes, and dermatoglyph metrics) are shared in Supporting Information.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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