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Notes on Patagium Morphology in the Gliding Flat-tailed House Gecko (*Hemidactylus platyurus*)

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Abstract.—Several species of geckos have independently evolved patagia, membranous features that facilitate gliding. Detailed morphological investigations of gecko patagia have largely been limited to gliding members of the genus *Gekko* (formerly in the genus *Ptychozoon*). Herein we describe the morphology of gliding patagia of the Flat-tailed House Gecko (*Hemidactylus platyurus*), a species with an independent evolutionary origin of gliding patagia from *Gekko* and an important species for researching gliding biomechanics. We compared morphology of *H. platyurus* with a closely related non-gliding species, the Common House Gecko (*Hemidactylus frenatus*). Using external examination and histological techniques, we compared and contrasted three regions that exhibit patagia (trunk, femoral region, and tail) in *H. platyurus* but not in *H. frenatus*. We find that patagia in a gliding *Hemidactylus*, like patagia in gliding members of the genus *Gekko*, are derived from expansion of lateral fat bodies, suggesting analogous processes to achieve similar phenotypic outcomes.

Gliding has evolved in many tetrapod lineages and has necessitated specialized morphology to create drag and slow aerial descent (Norberg 1994; Dudley et al. 2007). Specialized morphologies attributed to gliding include increased digital webbing in addition to lateral folds along the limbs, tail, and trunk (i.e., patagia) (Russell 1979; Socha et al. 2015). Geckos have evolved gliding behavior in at least seven lineages, most notably in the Southeast Asian *Gekko* clade (Boulenger 1890; Honda et al. 1997; Vitt and Zani 1997; Brown et al. 1997, 2007, 2012; Bauer et al. 2010; Wood et al. 2020). Most of the morphological investigations into gecko gliding structures have been conducted on members of the *Gekko* subgenus *Ptychozoon*, such as *Gekko kuhli* (Russell 1979; Russell et al. 2001; Young et al. 2002). This particular species of gecko is known for its gliding capabilities and exhibits elaborate membranous patagia in the lateral portions of the postocular region, trunk, hind- and forelimbs, and tail (Russell 1979; Young et al. 2002). They also possess substantial interdigital webbing. The trunk patagium of *G. kuhli* consists of epidermis, dermis, and adipose tissue, with integumentary layers exhibiting differences in relative thickness between dorsal and ventral areas (Russell 1979; Russell et al. 2001). The scales of trunk patagia exhibit distinct sizes and shapes depending on their location, with the dorsal patagial scales appearing much larger and more rectangular in shape when compared to the non-patagial dorsum, or the ventral patagium and non-patagial ventral regions (Russell et al. 2001). Patagia are hypothesized to have evolved in *G. kuhli* through the accumulation of adipose tissue (Russell 1979). These enlarged lateral folds prove useful for crypsis (de Rooij 1915) and were likely co-opted for gliding behavior (Russell 1979).

Gliding also has evolved in a southeast Asian clade of *Hemidactylus* geckos (Honda et al. 1997; Grismer 2006; Bauer et al. 2010). Gliders in this lineage (*H. platyurus*, *H. craspedotus*) also exhibit membranous trunk patagia, membranous folds on the hindlimbs, as well as tail patagia. These patagia are relatively smaller than those of *G. kuhli*, but still sufficient to assist in gliding (Honda et al. 1997; Grismer 2006). Indeed, *H. platyurus* (Fig. 1) has become the most commonly studied gliding gecko in the context of biomechanics (Jusufi et al. 2008, 2011; Siddall et al. 2021a, 2021b) and has recently become the focus of studies of morphological development (Griffing et al. 2020, in press). Despite their charismatic behavior and importance in biomechanical studies, and beyond a very brief description of patagium morphology by Russell (1979), no morphological

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Figure 1. A Flat-tailed House Gecko (*Hemidactylus platyurus*) showing the patagia on the trunk, hindlimbs, and tail. Photograph by Tony Gamble.

investigations have detailed the gross morphology of any gliding structures in *H. platyurus*.

We conducted a preliminary investigation into the morphology of gliding membranes in *Hemidactylus* geckos. To determine whether convergently evolved gliding patagia differ morphologically between two evolutionary origins of gecko gliding, we investigated the external and internal anatomy of gliding structures in *H. platyurus*. We compared the patagia of *H. platyurus* with homologous regions in a closely related species (*Hemidactylus frenatus*) that does not exhibit patagia.

Methods

We acquired individuals of *Hemidactylus platyurus* commercially and collected *Hemidactylus frenatus* in Kona, Hawaii. Geckos were housed in a live-animal facility for >2 months and fed the same diet of crickets and mealworms before euthanasia. We sacrificed one adult male of each species (*H. platyurus* TG 3807 and *H. frenatus* TG 2332) following Conroy et al. (2009) and subsequently fixed them in 10% neutral-buffered formalin. Both specimens were similar in size (*H. platyurus* SVL 51.2 mm; *H. frenatus* SVL 52.6 mm). We compared areas where *H. platyurus* exhibits lateral gliding patagia (femoral region, trunk, and base of the tail) with similar regions in the non-gliding *H. frenatus* (Fig. 2). We visualized the external morphology of these regions using a Nikon SMZ 74ST stereoscope and collected measurements using Fiji v2.0.0 (Schindelin et al. 2012). We calculated average scale measurements by measuring the areas of 10 randomly selected scales from the region of interest and averaging the values. To examine internal anatomy, we excised samples of the femoral region, the trunk, and the base of the tail and decalcified them in Formical-2000™ for approximately 92 hours. We cut 8-µm thick transverse sections using a Leica CM1900 cryostat, stained sections using a Hall-Brunt Quadruple stain, modified from Hall (1986) and Kerney et al. (2009), and imaged slides using a Nikon SMZ 74ST stereoscope and a Nikon ECLIPSE Ni-E compound microscope.

Results

Patagia of Hemidactylus platyurus.—Both the trunk and femoral patagia curl ventrally, whereas the caudal patagium extends laterally without curling (Fig. 1). Scales are on average larger in the dorsal regions of the trunk and femoral patagia (Fig. 3; Table 1). Scales are on average larger in the ventral portion of the caudal patagium than the dorsal portion. At their widest points, the patagia of the trunk, femoral region, and tail extend laterally by 2.2 mm, 2.5 mm, and 2.5 mm, respectively.

The trunk, femoral, and caudal patagia are composed of epidermis, dermis, and adipose tissue (Fig. 4). In all patagia, adipose tissue is the thickest proximally and is continuously thinner toward the distal axis. The trunk and caudal patagia exhibit thicker dorsal epidermal and dermal layers compared to the ventral integumentary layers (Fig. 3). Inversely, the femoral patagium exhibits thicker ventral epidermal and dermal layers than the dorsal integumentary layers. In the trunk patagium sections, dorsal and ventral epidermis occupy 15.1% and 8.6% of the total area, respectively, dorsal and ventral dermis occupy 27.9% and 6.5% of the total area, respectively, and the adipose tissue occupies 41.9% of the total area. In the femoral patagium sections, dorsal and ventral epidermis occupy 13.9% and 17.6% of the total area, respectively, dorsal and ventral dermis occupy 17.9% and 21.2% of the total area, respectively, and the adipose tissue occupies 29.4% of the total

Table 1. Average scale measurements of *Hemidactylus platyurus* patagia of trunk, hindlimb (femoral), and tail (caudal) regions.

Region	Average area (mm^2)
Trunk patagium (dorsal)	0.0475
Trunk patagium (ventral)	0.0108
Femoral patagium (dorsal)	0.0340
Femoral patagium (ventral)	0.0108
Caudal patagium (dorsal)	0.2482
Caudal patagium (ventral)	0.3780

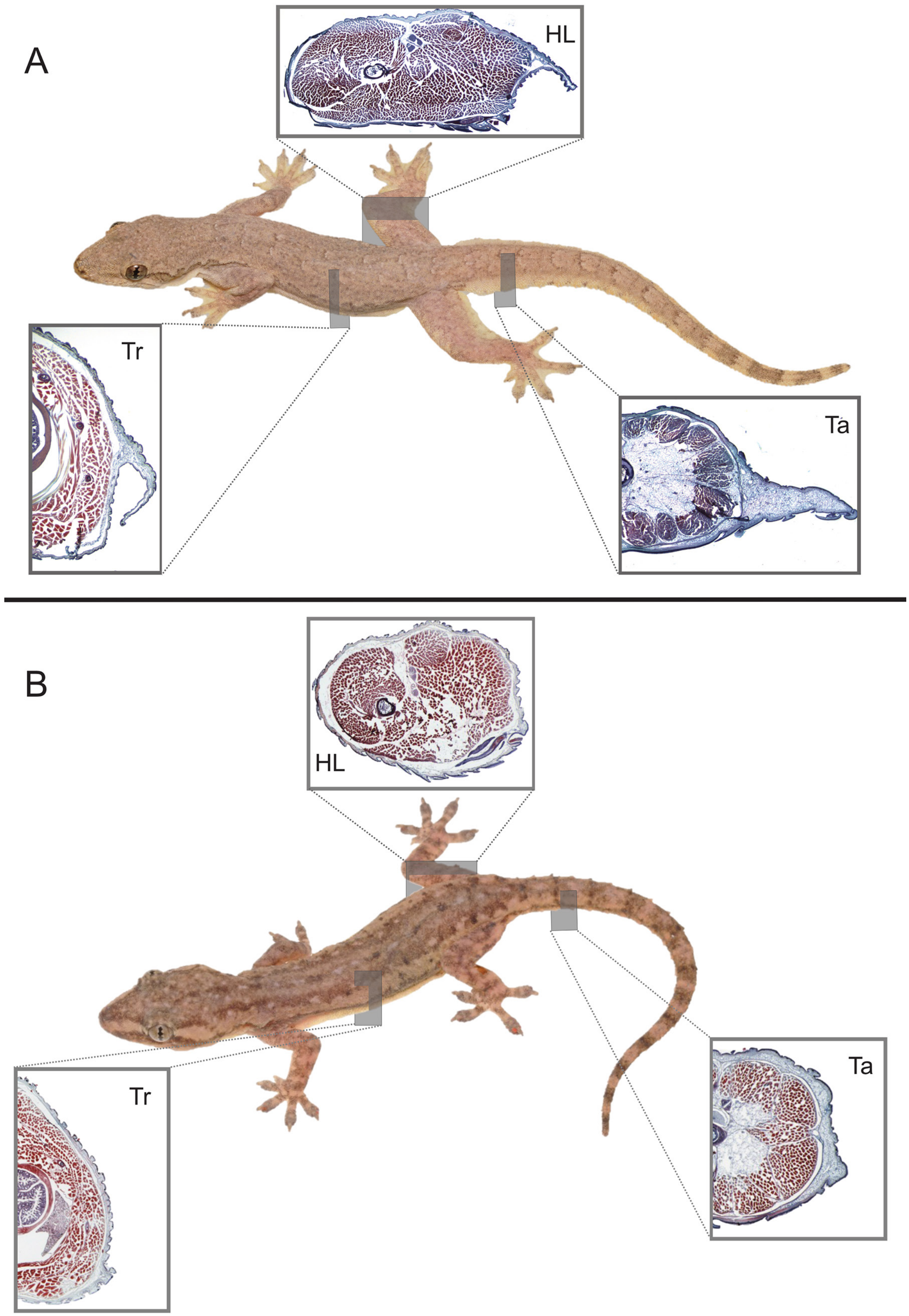

Figure 2. Overview of histology sampling in both *Hemidactylus platyurus* (A) and *Hemidactylus frenatus* (B). HL = hindlimb; Ta = tail; Tr = trunk. Photographs courtesy of Stuart Nielsen.

area. Finally, in the caudal patagium sections, dorsal and ventral epidermis occupy 8.3% and 5.8% of the total area, respectively, dorsal and ventral dermis occupy 12.9% and 5.6% of the total area, respectively, and the adipose tissue occupies 67.4% of the total area.

Homologous regions of Hemidactylus frenatus.—Beyond the presence of dorsal tubercles and caudal spines, the scales of *H. frenatus* do not differ noticeably from those of *H. platyurus* (Fig. 2). Although not noticeable from preserved specimens, histology reveals relatively small lateral outgrowths in the trunk, femoral, and caudal regions (Fig. 5). The trunk lateral outgrowth is situated more ventrally than the patagium of *H. platyurus* and exhibits adipose tissue, dermis, and epidermis, as well as loose connective tissue (Fig. 4). The femoral lateral outgrowth exhibits both dermis and epidermis, but no obvious adipose tissue is visible. The caudal lateral outgrowth, as well as the majority of the outer tissue layers of the tail, exhibit adipose tissue, dermis, and epidermis.

Discussion

Hemidactylus platyurus exhibits similar morphology in gliding structures to those of the more well studied *Gekko kuhli* (Russell et al. 2001). Both species possess patagia on their trunk, hindlimbs, and tail, with *G. kuhli* possessing additional patagia alongside the postocular region and forelimbs. Both *H. platyurus* and *G. kuhli* exhibit similar tissue composition and curving morphology. The ratio of these tissues, however, differ between the two species. In *G. kuhli* the dorsal dermis is the largest tissue layer (Russell et al. 2001), whereas in *H. platyurus* the adipose layer is the most prominent layer (Fig. 3). In *H. platyurus* the dorsal dermis is the second thickest tissue; both *G. kuhli* and *H. platyurus* have thin ventral dermis areas compared to their dorsal counterparts. The dorsal scales of the trunk patagium of *G. kuhli* were shown to be almost rectangular in shape with the ventral scales of the trunk being much smaller and more irregular and rounded in shape (Russell et al. 2001). Alternatively, *H. platyurus* exhibits very rounded and irregular dorsal trunk scales with ventral trunk

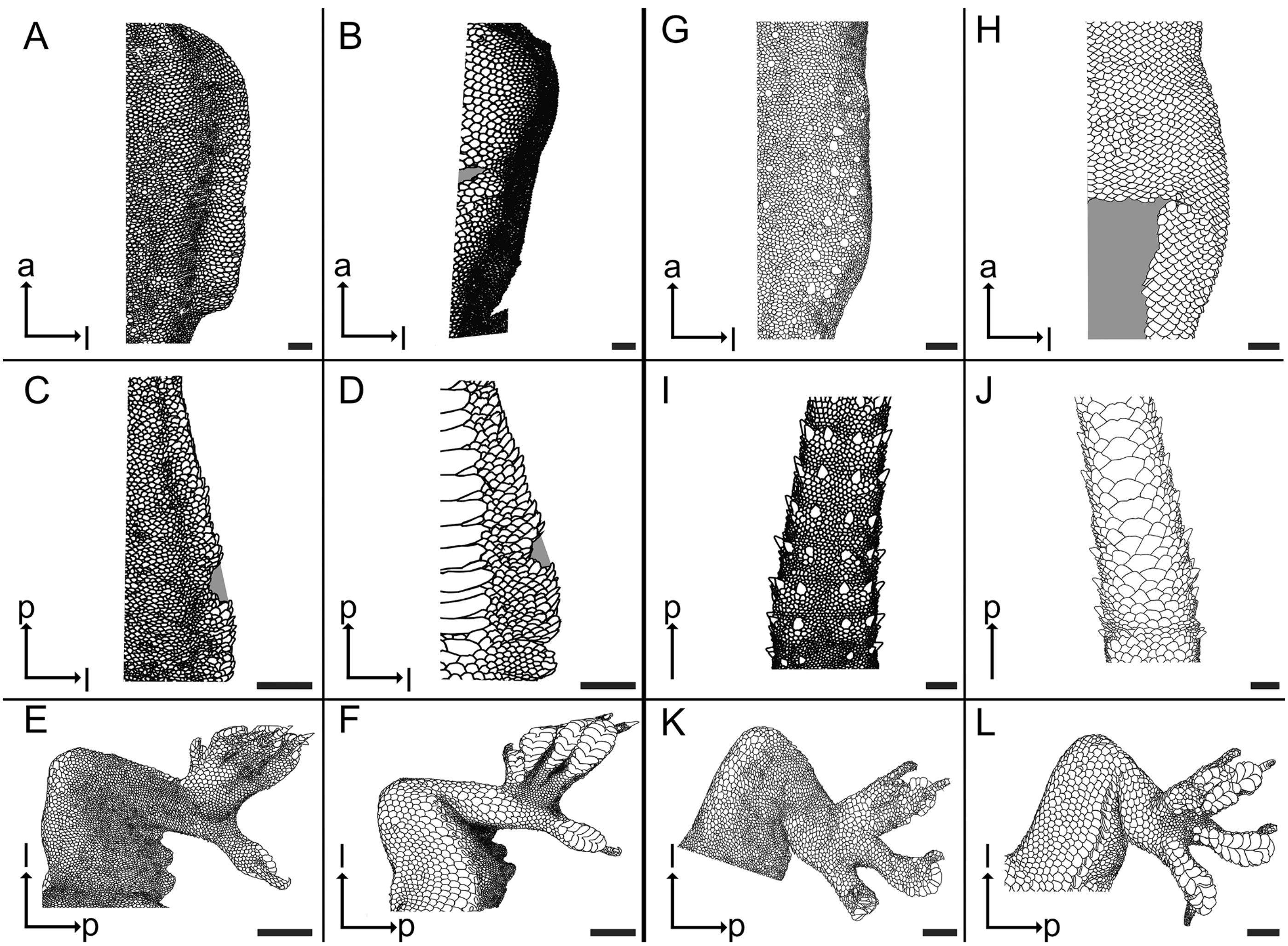

Figure 3. Illustrations of scalation in *Hemidactylus platyurus* (A–F) and *Hemidactylus frenatus* (G–L) for the trunk regions (A–B, G–H), caudal region (C–D, I–J), and femoral region (E–F, K–L). Dorsal views (A, C, E, G, I, K) and ventral views (B, D, F, H, J, L). Arrows illustrate directional planes — a = anterior; l = lateral; p = posterior. Gray regions denote areas of scale damage in the preserved specimen. Scale bars = 2 mm. Illustrations by Amber Petty.

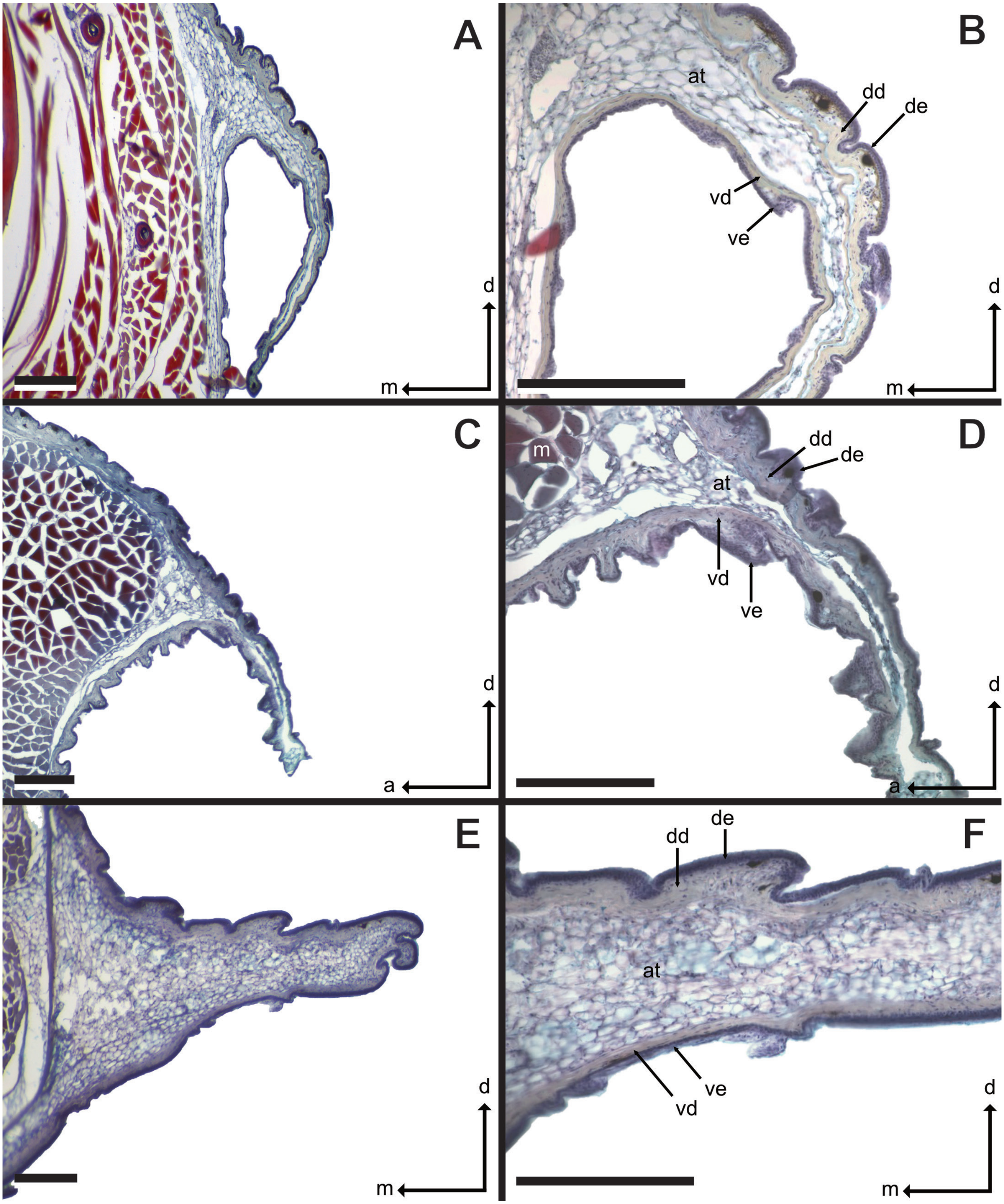

Figure 4. Hall-Brunt Quadruple-stained histological sections of *Hemidactylus platyurus* patagia. Transverse sections of the *H. platyurus* trunk patagium (A, B), femoral patagium (C, D), and tail patagium (E, F). Images at 10x (A, C, E) and 20x magnification (B, D, F). Arrows illustrate directional planes — a = anterior; d = dorsal; m = medial; at = adipose tissue; dd = dorsal dermis; de = dorsal epidermis; vd = ventral dermis; ve = ventral epidermis. Scale bars = 400 µm. Photographs by Aaron Griffing.

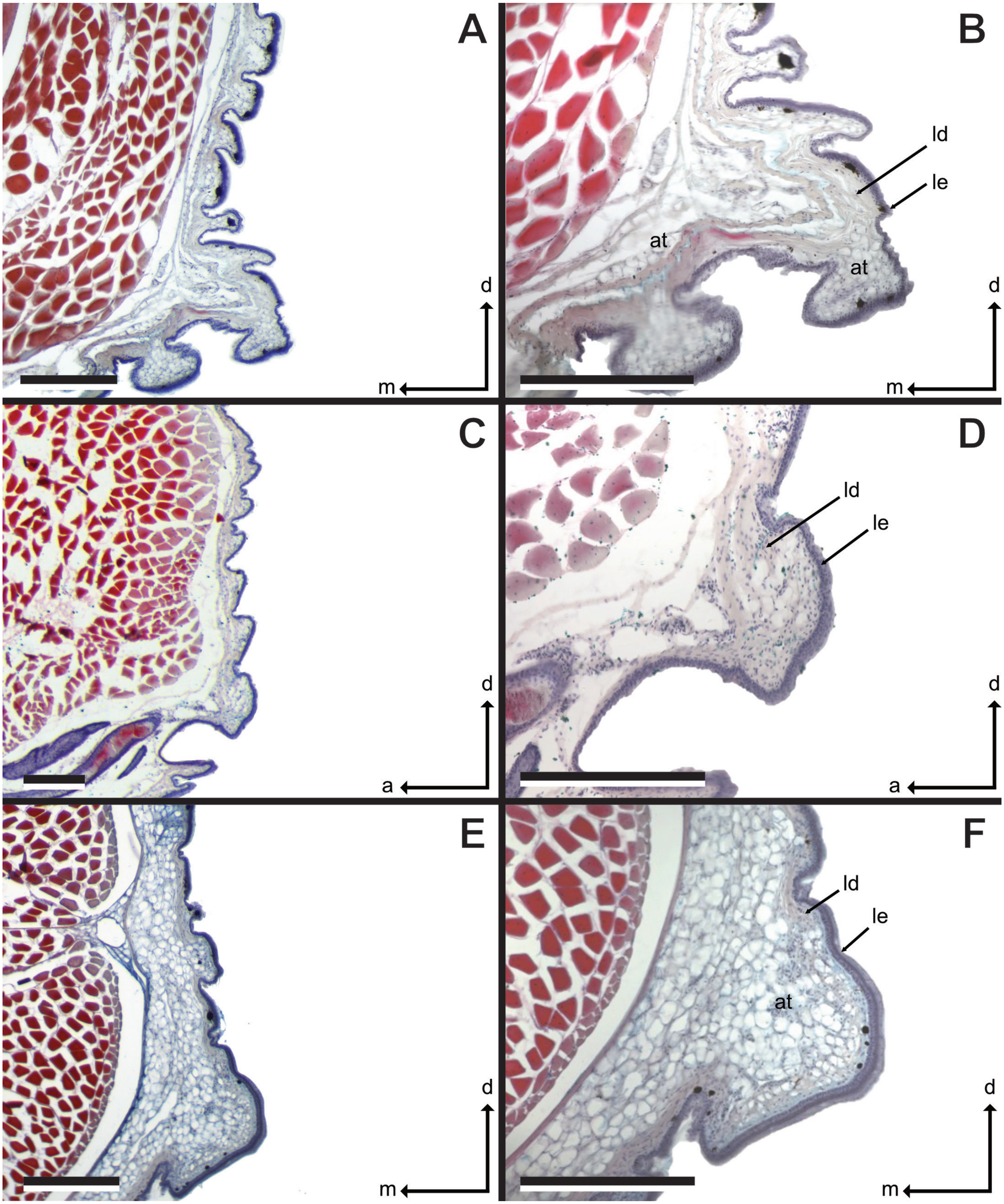

Figure 5. Hall-Brunt Quadruple-stained histological sections of *Hemidactylus frenatus* patagia-homologous regions. Transverse sections of the *H. frentatus* trunk (A, B), femoral region (C, D), and tail (E, F). Images at 10x (A, C, E) and 20x magnification (B, D, F). Arrows illustrate directional planes — a = anterior; d = dorsal; m = medial; at = adipose tissue; ld = lateral dermis; le = lateral epidermis. Scale bars = 1 mm. Photographs by Aaron Griffing.

scales similar in shape but slightly smaller. The ventral trunk scales also appear to have more space between them than those of *G. kuhli*. Patagia of gliding geckos differ substantially from other squamate and mammalian analogs. The patagia of *Draco* lizards are composed of heavily modified ribs, costal cartilage and ligaments, intercostal muscles, and very little adipose tissue (Russell and Dijkstra 2001). Unlike geckos, gliding rodents and marsupial mammals exhibit substantial striated muscle layers in their patagia (Johnson-Murray 1987; Panyutina et al. 2020). Despite these differences, the gliding patagium of scaly-tailed gliding squirrels (Anomaluridae) exhibits a thick dorsal dermal layer when compared to the ventral layer (Panyutina et al. 2020). Thick dorsal dermal layers of patagia may provide a level of rigidity required for aerial control, potentially preventing the ventral surface of the patagium from becoming convex during descent.

Hemidactylus frenatus, a close relative of *H. playturus*, lacks elaborate gliding structures. The trunk of *H. frenatus* appears to exhibit a lateral trunk outgrowth, with the same tissue components. Interestingly, the small lateral outgrowth that *H. frenatus* possesses is more ventrally oriented than the patagium of *H. platyurus*, which is almost directly in the middle of the lateral trunk. *Gekko gecko*, as well as many other non-gliding geckos with close phylogenetic affinities to *G. kuhli*, exhibit similar lateral fat deposits that have been considered patagial precursors that could later be exapted for crypsis and gliding (Russell 1979). As described herein, these parallels also are present in *Hemidactylus*, with *H. platyurus* possessing a thick layer of adipose tissue in its patagia and with *H. frenatus* also possessing thick adipose tissue on the lateral trunk. As posited by Russell (1979), accumulation of adipose tissue in the lateral regions of the trunk, tail, and limbs may underlie the evolution of gliding patagia in geckos. Although a sample size of one individual per species does not capture potential variation in gliding structures, these descriptions serve as a foundation to study comparative morphology and anatomy of gecko gliding membranes.

We observed histological similarities between two independently evolved gliding geckos (*G. kuhli* and *H. platyurus*); however, several other gecko lineages also exhibit patagia-like structures or membranous flaps used for crypsis, including but not limited to species in the genera *Thecadactylus*, *Gehyra*, *Uroplatus*, and *Luperosaurus* (Heinicke et al. 2012; Bauer and Russell. 1989). Further investigations should be conducted on other parachuting taxa, as well as those groups that evolved lateral folds for crypsis, to better understand how the convergent evolution of gliding and cryptic membranes was achieved.

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