

Toe pad morphology and adhesion in the miniaturized gecko, *Chatogekko amazonicus* (Gekkota: Sphaerodactylidae)

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Abstract

Chatogekko amazonicus is a miniaturized gecko from northern South America and is among the smallest of toe pad bearing lizards. The toe pads of *C. amazonicus* are miniscule, between 18% and 27% of the plantar surface area. We aimed to investigate the relationship between adhesive toe pad morphology, body size, and adhesive capabilities. Using scanning electron microscopy, we determine that the adhesive pads of *C. amazonicus* exhibit branched setae similar to those of other geckos, but that are generally much smaller. When compared with other gecko taxa, we show that *C. amazonicus* setae occupy a similar range of seta length: snout–vent length ratio and aspect ratio as other gekkonoid species (i.e. Gekkonidae, Phyllodactylidae, and Sphaerodactylidae). We demonstrate that *C. amazonicus*—even with its relatively small toe pads—is capable of climbing a smooth glass surface at a nearly vertical angle. We suggest that sphaerodactylids like *C. amazonicus* offer an excellent system for studying toe pad morphology and function in relation to miniaturization.

KEYWORDS

lagartixinha, scanning electron microscopy, scansors, setae

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1 | INTRODUCTION

Adhesive toe pads evolved numerous times across gecko evolutionary history and are diverse in relative shape, size, and function (Russell et al., 2019; Russell & Gamble, 2019). Toe pads facilitate digital adhesion through an assemblage of modified scales (scansors) bearing dense collections of hypertrophied epidermal structures (i.e. setae; Maderson, 1970; Ruibal & Ernst, 1965). Of the hypothesized 14 evolutionary gains of toe pads in geckos, at least four occurred in the Sphaerodactylidae (Russell & Gamble, 2019). The Sphaerodactylidae is a family comprising 230 described species, disproportionately split into 12 morphologically heterogeneous genera, inhabiting diverse habitats across western Asia, southern Europe, northern Africa, and the Neotropics (Gamble et al. 2008; Uetz et al., 2022). In addition to the incipient frictional adhesion described in the “padless” genus *Gonatodes* (Higham et al., 2017; Russell et al., 2015), sphaerodactylid toe pads are limited to *Aristelliger* (both basal and distal toe pads), *Euleptes* (distal leaf-toe pads), *Sphaerodactylus* (distal pad), *Coleodactylus* (distal pad), and *Chatogekko* (distal pad; Bauer and Russell, 1993; Gamble et al., 2012; Kluge, 1995; Russell & Gamble, 2019). The digital unguis sheath is a derived scale condition exhibited by the miniaturized sphaerodactyl geckos *Lepidoblepharis*, *Pseudogonatodes*, *Sphaerodactylus*, *Coleodactylus*, and *Chatogekko* (Kluge, 1995; Noble, 1921; Parker, 1926; Russell, 1972). In the latter three genera, the sheath is asymmetric, with one scale expanded, forming a toe pad with dense fields of setae (Gasc & Renous, 1980; Kluge, 1995; Röhl, 1995; Vanzolini, 1957; Figure 1a). *Sphaerodactylus cinereus* exhibits the largest asymmetric toe pad compared to those of other sphaerodactyls (Kluge, 1995); however, the more diminutive toe pads of *Chatogekko* also exhibit branching setae inferred to aid this lizard in clinging to heterogeneous surfaces in the leaf litter it inhabits (Gasc et al., 1982; Gasc & Renous, 1980).

Chatogekko amazonicus is a miniaturized species-complex of geckos from northern South America, previously considered a member of the genus *Coleodactylus* based on unguis sheath morphology (Gamble, Bauer, et al., 2011; Gamble, Daza, et al., 2011; Geurgas & Rodrigues, 2010; Kluge, 1995; Parker, 1926). Due to its volatile position in phylogenetic hypotheses and generally poor phylogenetic resolution at the base of the Sphaerodactylini, it is unclear whether *Chatogekko* represents an additional evolutionary gain of toepads, or if there was a single origin with subsequent loss of adhesive digits in *Lepidoblepharis*, *Gonatodes*, and *Pseudogonatodes* (Correia et al., 2016; Gamble et al., 2012, 2015; Gamble, Bauer, et al., 2011; Gamble, Daza, et al., 2011). Currently monotypic, *Chatogekko* appears to be a cryptic

species-complex comprising several undescribed, species-level lineages (Gamble, Bauer, et al., 2011; Gamble, Daza, et al., 2011; Geurgas & Rodrigues, 2010; Moretti, 2009). The miniature size of this lizard (average snout-vent length [SVL] = 21 mm; Gamble, Bauer, et al., 2011; Gamble, Daza, et al., 2011), coupled with its relatively small toe pads, makes *C. amazonicus* an ideal species-complex for studying the relationship between body size, seta size, and their effect on adhesive function in lizards. Gasc and Renous (1980) briefly described toe pad surface morphology of *C. amazonicus* from French Guiana, demonstrating that they do indeed exhibit branching setae as well as spinules and spines (sensu Garner & Russell, 2021). Gasc et al. (1982) demonstrated that microscopic surfaces on leaf litter in *C. amazonicus* habitat provide texture and relief that the setae, spines, and spinules likely exploit during locomotion. Beyond these two studies, no investigations have focused on *Chatogekko* toe pads. Here, we reinvestigated the surface morphology of the manus of *C. amazonicus* to test whether the minute size of this species and its toe pads facilitate vertical locomotion on a smooth glass surface. We compared the results of our morphological investigation with those of other seta-bearing species.

2 | METHODS

We investigated an ethanol-preserved specimen of *C. amazonicus* (specimen ID: MTR 12705). The specimen was not collected and euthanized for the purpose of our study. Rather, this specimen was donated to JDD by Miguel Trefaut Rodrigues (MTR) who collected it from Igarapé-Açu, Rio Abacaxis, Brazil, placing it in the geographic range of the central Amazonian clade (sensu Geurgas & Rodrigues, 2010). We removed the right manus from the specimen and then fixed the sample overnight with 2.5% paraformaldehyde and 2% glutaraldehyde in 0.1 M phosphate-buffered saline. Next, we washed the sample with 0.1 M phosphate-buffered saline, dehydrated it in ethanol serially, and fully dehydrated it with Hexamethyldisilazane. Finally, we mounted the sample on a carbon-tape stub and sputter coated it with Au (~200 Å for 60 s) before imaging it using a Hitachi SU3500 scanning electron microscope at Sam Houston State University (Huntsville, Texas USA).

We obtained scansor measurements as well as seta length and diameter measurements for digits I and II from scanning electron micrographs (SEMs) using Fiji (Schindelin et al., 2012); however, we could not estimate setal density with any confidence due to the curvature of the setal shafts. Due to setal bending and distortion, our seta measurements are not as accurate as those taken

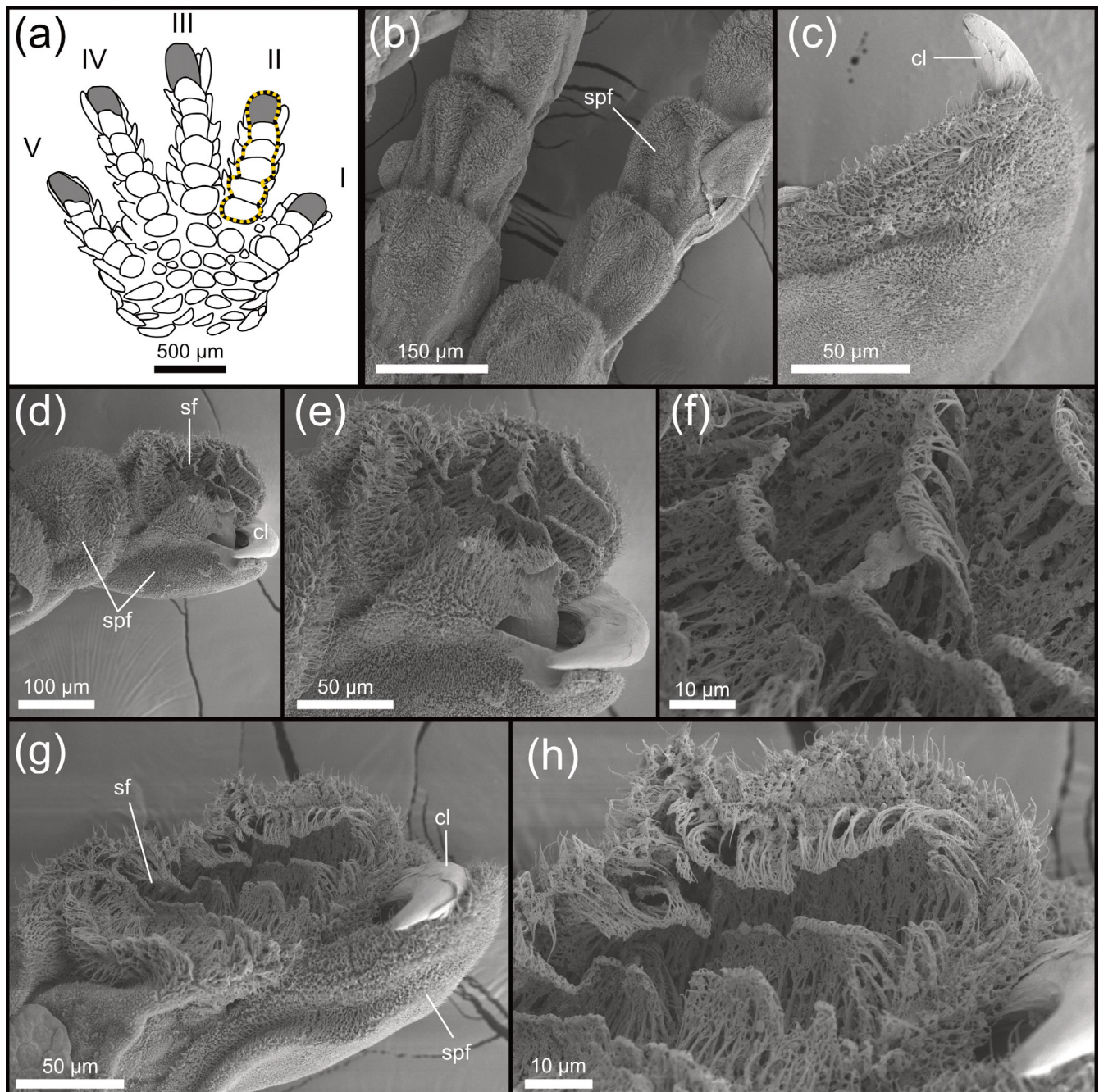


FIGURE 1 External manual morphology of *Chatogekko amazonicus*. (a) Illustration of the right manus in plantar view. Digits labeled I–V. Adhesive scansors shaded in gray. Yellow and black dashed line illustrates the boundary within which plantar digit area was measured. We also measured scansor area (gray within dashed line). (b) Scanning electron micrograph (SEM) of the plantar scales of digits III and II. (c) SEM of the non-adhesive unguis sheath of digit III in lateral view. (d) SEM of the distal tip of digit I in plantar view. (e) Magnified view of the adhesive scansor of digit I. (f) Magnified view of the field of branching setae on the scansor of digit I. (g) SEM of the distal tip of digit II in plantar view. (h) Magnified view of branching setae on the scansor of digit II. In all digit tips, the claw (cl) is situated between an unguis sheath incorporating a single adhesive scansor exhibiting a setal field (sf) and scale exhibiting a spinulate epidermal field (spf).

from longitudinal sections. Despite the non-ideal images for measurements, our setal length measurements are similar to those of Gasc and Renous (1980). We calculated the percentage of total scansor area in relation to the plantar surface of all digits using an image of the

manus prior to SEM processing using Fiji (Schindelin et al., 2012; Figure S1). We omitted measurements of digit IV due to distortion of the preserved specimen. Percentages of the scansor area and complete subdigital area were measured three times using the boundary illustrated

in Figure 1a and averaged. We selected digits I and II for setal measurements due to their undamaged condition and visibility in the micrographs. We compared our results with other published accounts of maximum setal length and maximum diameter (Table 1) and selected the other gecko taxa based on the presence of a maximum seta length and maximum diameter measurements in the literature and presence in the most comprehensive gecko phylogeny to date (Gamble et al., 2015). Because these data were presented independent of each other, there is no way of knowing if the setae with maximum lengths also exhibited maximum diameters. We therefore consider these seta measurements used in downstream analyses to represent idealized setae exhibiting maximum length and diameter values. To make these measurements comparable, we obtained reports of maximum SVL from the literature and calculated a maximum setal length: maximum SVL ratio (Table 1). Similarly, we used measurements from the literature to calculate seta aspect ratio (maximum setal length: maximum setal diameter; Table 1). We identified phylogenetic signal in these measurements using the phylogenetic hypothesis of Gamble et al. (2015) and using phylogenetic generalized least squares (Pagel's $\lambda = 1.029709$; Grafen, 1989). Because of the substantial phylogenetic signal in this sample, we corrected the relationships between maximum setal length, maximum setal diameter, and maximum SVL using phylogenetic independent contrasts (PICs; Felsenstein, 1985; geiger v2.0.7, Harmon et al., 2008; phytools v0.6-99, Revell, 2012; ape v5.3, Paradis & Schliep, 2019; nlme v3.1-142, Pinheiro et al., 2020) in R v4.1.2 (R Core Team, 2021).

We opportunistically obtained adhesion observations of *C. amazonicus* from the field. Obtaining adhesion data from miniaturized lizards can be difficult—typical instruments used to measure frictional adhesive performance are not sensitive enough for *Chatogekko* (Higham, pers. comm.; Higham et al., 2017). Therefore, we qualitatively examined the adhesive capability of two wild-caught *C. amazonicus* individuals from Manaus, Brazil (3.097083°S 59.986170°W; 27–28 July 2022). We observed animals moving through leaf litter on forest trails of Instituto Nacional de Pesquisas da Amazônia and caught them by hand (Instituto Chico Mendes de Conservação da Biodiversidade collecting permit #44832, granted to FPW). Animals were kept briefly (<1 h) in a ventilated plastic cup before each trial. The animals were placed on a pane of glass at a nearly vertical angle (recently cleaned with 70% EtOH) resting against the inside wall of a tall glass aquarium (L -39 cm \times W -15 cm \times H -31 cm; a repurposed setup generally used for live fish photography). The animals were encouraged to begin moving via light touches of their tail with the tip of a pen. We began

encouraging the animals to climb up the glass at a nearly vertical angle. Each individual was tested on the glass once. All videos were captured with a hand held iPhone 11.

3 | RESULTS

Scansors occupy 20.6%, 20.8%, 18.4%, and 27.0% of the plantar surface of manual digits I, II, III, and V, respectively (digit IV omitted due to specimen distortion). The plantar surface of the manual digits is covered with a spinulate Oberhäutchen epidermal field (Figure 1b). These spines are longer than those on the lateral portion of the digit (Figure 1c). Yet longer spines occur on the fringes of the single adhesive scansors (Figure 1d–h). The fringing spines are on average 8.6 μm in length ($N = 15$) with the longest being 10.5 μm . The adhesive scansors exhibit setal field areas of 6.06 and 6.47 mm^2 (for digits I and II, respectively). The setae themselves overlap in length with the fringing spines, ranging from 9.2 to 18.7 μm (average = 14.9 μm ; $N = 15$; Figure 1d–h; Table S1). The diameter of the setae range from 0.50 to 1.31 μm . Gasc and Renous (1980) reported a similar maximum seta length (20 μm) and diameter (1 μm) for their *C. amazonicus* from French Guiana. The setae themselves exhibit substantial branching, the initial branching being situated ca. 60% of the length of the seta from its base (Figure 1f,h). Smaller, spinulate projections are attached to the base of some setal stalks (Figure 1f). The setal lengths exhibited by *C. amazonicus* are short compared to those of other geckos (Table 1; Figure 2). When adjusted for phylogeny, maximum seta length is positively correlated with both maximum SVL and maximum diameter ($r^2 = 0.1742$, $F = 5.641$, $p = 0.02715$; $r^2 = 0.1746$, $F = 4.595$, $p = 0.04777$; Figure S2). The ratio of maximum seta length to maximum SVL for *C. amazonicus* sits within the range compiled for other pad-bearing gekkonoid species (i.e. gekkonids, phyllodactylids, and sphaerodactylids; Figure 3a). Of our sampled taxa, *S. cinereus* and *Thecadactylus rapicauda* exhibited the largest and smallest ratios in the Gekkonoidea, respectively (Table 1; Figure 3a). This range in ratio is well above the range of diplodactylid species sampled. The setal aspect ratio for *C. amazonicus* sits within the range compiled for diplodactylid species, but at the lower end of the range for other pad-bearing gekkonoid species (Figure 3b). Of our sampled taxa, *Aristelliger praesignis* and *Tarentola caboverdiana* exhibited the largest and smallest aspect ratios in the Gekkonoidea, respectively (Table 1; Figure 3b). The setal aspect ratios of diplodactylid species sampled generally sit in a lower range, but overlap the range for the species of the gekkonoidea sampled. Setal

TABLE 1 Setal measurements in some toe pad bearing geckos taken from the literature.

F	Species	MSL (μm)	MSVL (mm)	Seta: body size	MSD (μm)	Seta aspect ratio	Sources
S	<i>Chatogekko amazonicus</i>	20.0	24.0	0.833	1.3	15.4	Gasc, 1990; Gasc & Renous, 1980; This study
S	<i>Sphaerodactylus cinereus</i>	85.0	32.0	2.66	2.0	42.5	Röll, 1995; Schwartz & Henderson, 1991
S	<i>Aristelliger praesignis</i>	57.0	100.7	0.570	1.3	43.9	Griffing et al., 2017; Ruibal & Ernst, 1965
P	<i>Tarentola annularis</i>	114.0	114.5	0.996	—	—	Dellit, 1934; Schleich et al., 1996
P	<i>Tarentola caboverdiana</i>	68.0	73.0	—	4.5	15.1	Joger, 1993; Schleich & Kästle, 1986
P	<i>Thecadactylus rapicauda</i>	60	126.0	0.476	1.8	33.3	Schleich & Kästle, 1986; Vitt & Zani, 1997
G	<i>Chondrodactylus bibronii</i>	124.5	108.0	1.153	3.5	35.6	Heinz et al., 2021; Schleich & Kästle, 1986; Webster et al., 2009
G	<i>Hemidactylus bouvieri</i>	50	35.6	—	2.5	20.0	Schleich & Kästle, 1986; Vasconcelos et al., 2020
G	<i>Hemidactylus frenatus</i>	84.0	59.0	1.424	—	—	Dellit, 1934; Goldberg & Kraus, 2016
G	<i>Hemidactylus mabouia</i>	117.0	67.4	1.751	—	—	Ceríaco et al., 2021; Dellit, 1934
G	<i>Hemidactylus turcicus</i>	95.0	63.3	1.501	—	—	Dellit, 1934; Itescu et al., 2016
G	<i>Gekko gekko</i>	130.0	185.0	0.703	4.7	27.7	Conant & Collins, 1991; Ruibal & Ernst, 1965; Schleich & Kästle, 1986
G	<i>Gekko vittatus</i>	78.0	108.3	0.720	3.5	22.3	Rösler et al., 2012; Schleich & Kästle, 1986
G	<i>Gekko kuhli</i>	91.0	107.8	0.844	—	—	Brown et al., 1997; Schleich & Kästle, 1986
D	<i>Pseudothecadactylus lindneri</i>	37.0	107.0	0.346	1.2	30.8	Bauer, 1998; Cogger, 1975
D	<i>Correlophus ciliatus</i>	32.7	125.0	0.262	1.1	29.7	Bauer, 1990; Griffing et al., 2021
D	<i>Bavayia cyclura</i>	32.0	90.0	0.356	1.3	24.6	Bauer, 1998; Bauer et al., 2022
D	<i>Eurydactylodes viellardi</i>	19.0	57.0	0.333	—	—	Bauer, 1990, 1998
D	<i>Rhacodactylus auriculatus</i>	38.0	125.0	0.304	—	—	Bauer, 1990, 1998
D	<i>Amalasia lesueurii</i>	10.0	80.0	0.125	3	3.33	Cogger, 2014; Schleich & Kästle, 1986
D	<i>Woodworthia maculata</i>	13.0.0	82.0	0.159	0.6	21.7	Bauer, 1998; Towns, 1971
D	<i>Dactylochemis pacificus</i>	17.0	106.0	0.160	1.5	11.3	Bauer, 1990; Schleich & Kästle, 1986
D	<i>Toropuki stephensi</i>	17.0	80.0	0.212	0.8	21.3	Bauer, 1998; Robb, 1980
D	<i>Naultinus rudis</i>	21.0	75.0	0.292	0.8	26.3	Bauer, 1990, 1998
D	<i>Naultinus elegans</i>	15.0	72.0	0.200	0.8	18.8	Bauer, 1998; Robb & Hitchmough, 1979

Note: Maximum seta lengths (MSL), maximum snout–vent lengths (MSVL), the ratio of MSL to MSVL (seta: body size ratio), average setal diameter (MSD), and the ratio of MSL to MSD (Seta Aspect Ratio).

Abbreviations: D, Diplodactylidae; F, family; G, Gekkonidae; P, Phyllodactylidae; S, Sphaerodactylidae.

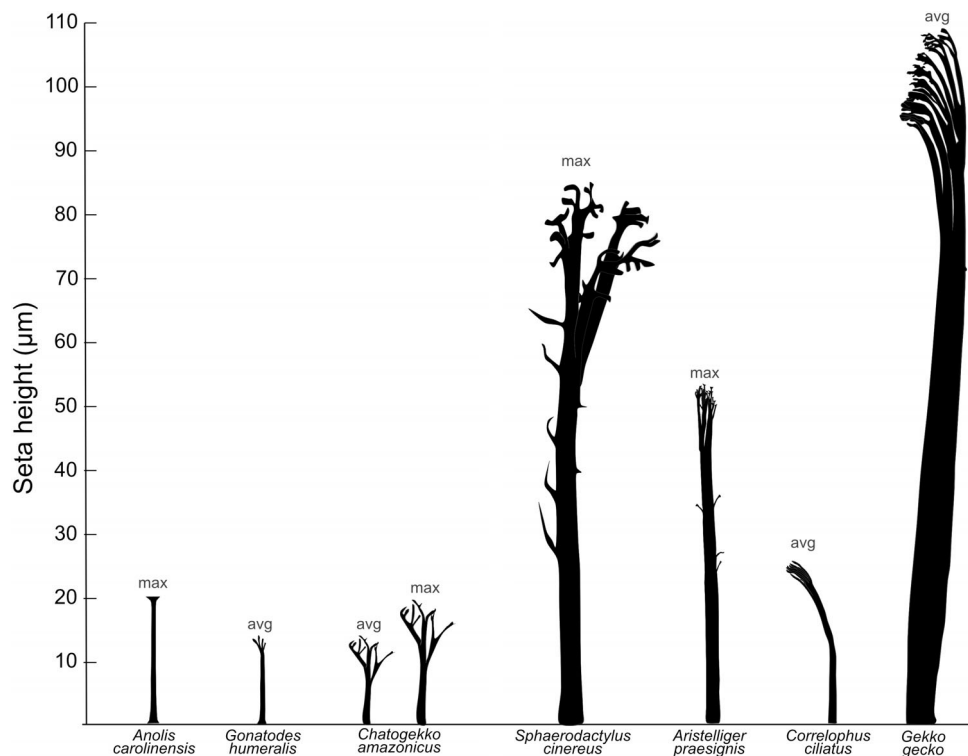


FIGURE 2 Comparisons of average setal length of *Chatogecko amazonicus* compared with average (avg) and maximum (max) setal length of other toe pad bearing species, reported from the literature. Other sphaerodactylids illustrated are *Gonatodes humeralis* (Russell et al., 2015), *Sphaerodactylus cinereus* (Röll, 1995; Ruibal & Ernst, 1965), and *Aristelliger praesignis* (Ruibal & Ernst, 1965). We also illustrate the average setal length of pad-bearing iguanian lizard, *Anolis carolinensis* (Ruibal & Ernst, 1965) and two non-sphaerodactylid geckos, *Correlophus ciliatus* (Griffing et al., 2021) and *Gekko gecko* (Ruibal & Ernst, 1965).

aspect ratio is positively correlated with maximum SVL ($r^2 = 0.7674$, $F = 60.37$, $p = 5.418 \times 10^{-7}$; Figure S3); however, after correcting for phylogeny, the relationship is not significant ($r^2 = 0.0222$, $F = 0.6313$, $p = 0.4385$).

The tested specimens of *C. amazonicus* were able to climb and adhere to glass at a near vertical angle (Figure 4a–c). At an angle of 80.7° the animal was able to reach the top of the glass slope but began slipping (Figure 4a; Figures S4–S6). The animal generally kept three autopodia in contact with the substrate at a time while climbing the surface.

4 | DISCUSSION

Manual toe pads of *C. amazonicus* occupy 18.4%–27.0% of subdigital area (21.7% average). Distal toe pads of several gekkotan species occupy less relative subdigital space when compared with basal toe pads (A. P. Russell, unpublished). The range of relative toe pad area we observe in *C. amazonicus* overlaps with pedal digit IV of other distal pad-bearing species (*Coleodactylus meridionalis*, *Diplodactylus pulcher*, *Lucasium byrnei*, *Lucasium steindachneri*) as well a reduced basal pad-bearing species (*Pachydactylus mariquensis*; A. P. Russell, unpublished). Although the range of relative toe pad area is quite small compared to many padded taxa, this range is larger than that of other non-miniaturized gekkotan taxa (*Lucasium stenodactylus*, *Dixonius siamensis*; A. P. Russell, unpublished).

Setal morphologies are diverse across pad-bearing species. The setae of *Anolis* spp. and *Prasinohaema* skins are spatulate and unbranched, whereas those of pad-bearing geckos generally exhibit distal branching (Ruibal & Ernst, 1965; Williams & Peterson, 1982). Even the nascent adhesive pads of the sphaerodactylid *Gonatodes humeralis* exhibit distally branching setae (Russell et al., 2015). The setae of *C. amazonicus* are profusely branched and of a similar length to those of *G. humeralis* (Figures 1f,h and 2). The unbranched spines surrounding the toe pad fall within a length range overlapping that of the setae, suggesting they may often come in contact with substrate during adhesion in *C. amazonicus* (Figure 1). The setae of *C. amazonicus* also exhibit the lateral spinulate projections from the main setal stalk exhibited by other sphaerodactylid species, *A. praesignis* and *S. cinereus* (Röll, 1995; Ruibal & Ernst, 1965). Whether this is a trait shared by all seta-bearing sphaerodactylid species requires further examination of additional species.

The ratio of maximum seta length to maximum SVL for *C. amazonicus* places this species well-within the ratio range of other sphaerodactylid, phyllodactylid, and gekkonid species (i.e. the Gekkonioidea; Table 1; Figure 3a). The short seta lengths of diplodactylids, regardless of body size, appear to be characteristic for the family and is likely related to relative density of setae (Bauer, 1998; Garner et al., 2021; Griffing et al., 2021; Russell & Garner, 2021). Setal length and frictional adhesive force have been shown to be positively related (Cobos &

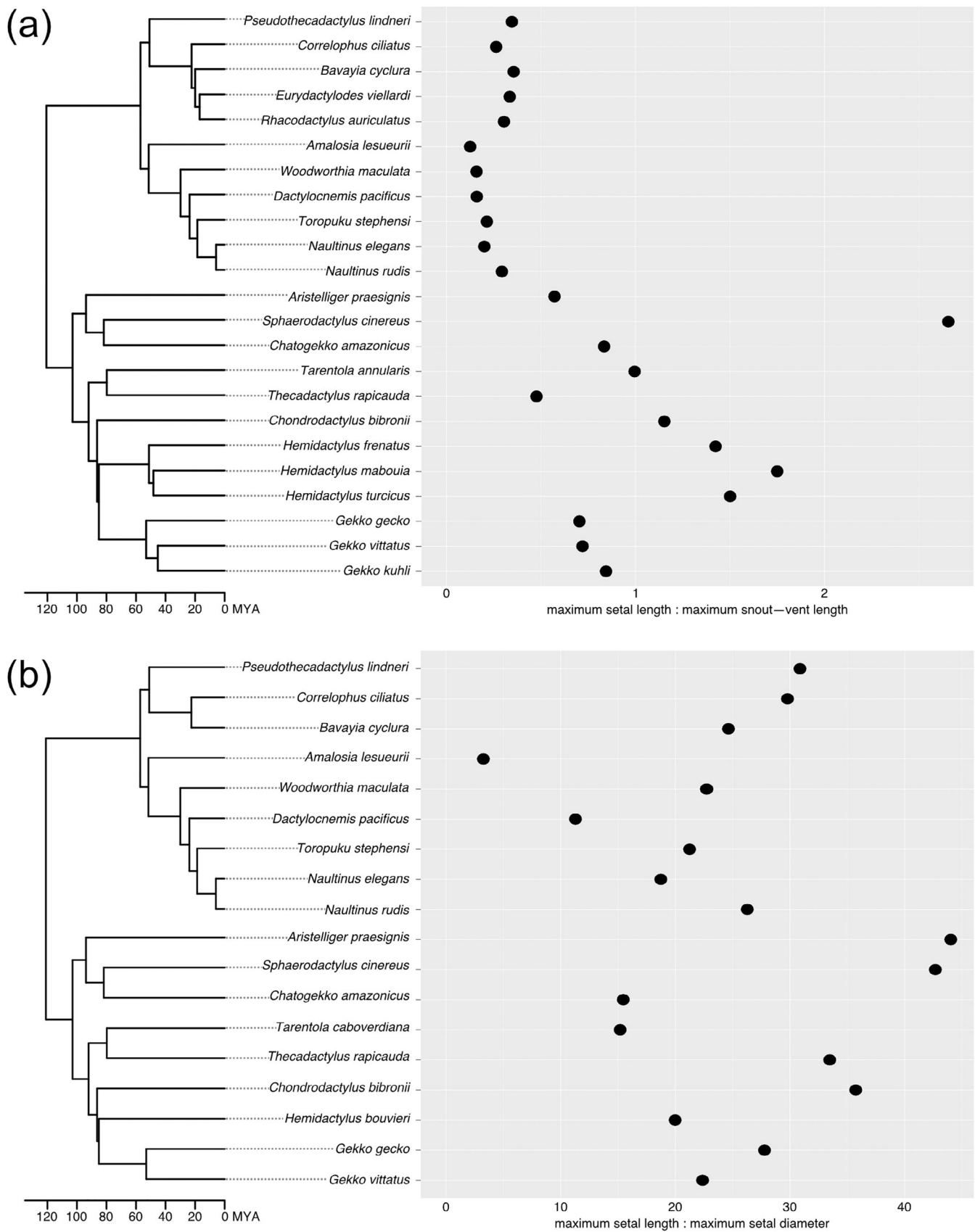


FIGURE 3 Setal morphology of *Chatogekko amazonicus* compared with other geckos. (a) Ratio of maximum seta length to maximum snout-vent length in a phylogenetic context. (b) Setal aspect ratio (maximum seta length to maximum setal diameter) in a phylogenetic context. Phylogenies adapted from Gamble et al. (2015). MYA, millions of years ago.

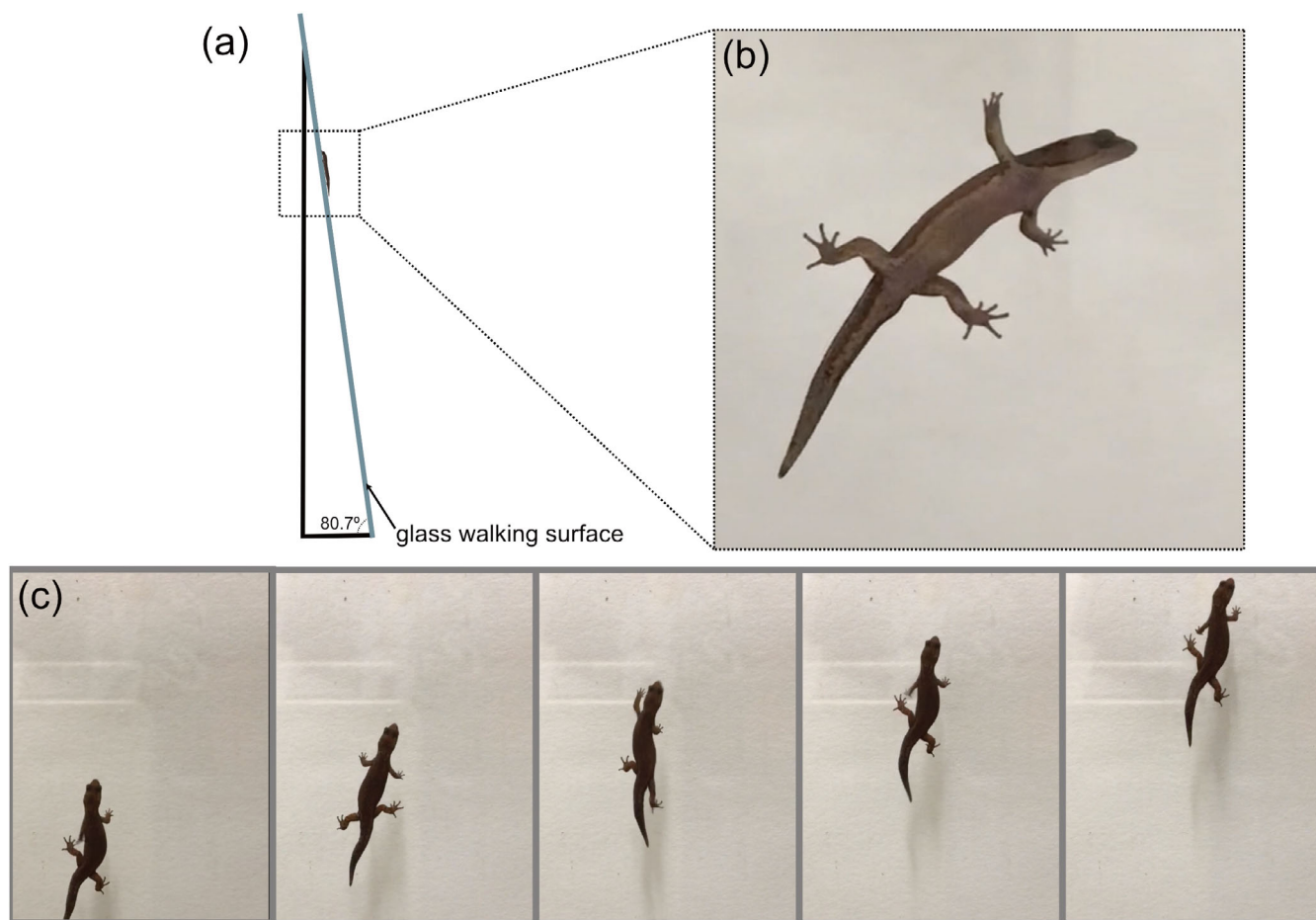


FIGURE 4 Digital adhesion of *Chatogekko amazonicus*. (a) Schematic of enclosure used to observe adhesive capability. The individual successfully walked up a smooth glass surface at an 80.7° angle. (b) View of the individual through glass while scaling slope. (c) Time series of the individual in dorsal view scaling the 80.7° slope.

Higham, 2022; Griffing et al., 2021). Additionally, synthetic fibrillar adhesives are generally more effective when fiber aspect ratio is higher—longer fibers with smaller diameters tend to require more pull-off force (Aksak et al., 2011; Gao & Yao, 2004; Paretkar et al., 2013). Gekkonoid species sampled generally exhibit a higher range of setal aspect ratios (15.1–43.8) than those of the diplodactylid species sampled (3.3–30.8; Table 1; Figure 3b). Given the above, one might expect setal aspect ratio to be positively correlated with SVL in scansorial geckos, due to the greater pull-off stress imposed by their large mass. Indeed, we initially found aspect ratio to be positively correlated with maximum SVL in species we examined (Figure S3); however, correcting for phylogeny renders this relationship not significant. Despite this, the setal aspect ratio of *C. amazonicus* sits within the range of other scansorial geckos (Figure 3b). When considering the exceptional miniaturized size of *Chatogekko* and its setal aspect ratio lying well within the range of other scansorial species, it would

not be surprising that the toe pads of *C. amazonicus* would be functionally comparable to those of other gekkonoid species. Indeed, we demonstrate that this species can climb a nearly vertical smooth surface (Figure 4); however, these geckos begin slipping on a smooth glass surface at an 80.7° angle. Considering their comparable setal lengths and aspect ratios, the reduced adhesive ability we observe may be due to the overall relatively small area of the adhesive surface, compared to that of other pad-bearing taxa (Garner et al., 2021). We were unable to investigate the toe pads of the pes, which likely exhibit different setal dimensions and may provide more insight into the adhesive capabilities of this species (Russell & Oetelaar, 2016). Unfortunately, we were unable to estimate the setal density of the *C. amazonicus* toe pad, which plays an important role in adhesive capability. When corrected for phylogeny, there is a significant relationship between maximum setal length and body size, however there are a few interesting outliers (Figure 3a). The relatively enormous setal length and aspect ratio of

S. cinereus compared to its miniaturized body size, in tandem with a relatively greater toe pad area, would suggest that the adhesive capabilities of miniaturized sphaerodactyls can be substantial.

Taken together, we have shown that the adhesive pads of *C. amazonicus* exhibit relatively long spines and setae, like those of other scansorial geckos. This collection of epidermal structures is sufficient to facilitate adhesion to smooth surfaces, not just the textured leaves that provide substrate on the forest floor as demonstrated by Gasc et al. (1982). Due to the miniaturized size of *C. amazonicus*, its ratio of maximum setal length to SVL and aspect ratio resides within the range of other gekkonoids. We note that this investigation was limited by the amount of detailed setal data published for geckos. Careful consideration must be paid when collecting data from the literature—in taxa bearing basal pads, setal length has been shown to vary along the disto-proximal axis of the toe pads, and must be considered when working with length averages (Garner et al., 2021; Garner & Russell, 2021; Johnson & Russell, 2009; Russell & Johnson, 2014; Russell & Garner, 2021). Future investigations should work towards further taxon sampling in characterizing setal morphology, density, and toe pad area. Due to the different mechanisms by which leaf-toe pads and basal-toe pads functionally operate (Russell & Delauger, 2016), future investigations should focus on setal measurements based on toe pad type. Clades such as the Sphaerodactylidae are ideal for investigations that explore how digital morphology and body size adapt to the diverse environments encountered by different species.

AUTHOR CONTRIBUTIONS

Aaron H. Griffing: Conceptualization; investigation; methodology; formal analysis; writing – review and editing; writing – original draft. **Juan D. Daza:** Writing – review and editing; methodology; writing – original draft; visualization; investigation; conceptualization. **Stuart V. Nielsen:** Investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; visualization. **Fernanda P. Werneck:** Funding acquisition; writing – original draft; writing – review and editing; methodology. **Patrik F. Viana:** Writing – review and editing; writing – original draft; methodology. **Tony Gamble:** Conceptualization; investigation; writing – original draft; writing – review and editing; methodology.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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