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Developmental Patterns Underlying Variation in Form and Function Exhibited by House Gecko Toe Pads

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Synopsis Adhesive toe pads have evolved numerous times over lizard evolutionary history, most notably in geckos. Despite significant variation in adult toe pad morphology across independent origins of toe pads, early developmental patterns of toe pad morphogenesis are similar among distantly related species. In these distant phylogenetic comparisons, toe pad variation is achieved during the later stages of development. We aimed to understand how toe pad variation is generated among species sharing a single evolutionary origin of toe pads (house geckos—*Hemidactylus*). We investigated toe pad functional variation and developmental patterns in three species of *Hemidactylus*, ranging from highly scansorial (*H. platyurus*), to less scansorial (*H. turcicus*), to fully terrestrial (*H. imbricatus*). We found that *H. platyurus* generated significantly greater frictional adhesive force and exhibited much larger toe pad area relative to the other two species. Furthermore, differences in the offset of toe pad extension phase during embryonic development results in the variable morphologies seen in adults. Taken together, we demonstrate how morphological variation is generated in a complex structure during development and how that variation relates in important functional outcomes.

Introduction

Morphological variation is shaped by both extrinsic and intrinsic processes (Wake and Roth 1989; Müller and Wagner 1991; Wake and Larson 2003). Therefore, understanding how morphological variation is generated requires detailed investigation of extrinsic factors, such as function, along with intrinsic factors, such as developmental patterns. The digits of gecko lizards (Infraclass Gekkota), particularly those exhibiting adhesive toe pads, offer an excellent structural complex for studying how morphological variation is generated during development and subsequently relates to particular functions. Toe pads have independently evolved at least 15 times in geckos (Gamble et al. 2012; Higham et al.

2017; Russell and Gamble 2019; Riedel et al. 2021), and relatively large-scale variation in toe pad morphology exists among these clades (Russell and Gamble 2019). More subtle variation is evident in the size, organization, and the number of adhesive scales among species within each of those independent origins. Although the developmental bases of gross toe pad diversity were previously described (Griffing et al. 2022a), nothing is known about how toe pad variation is generated within a clade ancestrally sharing a single evolutionary origin of toe pads.

Toe pads consist of specialized scales (scansors and basal lamellae) that bear microscopic, hypertrophied, branching epidermal structures (setae; Ruibal and Ernst

1965; Maderson 1970; Russell 2002; Bergmann and Russell 2003). The underlying musculoskeletal features and histology of toe pads are also specialized for control of the adhesive apparatus (Maderson 1966; Russell 1972, 1975, 1976, 1979, 1981; Russell and Bauer 1988, 1990). Working together, this collection of specialized morphologies allows geckos to adhere to smooth surfaces through frictional and adhesion forces (Russell 1981, 1986; Autumn et al. 2002; Autumn 2006). The efficacy of toe pad adhesion results from myriad factors, including toe pad configuration, setal dimensions and morphology, adhesive contact area, substrate roughness, and humidity (Russell 1979; Autumn and Peattie 2002; Stark et al. 2012; Collins et al. 2015; Niewiarowski et al. 2016; Russell and Delaugerre 2016; Higham et al. 2019; Russell et al. 2019; Griffing et al. 2021).

Despite distant phylogenetic relationships between some toe pad-bearing gecko lineages, patterns of early toe pad development are similar among those examined. More specifically, the pad-bearing geckos *Correlophus*, *Hemidactylus*, *Lepidodactylus*, *Ptyodactylus*, and *Tarentola* have distinct toe pad morphologies, yet share similar stages of pad initiation (presence of an enlarged subdigital pad) and initial formation of the adhesive scansors or lamellae (Rosenberg et al. 1992; Khannoon 2015; Alturk and Khannoon 2020; Griffing et al. 2022a). Variation in toe pad morphology arises through differential distal-to-proximal expansion of the adhesive scales (Griffing et al. 2022a). The observed pattern of development in pad-bearing species is also distinct from the hypothesized ancestral patterns of non-padded species (Griffing et al. 2022a). Griffing et al. (2022a) hypothesized that early patterning of toe pads is subjected to developmental constraint, which is subsequently released during later stages of pad development when variation appears between different species.

House geckos (*Hemidactylus*) are a diverse lineage of gekkonid lizards, with a natural distribution spanning tropical Asia, much of Oceania, Africa, Mediterranean Europe, the Caribbean, and South America (Bauer and Henle 1994; Uetz et al. 2023). *Hemidactylus*, along with its sister lineage *Dravidogecko*, all exhibit adhesive toe pads (Russell 1976; Gamble et al. 2012; Chaitanya et al. 2019). This clade is considered by previous investigations to exhibit an unambiguous gain of toe pads from a padless ancestor (Russell 1976; Gamble et al. 2012; Russell and Gamble 2019). Digital morphology of *Hemidactylus* is considered extraordinarily derived, exhibiting extreme reduction of antepenultimate phalanges, tendinous insertions of interossei muscles into individual scansors, the presence of paraphalanges, and scansors that are often divided (Russell 1976, 1977; Russell and Bauer 1988; Griffing et al. 2022b). Toe pad morphology is diverse within this lineage, including in-

terspecific variation in the number of scansors, dimensions of individual scansors, and degree of pad bifurcation (Russell 1972). Toe pad variation is most evident when comparing the toe pads of arboreal species to those with terrestrial lifestyles (Lajmi et al. 2020). How this variation in toe pad morphology is achieved remains unknown. Specifically, we do not know whether variation in toe pads is due to heterochronic shifts in development or secondary elaboration/reduction in toe pads.

We investigated the development of *Hemidactylus* toe pads to better understand how variation in toe pad expression is generated within a single evolutionary lineage, as opposed to the squamate-wide phylogenetic breadth of Griffing et al. (2022a). To place this variation in a functional context, we also collected frictional adhesion measurements for all three species. Herein, we describe embryonic toe pad development and clinging ability of three species with variable toe pad morphologies (*Hemidactylus turcicus*, *H. platyurus*, and *H. imbricatus*). *Hemidactylus turcicus* and *H. platyurus* are scansorial species and exhibit wider, mostly deeply cleft scansors than those of terrestrial species, like *H. imbricatus* (Fig. 1). We hypothesized that heterochronic shifts in development result in the variable toe pad morphologies we see in these species. Furthermore, we hypothesized that different species of *Hemidactylus* exhibit significantly different adult toe pad morphology and varying adhesive capabilities. As such, we predicted species-specific differences between the onset and offset of toe pad development and that smaller toe pads are less effective in respect to adhesion.

Materials and methods

We collected embryonic material from eggs produced by captive colonies of *H. turcicus*, *H. platyurus*, and *H. imbricatus*. We selected these species based on their differing toe pad morphologies, diverse ecologies, and availability in the pet trade and from introduced populations. *Hemidactylus turcicus* is a scansorial gecko with a native range spanning the Mediterranean region of southern Europe, northern Africa, and the Middle East, and also has an introduced range primarily in southern North America (McCoy 1970; Weterings and Vetter 2018). Although largely commensal with humans and found primarily on buildings in both its native and introduced ranges, *H. turcicus* can often be found on or underneath rocks and dead trees (Loveridge 1947; Davis 1974; Moravec et al. 2011). The digits of this species lack interdigital webbing, and digit IV possesses 9–10 mostly bifurcated, broad scansors that run from the base of the digit up to the end of the pad (McCoy 1970; Fig. 1). *Hemidactylus platyurus* is a scansorial

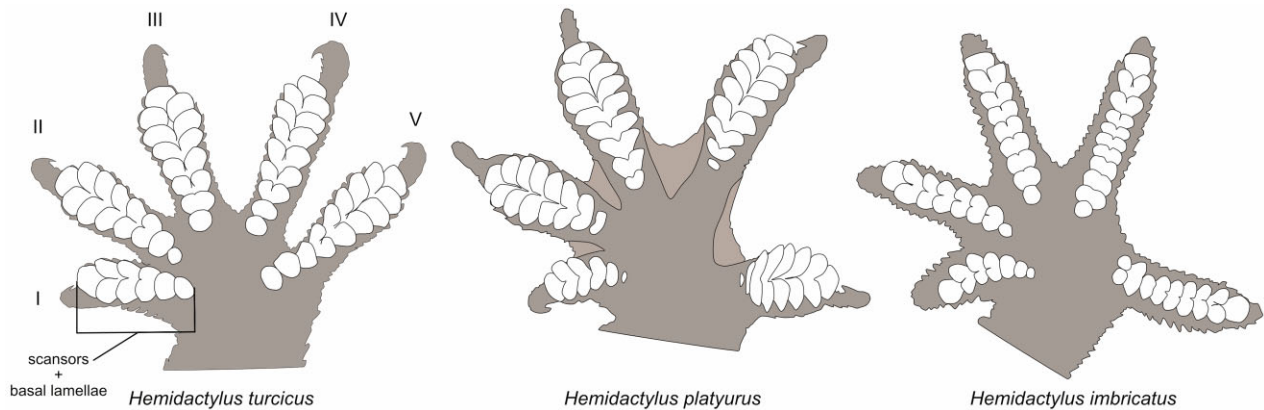


Fig. 1 Surface toe pad morphology of the left pes in three species of *Hemidactylus*. White structures correspond to scansors and basal lamellae. Digits are labeled I–V.

gecko found throughout Southeast Asia, parts of the Indian subcontinent, as well as being now introduced to Florida, USA (Smith 1935; Taylor 1963; Meshaka and Lewis 1994). Similar to *H. turcicus*, *H. platyurus* is a human commensal and is found primarily on buildings, but sometimes frequents low-elevation forest tree trunks, rocks, and forest floors (Smith 1935; Zug et al. 2007; Kaiser et al. 2011). The digits of this species possess substantial interdigital webbing and digit IV possesses 5–9 mostly bifurcated, extremely broad scansors that run from half of the length of the digit to the end of the pad (Smith 1935; Fig. 1). *Hemidactylus imbricatus* is a terrestrial gecko native to portions of the Indian subcontinent and is primarily found beneath cover objects on loose, dry soil (Smith 1935; Anderson 1964). The digits of this species lack interdigital webbing and digit IV possesses 9–11 narrow scansors, the distal ones being bifurcated, that extend from the base of the digit to the distal end of the pad (Smith 1935; Anderson 1964; Fig. 1).

We obtained *H. turcicus* for our colony from non-native populations in Oklahoma, USA (Permit: ODWC-6945). We obtained both *H. platyurus* and *H. imbricatus* for our colonies from the pet trade. Live animals were housed at Marquette University (Milwaukee, WI, USA) under Institutional Animal Care and Use Committee (IACUC) protocols AR279, AR288, and AR298 or at University of California (Riverside, CA, USA) under IACUC protocol 20170039.

We collected and preserved embryos in 4% paraformaldehyde in phosphate-buffered saline following Griffing et al. (2018) and assigned developmental stages based on previously published gecko staging series (Griffing et al. 2019, 2022b). Embryo sample sizes were 42 (*H. imbricatus*), 159 (*H. platyurus*), and 222 (*H. turcicus*). We subsampled these embryo collections for scanning electron microscopy (SEM) imaging ($N = 9$,

H. imbricatus; $N = 8$, *H. platyurus*; $N = 13$, *H. turcicus*). SEM images for *H. turcicus* toe pad development and embryonic staging are described in detail in Griffing et al. (2022a, 2022b).

We visualized toe pad development using SEM. After identifying preserved specimens within the developmental range of toe pad morphogenesis (stages 36–42; Griffing et al. 2022a), we removed hindlimbs at the ankle and post-fixed tissue in 1% glutaraldehyde at 4°C overnight. Following post-fixation, we treated the tissue with 1% osmium tetroxide for 1–2 h (depending on sample size) at room temperature and subsequently critical point dried the tissue. We sputter coated all specimens with gold/palladium (1 Å) and then imaged the specimens using a SU3500 scanning electron microscope (Loyola University Chicago, Chicago, IL, USA). We then compared toe pad morphology between species. Following previous investigations, we focused on pedal digit IV, which is often the longest digit in lizards (Losos and de Queiroz 1997; Knox et al. 2001; Pinto et al. 2008; Griffing et al. 2022a). In the case of stage 37 *H. imbricatus*, pedal digit IV was damaged or not in view of the SEM, therefore, we visualized pedal digit III.

To investigate the functional capacity of *Hemidactylus* toe pads, we collected frictional adhesive force measurements for three individuals ($N = 3$) for each of the three species. To measure relative toe pad size, we recorded mass using a standard high precision lab scale (Ohaus Scout Pro 400 g) and measured snout–vent length with digital calipers. We measured toe pad area by pressing the manus against a clear acrylic sheet and taking a ventral photo with scale using a Nikon D7000 camera. The toe pad area of digit IV was measured by importing the photo into ImageJ (Schneider et al. 2012) and using the area measurement tool. The area of all toes was measured, but we focused on digit IV.

Following specimen measurements, we connected a 6 × 2 cm acrylic sheet to a portable force gauge (Model M5-10, accuracy = ±0.1% full-scale) using a silk suture. We wiped the sheet with 100% ethanol between every trial. We measured clinging force by holding the gecko in our hand and placing the right manus of each individual on the acrylic surface, allowing it to adhere before steadily pulling the individual horizontally along the surface until either slippage occurred or there was no additional room to pull (i.e., the toes slipped off the sheet). We performed this force gauge measurement five times in succession and repeated these measurements the following day. For each individual, we retained a single maximum value. In addition to our measurements, we included clinging force measurements of *H. frenatus* from Irschick et al. (1996). However, it is important to note that the material used in our study (acrylic) differs from the material used by Irschick et al. (1996; acetate). Although both materials are smooth, we cannot rule out differences due to the chemical composition of the materials.

To examine the differences in toepad area (digit IV relative to body mass), frictional adhesive force, and relative adhesive force (maximum adhesive force of the manus by the total area of all toepads on a single manus), we used one-way ANOVAs with species as the categorical independent variable and force and area as continuous dependent variables. Tukey's post-hoc tests were used to determine pairwise relationships if the overall ANOVA was significant. Without a significant ANOVA, we performed two-sample *t*-tests to determine differences between pairs of species. In addition, a linear regression was used to determine the relationship between body mass and toepad area, and a subsequent one-way ANOVA was used to determine if the residuals were different among species. All statistics were performed in SYSTAT 8.0.

Results

Embryonic staging of *Hemidactylus*

Embryonic development in both *H. platyurus* and *H. imbricatus* proceeds similarly to other gekkonid geckos, including *H. turcicus* (Noro et al. 2009; van der Vos et al. 2018; Griffing et al. 2019, 2022b). Postovipositional embryonic development lasts for an average of 51 days ($N = 12$) when incubated at 27°C for *H. platyurus*. We identified 18 postovipositional embryonic stages (Fig. 2), with the earliest stage at oviposition being 26 (25 somites; *sensu* Dufaure and Hubert 1961). Postovipositional embryonic development lasts for an average of 52 days ($N = 20$) when incubated at 27°C for *H. imbricatus*. We identified 20 postovipositional embryonic stages

(Fig. 3), with the earliest stage at oviposition being 24 (17 somites; *sensu* Dufaure and Hubert 1961). For both species, the final embryonic stage (43) is characterized by an opaque ventrum, hydrophobicity of the skin (air pockets being visible on the embryo when submerged in buffer), and inversion of the hemipenes (*sensu* Griffing et al. 2019). Stage-by-stage descriptions of embryonic development for both *H. platyurus* and *H. imbricatus* can be found in Supplemental Material S1 and S2. In all species examined, toe pad development is initiated following the end of digital webbing recession (stage 36). For this reason, we selected stage 36 and later stages for our SEM investigation.

Hemidactylus toe pad development

For all three species, following digital webbing recession at stage 36, the pad is undivided and distinct from the distal portion of the digit (*H. platyurus* retains most of its interdigital webbing; Fig. 4). In *H. turcicus*, the pad is initially subdivided into five transverse ridges in the distal portion of the pad (stage 37; Fig. 4). The distalmost ridge exhibits a dome-like shape. Later in development (stage 38), additional transverse rows form further proximally, while the second and third distalmost ridges assume a curved shape. Eventually (stages 39–40), the second through fifth distalmost expand distolaterally, creating “V”-shaped, imbricating scansors that are cleft in the midline. A furrow is evident in the midline of the scansors. Non-adhesive digital scales begin to be visible during these stages as dome-shaped integumentary thickenings. Nearing the end of *in ovo* development (stage 41), scansors are plate-like and reflect the morphology that will persist to adulthood (Figs. 1 and 4).

In *H. platyurus*, the pad is initially subdivided into five transverse ridges in the distal portion of the pad (stage 37; Fig. 4). The distalmost ridge exhibits a dome-like shape, while the second and third distalmost ridges exhibit curved shapes. Later in development (stage 38), additional transverse rows form further proximally while the initially formed ridges expand laterally. Eventually (stages 39–40), the second through seventh distalmost ridges expand distolaterally, creating wide “V”-shaped, imbricating scansors. By stage 40, non-adhesive scales are evident on the tarsal region of the foot as dome-shaped integumentary thickenings. A furrow is evident in the midline of the scansors at stage 39. From stages 41 and on, scansors are plate-like and reflect the morphology that persists into adulthood (Figs. 1 and 4).

In *H. imbricatus*, the pad is initially subdivided into three transverse ridges in the distal portion of the pad

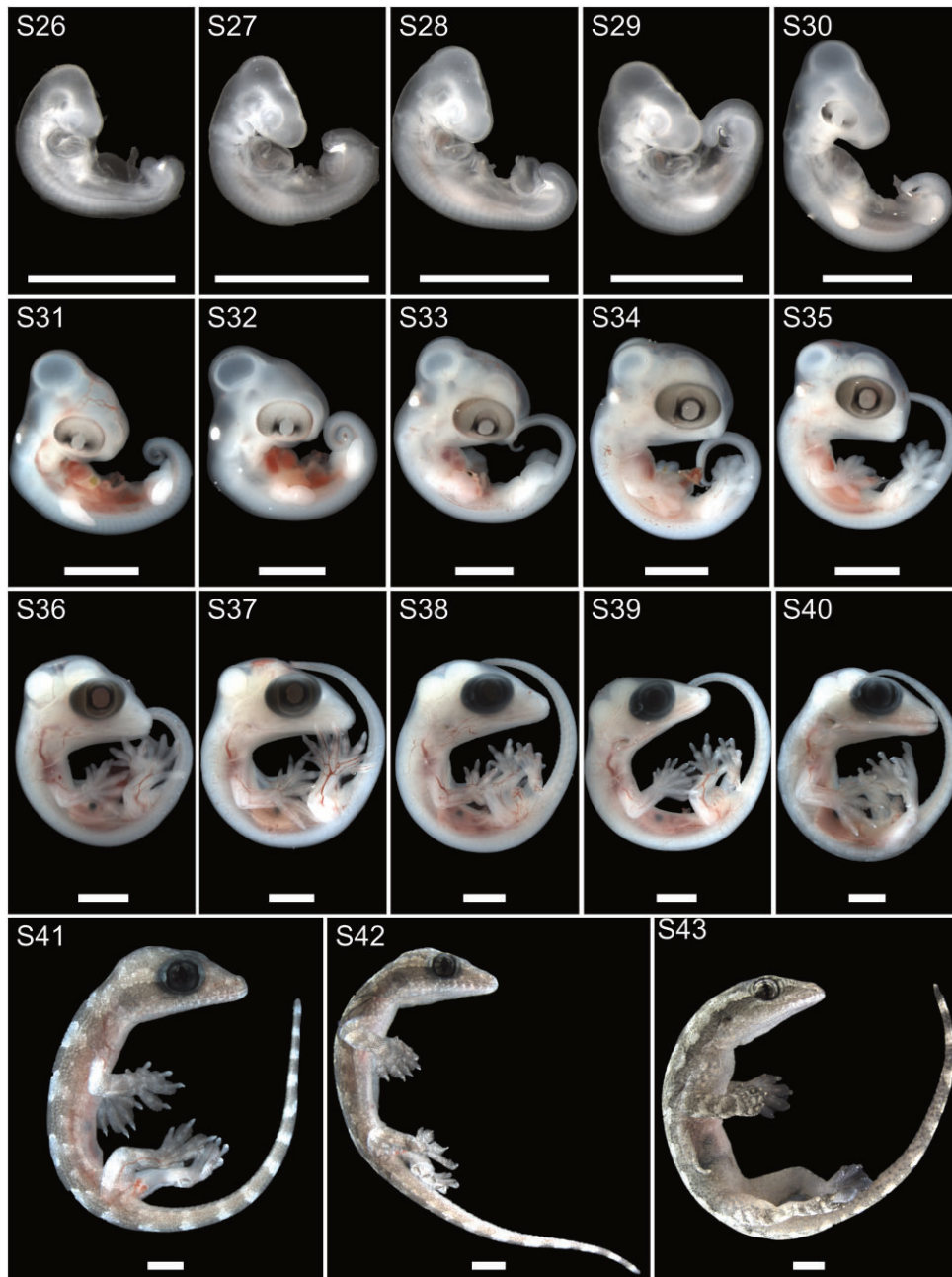


Fig. 2 Embryonic *in ovo* stages (S) 26–43 of *H. platyurus* development. Lateral views of whole embryos. Scale bars = 2 mm.

(stage 37; Fig. 4). Later in development (stages 38), additional transverse rows form further proximally. The distalmost ridge exhibits a dome-like shape, while the penultimate one exhibits a curved shape. The penultimate and antepenultimate ridges appear to grow distolaterally, creating a “U”-shape. By stage 40, non-adhesive digital scales are evident on the sides of the digits. Beyond slightly more raised proximal ridges, no additional morphological change is visible. By stage 41, scansors are imbricate and reflect the morphology that persists into adulthood (Figs. 1 and 4).

Adhesive performance measurements

Relative to body mass, digit IV toe pad area was significantly greater (ANOVA with Tukey’s post hoc test, $P < 0.001$) for *H. platyurus* (6.54–6.99 mm²) compared to *H. turcicus* (2.66–4.19 mm²) and *H. imbricatus* (2.43–2.81 mm²; Fig. 5A; Supplemental Material S3). Total toepad area for a single manus ranged from 20.9 to 22.3 mm² for *H. platyurus*, 11.2 to 17.6 mm² for *H. turcicus*, and 8.3 to 9.5 mm² for *H. imbricatus*. When the total toepad area (relative to body mass) was quantified, all species differed from one another (Tukey’s

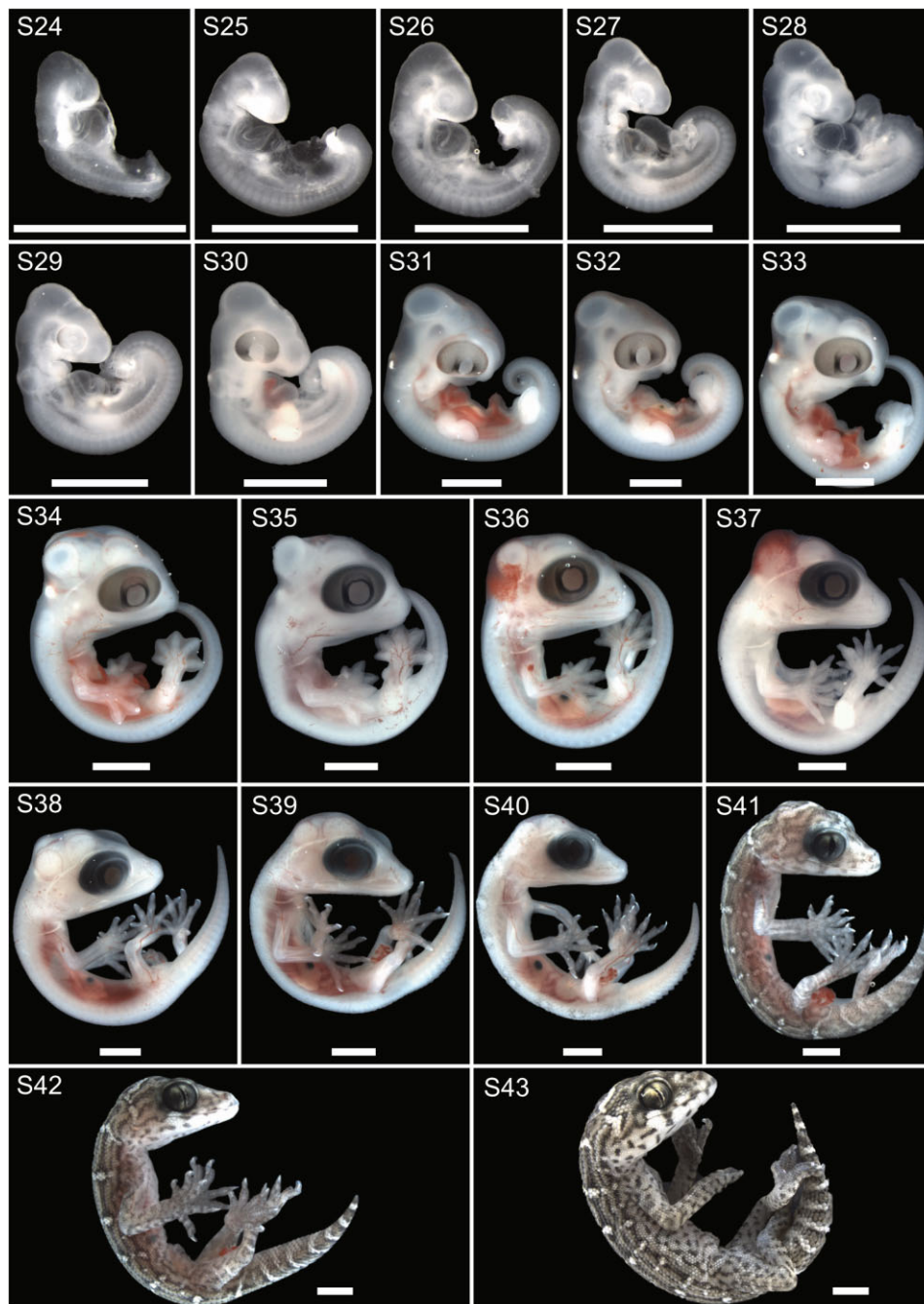


Fig. 3 Embryonic *in ovo* stages (S) 24–43 of *H. imbricatus* development. Lateral views of whole embryos. Scale bars = 2 mm.

post hoc test, $P < 0.001$ for *H. platyurus* compared to other species and $P = 0.006$ for *H. turcicus* compared to *H. imbricatus*). *Hemidactylus platyurus* exhibited the greatest adhesive strength of the species we investigated (0.65–1.85 N for single manus), followed in order by *H. turcicus* (0.05–1.12 N) and *H. imbricatus* (0.00–0.11 N; Fig. 5B; Supplemental Material S3). Measurements of *H. frenatus* are similar to those of *H. turcicus* (Irschick et al. 1996). The adhesive force of the

three species in our study only differed significantly between *H. platyurus* and *H. imbricatus* (Tukey's post hoc test, $P = 0.01$). The relative adhesive force (maximum force divided by the toepad area of all digits on the manus) for *H. turcicus*, *H. platyurus*, and *H. imbricatus* was 0.14, 0.20, and 0.03 N/mm², respectively. Relative adhesive force was only different between *H. platyurus* and *H. imbricatus* (pooled variance two-sample *t*-test, $P = 0.029$).

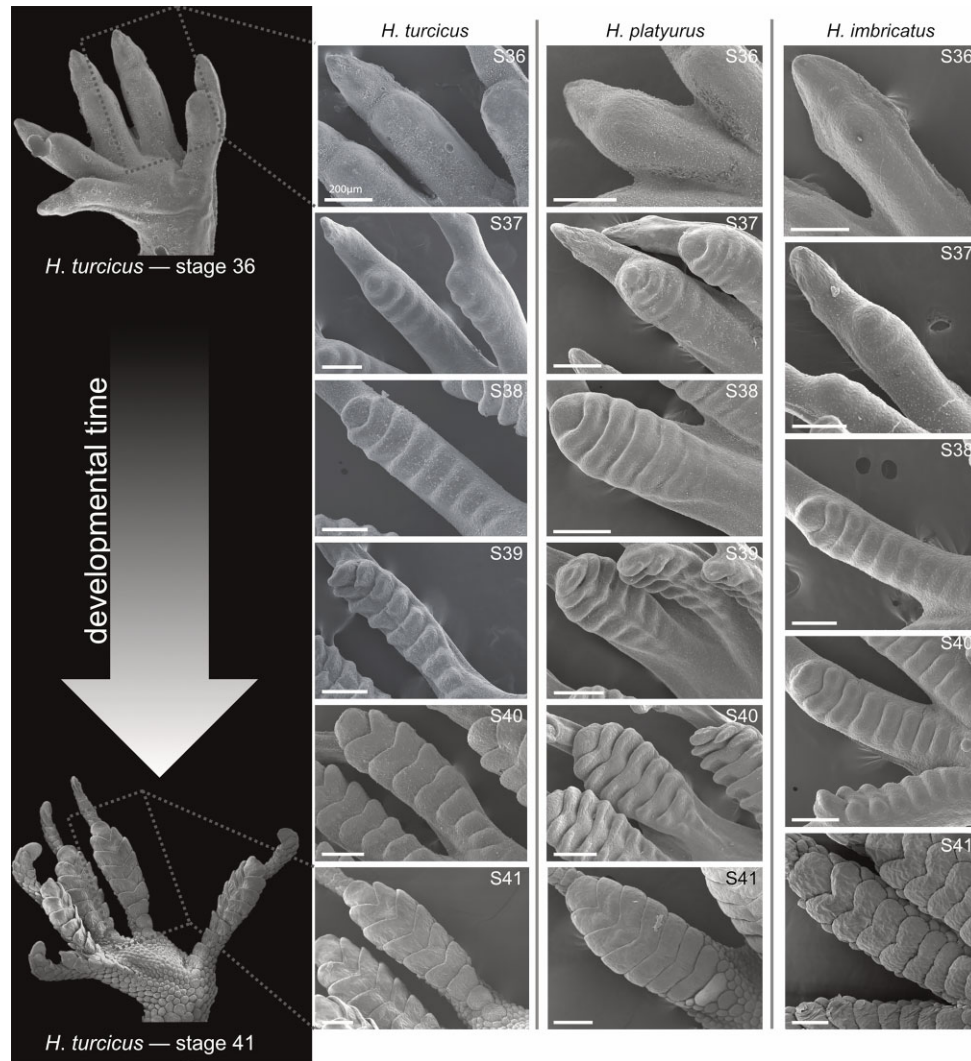


Fig. 4 Scanning electron micrographs depicting the stages (S) of toe pad development of *H. turcicus*, *H. platyurus*, and *H. imbricatus*. Plantar views of pedal digit IV (except *H. imbricatus* stage 37, which is digit III). Development progresses from top to bottom. SEMs of *H. turcicus* originally from Griffing et al. (2022a). Scale bars = 200 μ m.

Discussion

Beyond small differences in the developmental stage at oviposition between the three species we examined, gross embryonic development in *H. turcicus*, *H. platyurus*, and *H. imbricatus* appears to proceed similarly (Figs. 2 and 3; Supplemental Material S1 and S2; Griffing et al. 2022b). However, at the level of toe pad morphogenesis, the three species exhibit slight modifications of the patterns of development following the establishment of scansor ridges. Our results unsurprisingly demonstrate that *H. platyurus* and *H. imbricatus* exhibit the pattern of adhesive pad development in which plantar scansors develop in a distal-to-proximal series (Fig. 4; Griffing et al. 2021, 2022a). This pattern appears to be decoupled from the development of the non-adhesive digital scales which arise later in embryonic development. The initial scansor ridges form after the pad be-

comes distinct from the distalmost portion of the digit, foreshadowing the characteristic angled claw of *Hemidactylus* (Russell 1976; Griffing et al. 2022b). This pattern does not occur in other toe pad bearing taxa and therefore appears to be a derived characteristic of *Hemidactylus* toe pad morphogenesis (Griffing et al. 2022a). Scansor development following the formation of the expanded pad is typical for all pad-bearing lizards investigated to date (Rosenberg et al. 1992; Khannoon 2015; Alturk and Khannoon 2020; Griffing et al. 2022a). During initial scansor ridge formation, we found that *H. turcicus* and *H. platyurus* exhibit the same number of scansor rows at the earliest stages of pad subdivision, while *H. imbricatus* exhibited fewer (Fig. 4). *Hemidactylus imbricatus* subsequently develop additional rows until achieving a similar number of rows as *H. turcicus*. Whether the deviation by *H. imbricatus* from the

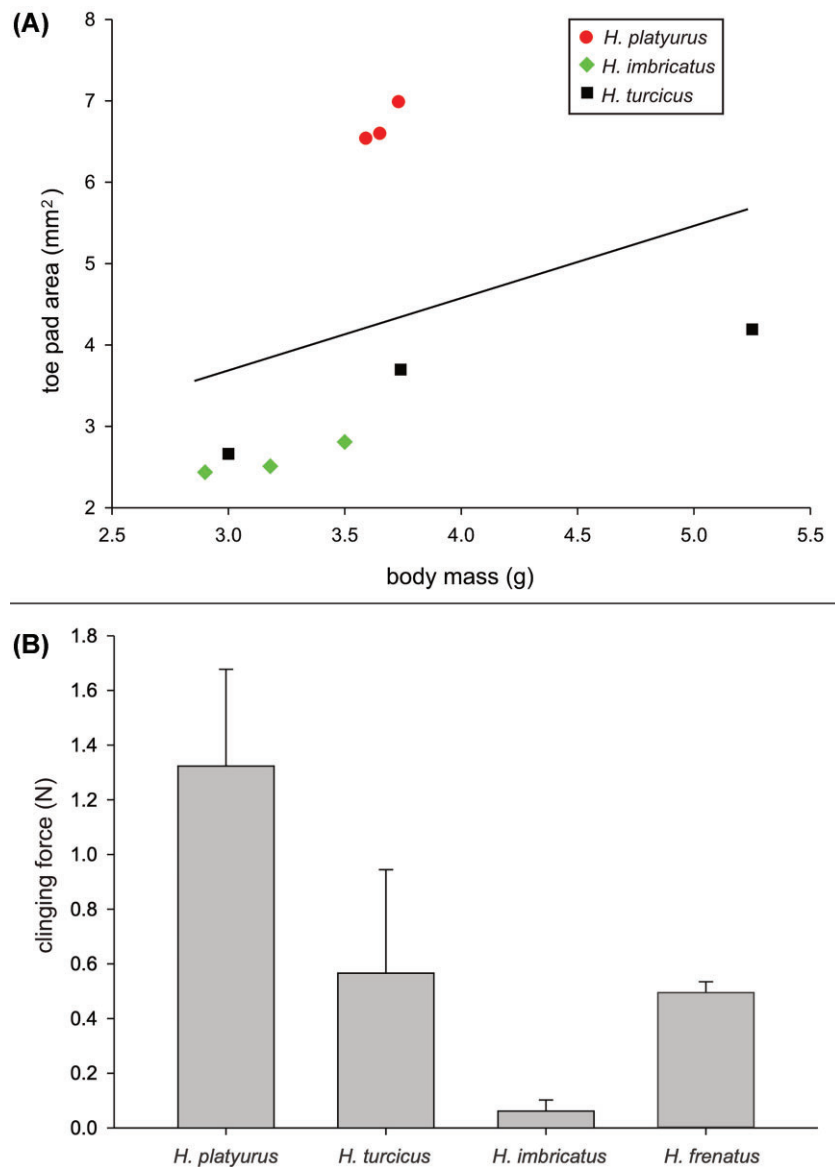


Fig. 5 (A) Relationship between body mass and toe pad area of three species of *Hemidactylus*. **(B)** Toe pad clinging force exhibited by four *Hemidactylus* species. Measurements of *H. frenatus* from Irschick et al. (1996).

pad subdivision pattern observed in *H. turcicus* and *H. platyurus* is an artifact of sampling is unclear, but *H. imbricatus* differs in other ways. *Hemidactylus imbricatus* suppresses distolateral growth or any further elaboration following the initial patterning of the scansors (Fig. 4). This developmental pattern exhibited by *H. imbricatus* likely represents a relatively early offset (i.e., progenic; Alberch 1980; McNamara 1986) of the toe pad morphogenetic pathway. Compared to *H. turcicus* and *H. imbricatus*, it takes longer for *H. platyurus* to complete the patterning of the scansors. Unlike what we observed during *H. imbricatus* toe pad development, *H. platyurus* exhibits immediate lateral expansion of the pad and distolateral growth of individual scansors.

In *Anolis* lizards, a non-gekkotan clade exhibiting an independent and unique single origin of toe pads, the initial number of lamellar ridges during development is consistent between species, despite exhibiting different toe pad morphologies as adults (Griffing et al. 2022a). Earlier offset of the toe pad extension phase appears to produce the differences in adult morphology between *Anolis carolinensis* and *A. sagrei* (Griffing et al. 2022a). These findings mirror our own observations in how variation is generated in the ancestrally shared toe pads of *Hemidactylus*.

Our measurements of adult *Hemidactylus* suggest that differences in morphology between *H. turcicus*, *H. platyurus*, and *H. imbricatus* result in distinct func-

tional capabilities. The primarily scansorial *H. platyurus* exhibits relatively larger toe pad areas and significantly greater frictional adhesive forces than the terrestrial *H. imbricatus* (Fig. 5). The superior adhesive force of *H. platyurus* is likely attributable to their relatively larger toe pads (Figs. 1, 4, and 5). However, when comparing relative adhesive force (force divided by the total toepad area from a manus), the difference still prevails. Thus, other attributes of the adhesive system likely play a role. Indeed, it should be noted that *H. platyurus* exhibit large setal lengths and high setal density when compared to other gekkotans (Peattie 2007). Future work comparing the microstructures of adults from the three species in our study would illuminate any differences in setal morphology and density. It is important to note that there is variation among the three individuals per species that we measured and that a single individual of *H. turcicus* did not generate any adhesive force (Supplemental Material S3). This lack of performance may be due to timing of the shedding cycle, adhesive pad damage, or unobservable fine control of the adhesive mechanism (Hiller 1968; Pillai et al. 2023).

Our investigation of the ontogeny of the toe pads among species of *Hemidactylus* demonstrates variation in their expression and its associated correlation with their differential adhesive capabilities, supporting our initial hypotheses. The slight differences in toe pad expression we observed in three species of *Hemidactylus* have led to downstream shifts in morphology and concomitant influences on functional performance. Our characterization of external morphological development, as well as other SEM investigations (Rosenberg et al. 1992; Khannoon 2015; Alturk and Khannoon 2020; Griffing et al. 2022a) provides an important foundation for studying toe pad evolution and development. However, future investigations may reveal more fine-scale differences in development (of both toe pads and non-adhesive scales) by taking a more complete anatomical approach and examining histology, cellular activity, and spatial gene expression data (e.g., Rosenberg et al. 1992; Alibardi 1996, 1997; Di-Poi and Milinkovitch 2016; Cooper et al. 2019). Additional sampling of *Hemidactylus* gecko development, seta morphology, and adhesive performance, in tandem with additional sampling of closely related padded and non-padded lineages (*Dravidogecko* and *Cyrtodactylus*, respectively) may reveal further modifications to the evolution of the lizard adhesive apparatus.

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Supplementary data

Supplementary Data available at *ICB* online.

Conflict of interest

The authors listed above declare no conflicts of interest.

Data availability

The data used in this article are available in the article itself and in its Supplementary Materials.

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