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Left in the dust: differential effectiveness of the two alternative adhesive pad configurations in geckos (Reptilia: Gekkota)

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adhesion; anatomy; colonization; competition; invasive species; locomotion; geckos; gripping.

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Abstract

Two distinctive patterns of adhesive toepad are found in the Gekkota - terminal leaf-like pads situated at the distal ends of the digits, and basal pads that encroach more proximally along the digits, are proportionally larger and are associated with more than just the ungual and distal portion of the penultimate phalanges. Although these two configurations have long been recognized, there has been no explanation of whether or not they are functionally different. A small offshore island provided a potential arena for testing the possibility of differential functionality of these two patterns. Euleptes europaea, a leaf-padded taxon, is widespread on Giraglia Island (Corsica), whereas Tarentola mauritanica, a basally padded recent colonizer, has remained restricted to its one concrete building. Challenges to adhesion occur on dusty surfaces, and the self-cleaning mechanism of gecko setal fields can be rendered ineffective if the dust is ubiquitous. Giraglia is composed of prasinite, an inherently friable and dusty schist. The leaf-like terminal pads of E. europaea can be withdrawn from close contact with dusty surfaces, leaving the claws alone to provide traction. The digits of T. mauritanica more fully integrate the claws and adhesive pad, with full-digit hyperextension rendering the claws alone incapable of gripping the surface. Colonization of Giraglia by T. mauritanica has failed because its adhesive system is incompatible with the island's rocky terrain. This has permitted the relictual E. europaea to persist in the face of potentially intense competition. Our findings shed light on the previously noted association of leaf-like pads with rupicolous habits, and indicate that an enhanced understanding of particular surfaces that leaf-padded geckos exploit may further clarify how definitive these associations are.

Introduction

Gamble et al. (2012) concluded that the gekkotan adhesive system arose independently at least 11 times, and noted two configurations of the adhesive apparatus: leaf-like terminal adhesive pads (Fig. 1a) and the alternative pattern (unnamed by Gamble et al., 2012), referred to here as basal pads (Fig. 1b). The phylogenetic analysis of Gamble et al. (2012; fig. 1) indicates that the leaf-like configuration of adhesive plates originated independently a minimum of six times: thrice within the Gekkonidae (Gamble et al., 2012; fig. 1) (one for the clade descended from the most recent common ancestor of Goggia and Afroedura, a second for the clade descended from the most recent common ancestor of Afrogecko and Uroplatus and a third on the stem of Dixonius), and at least once in each of the Phyllodactylidae, Sphaerodactylidae and Diplodactylidae (Gamble et al., 2012; fig. 1). Similarly, at least five origins of the basal pad configuration (Fig. 1b) are evident (Gamble

et al., 2012; fig. 1): two in the Gekkonidae (in the clade descended from the most recent common ancestor of *Pachydacty-lus* and *Luperosaurus*, and on the stem of *Hemidactylus*), and minimally once in each of the Phyllodactylidae, Sphaerodactylidae and Diplodactylidae (Gamble *et al.*, 2012; fig. 1).

Although considerable attention has been paid to the functional attributes of adhesion in geckos (Dellit, 1934; Hiller, 1968; Autumn *et al.*, 2000; Russell, 2002; Autumn, 2006*a,b*; Russell & Johnson, 2007; Santos *et al.*, 2007; Autumn & Gravish, 2008; Autumn, Niewiarowski & Puthoff, 2014), little is known of why these two configurations of the adhesive apparatus exist. The multiple origins of each suggest that they differ functionally. Niewiarowski, Stark & Dhinojwala (2016) opined that our current level of understanding of gecko adhesion is now sufficient to prompt investigation of the performance consequences of variations in toepad size and shape. The current contribution explores this by examining the outcome of a natural experiment in which the two aforementioned



Figure 1 Pedal structure of the geckos inhabiting Giraglia Island, Corsica, and large-scale aspects of their habitat. (a) Right pes of Euleptes europaea in ventral view. Roman numerals I-V indicate the individual digits. The terminal, leaf-like pad, comprised of a pair of adhesive plates, is encircled at the distal end of digit III. (b) Right pes of Tarentola mauritanica in ventral view showing the extent of the basal pads (encircled on digit IV) which consist of multiple plates that extend far proximally along the digits. (c) Giraglia Island, Corsica showing the extent of the rocky prasinite outcrops along the spine of the island (the habitat of E. europaea), and its three buildings. The lighthouse (built in 1848) and tower (built in 1584) are constructed of prasinite and are situated at the northern end of the island, whereas the physical plant (built in 1950) (the only habitat of T. mauritanica on the island) is constructed of concrete and is located a little further south. (d) The physical plant building on Giraglia, with the lighthouse and the tip of the tower in the background. (e) Prasinite rock of Giraglia showing the film of dust released when a finger is dragged across it.

adhesive pad configurations are challenged by a particular type of locomotor substratum.

Russell & Bauer (1989) suggested that terminal, leaf-like adhesive pads are associated with the exploitation of rupicolous habitats, but lack of data precluded further exploration. New observations (Cole, Jones & Harris, 2005; Delaugerre, Gauthier & Leoncini, 2014) now provide potential insights. Cole *et al.* (2005) examined the possible advantages of the padless gekkonid *Nactus* on certain types of substrata in the face of invasion by the basally padded aggressive competitor Hemidactylus frenatus. Delaugerre et al. (2014) found that substratum was a key factor in inhibiting the colonization of Giraglia Island (Fig. 1c) by a basally padded gecko. Giraglia is a small (10 ha, highest point 65 m a.s.l.) island 1.4 km off the north coast of Corsica, from which it has been separated for about 5000 years (Delaugerre, 2013). The leaf-padded (Fig. 1a) western Mediterranean relictual (Delaugerre, Ouni & Nouira, 2011) sphaerodactyl gecko Euleptes europaea is native to Giraglia, and is widely distributed on its extensive rocky outcrops (Fig. 1c), upon which it forages at night (Delaugerre, 2013). It is also found in the two buildings constructed of the island's native prasinite rock. The basally padded (Fig. 1b) phyllodactylid Tarentola mauritanica arrived on the island no earlier than the 1950s. Tarentola mauritanica is known to be an aggressive colonizer elsewhere, having spread across the entirety of the Tunisian island of Galita (725 ha, highest point 391 m a.s.l.), since its first occurrence there in the 1950s (Delaugerre et al., 2014). Euleptes europaea has been extirpated from Galita (Delaugerre et al., 2011), although whether or not this is an outcome of the invasion by T. mauritanica is not known. On Giraglia, however, T. mauritanica has remained restricted to the island's only concrete structure (Fig. 1c,d), the physical plant building erected in 1950 to house the power generator for the lighthouse. Similar restriction of T. mauritanica to masonry, and its absence from local bedrock outcrops, was noted on Crete by Arad, Schwarzbaum & Werner (1997).

Experiments conducted by Delaugerre et al. (2014) revealed that E. europaea is able to move freely on vertically and horizontally oriented prasinite, and when climbing on this rock keeps its leaf-like adhesive pads curled towards the mid-line long axis of the digits (Fig. 2a,b), whereas when moving on concrete its pads are adpressed firmly to the substratum (Fig. 2c,d). In contrast, T. mauritanica kept its adhesive pads adpressed to the substratum on both concrete and prasinite vertical surfaces (Fig. 2e,f), and slipped when it attempted to run on horizontally oriented prasinite. In vertical traverses, it was effectively unable to move after a few metres had been traversed, because particles of the friable prasinite surface fouled the toepads, rendering them adhesively ineffective (Delaugerre et al., 2014), resulting in station-holding using the claws alone (Fig. 2f). A similar fouling of the basal adhesive pads of H. frenatus is reported for powdery tuff outcrops on Flat Island (253 ha) north of Mauritius (Cole et al., 2005).

Prasinite is a basaltic, crystalline metamorphic green schist with a fine-grained texture (Leardi, Rosetti & Crisci, 1986; Balatzis, 1996) that is powdery to the touch (Fig. 1e). *Euleptes europaea* occurs on outcroppings of prasinite in other areas of Corsica, whereas such surfaces are eschewed by *T. mauritanica* (Delaugerre *et al.*, 2014). To explore why this might be, we examined the structure of the digits of *E. europaea* and *T. mauritanica*, and compared our findings to those for the structure of leaf-like terminal pads and basal pads throughout the Gekkota (Russell, 1976; Data S1). In parallel, we examined the surface structure of prasinite in relation to how it might relate to adhesive toepad functioning and fouling.



Figure 2 (a) and (b) *Euleptes europaea* on a prasinite surface showing the edges of the terminal adhesive plates hyperextended away from the surface (black arrows) and the claws engaging with the surface (white circles). (c) and (d) *Euleptes europaea* on a concrete surface showing the edges of the terminal adhesive plates adpressed to the substratum (black arrows) and the claws engaging the surface (white circles). (e) Pedal digit III of *Tarentola mauritanica* attaching to a concrete surface using its claw (white circle) and adhesive pad (black bracket). (f) Pedal digit IV of *T. mauritanica* on a prasinite surface attaching by way of its claw (white circle) but with its adhesive pad bowed away from the surface (black bracket) and fouled with prasinite dust.

Materials and methods

We examined and dissected the digits of *E. europaea* and *T. mauritanica* (Data S1) to ascertain details of their anatomy that might relate to the differential ability of these two taxa to exploit the prasinite rocks of Giraglia Island. Because of their large size (see below), we also examined and dissected the digits of the phyllodactylid *Haemodracon riebeckii* and *Tarentola gigas* (Data S1). We broadened our comparative scope by studying the structure of the digits of leaf-padded gekkotans in general (Data S1), examining 4 genera of phyllodactylids (23 species, 8 of which were dissected); 10 genera of gekkonids (23 species, 11 dissected); 1 genus of sphaerodactylid (1 species, 1 dissected). The anatomy of these examples was compared

among themselves and with the anatomy of basally padded gekkotans as reported by Russell (1976).

We also examined the particulate material that is released from the surface of prasinite. Scanning electron microscope images were obtained using a Philips XL 30 SEM in the Microscopy and Imaging Facility, Cumming School of Medicine, University of Calgary. Rock specimens were mounted on aluminium stubs and coated with a 3-5 nm layer of platinum in a Technics Hummer 1 sputter coater. Colloidal graphite was applied to the junction between the specimen and the stub to enhance conductivity. Images were captured in the extra high definition (XHD) mode. Particles were also visualized by making adhesive tape (Scotch Tape®, 3M Canada, London, Ontario, Canada) peels. A strip of adhesive tape was placed, adhesive side down, onto the surface of prasinite and then lifted free, collecting the surface material released. This was examined by placing the strip of tape, adhesive surface uppermost, onto a microscope slide and viewing it with a Nikon Eclipse 50i compound microscope equipped with a Nikon DS 5Mc camera head and a DS-L1 camera control unit (Nikon Instruments, Inc., Melville, NY, USA).

Results

Digit anatomy

Anatomical details of the leaf-padded condition are reported here for the large phyllodactylid *H. riebeckii*, but the anatomy of the digits of *E. europaea* is identical to that reported for *Haemodracon* in all salient aspects. Similarly, the details of the anatomy of the digits of *T. gigas* are presented, although the structure displayed by *T. mauritanica* is identical. Descriptions are provided for the fourth digit of the pes unless otherwise stated, but the pertinent details for the adhesive apparatus remain constant between digits. Attention is paid chiefly to those muscles and tendons that relate directly to the control of the claws and the adhesive scansorial plates.

Haemodracon riebeckii (Fig. 3a) and E. europaea (Fig. 1a) bear a pair of leaf-like plates distally on each digit, with a retractable claw between them. Dissection of the dorsal (extensor) surface of the digits reveals a large flat tendon emanating from the m. extensor digitorum brevis (Fig. 3a,b) and coursing along the mid-dorsal aspect of the phalanges. At the joint between the antepenultimate and penultimate phalanges this tendon passes deep to a retinacular band and gives rise to one central and two (one preaxial and one postaxial) lateral branches (Fig. 3b). The mid-line branch continues distally to insert on the proximal end of the dorsal aspect of the ungual phalanx. The lateral branches diverge and enter the terminal leaves constituting the adhesive pad (Fig. 3a,b), fanning out and attaching broadly, by a tendinous sheath, to the region of a large shield of scales on the dorsal face of the distal end of the leaves (Fig. 3a,b).

The mm interossei dorsales give rise to tendons (lateral digital tendons) that course along the preaxial and postaxial margins of the phalanges (Fig. 3a,b). These are bound down firmly at the penultimate interphalangeal joint, but continue distally to insert, via tendinous sheets, onto the proximal half



Figure 3 Anatomy of the digits of Haemodracon riebeckii. (a) Digit III, left pes in dorsal view with the m. extensor digitorum brevis reflected, showing its tendinous insertion onto the ungual phalanx and the distal extremities of the terminal adhesive plates. (b) Dissection of the dorsal aspect of digit IV, left pes showing the tendons associated with the extensor control of the claw and leaf-like pads. (c) Dissection of the ventral aspect of digit IV, left pes showing the tendons associated with the flexor control of the claw and leaflike pads. The upper scale bar relates to panel (a) and the lower scale bar to panels (b) and (c). ahedb, accessory head of the m. extensor digitorum brevis; cbtedb, central branch of the motor tendon of the edb; cbtfdl, central branch of the motor tendon of the fdl; cts, connective tissue sheet of the edb; edb, m. extensor diaitorum brevis: id. mm. interossei dorsales: lbtedb. lateral branch of the motor tendon of the edb; lbtfdl, lateral branch of the motor tendon of the fdl; ldt, lateral digital tendon; plap, tendon from the plantar aponeurosis to the metatarsophalangeal joint capsule; mtIV, fourth metatarsal; ph1, first phalanx; rb, retinacular band; ss, dorsal shield of scales lying above the insertion of the ctsedb; tedb, motor tendon of the m. extensor digitorum brevis; tfdl, motor tendon of the m. flexor digitorum longus; tsldtid, tendinous sheet of the id from the ldt.

of the lateral borders of the adhesive plates (Fig. 3b). The bellies of neither the m. extensor digitorum brevis nor the mm. interossei dorsales extend fleshly beyond the metapodial–phalangeal joint capsules (Fig. 3a,b).

On the ventral surface the plantar aponeurosis sends a branch to the metapodial-phalangeal joint capsule of each digit (Fig. 3c), which spreads broadly across the capsule. A tendinous branch of the m. flexor digitorum longus courses midventrally along the digit and divides at the penultimate joint (Fig. 3c), sending a pair of parasagittal branches to the flexor process of the ungual phalanx and a preaxial and postaxial branch to the proximal end of the scansorial plates. Here, the latter merge with the dense connective tissue of the stratum compactum of the dermis of the ventral scansor surface. Slips of the m. flexor digital tendons on the ventral aspect of

the digit, inserting ventrolaterally onto the distal end of all phalanges proximal to the penultimate one (because of the different number of phalanges in each digit there is one such phalanx in digit II, two in digit III, three in digit IV and two in digit V of the pes). These serve to hold the proximal region of the digit flat against the substratum when the foot is plantar flexed, but they have no direct relationship with the claw or adhesive pads.

The anatomical pattern described above for *E. europaea* and *H. riebeckii* pertains in its basic details to all other species of leaf-toed gekkotans dissected (Data S1). In all of these taxa the leaf-like scansorial plates exhibit independence of control from the ungual phalanges and claws (when present), thus differing from the condition encountered in gekkotans with basally located pads (as exemplified by *T. mauritanica* – see immediately below).

Tarentola mauritanica (and T. gigas) exhibit a large basal adhesive pad beneath each digit of the manus and pes (Fig. 1b). In Tarentola, only the third and fourth digits of the manus and pes are strongly clawed (Fig. 1b), the remaining pedal digits bearing minute, essentially straight, needle-like claws and the manual ones lacking claws entirely (Khannoon, Russell & Tucker, 2015; fig. 1P). Dissection of the dorsal (extensor) surface of the digit (Fig. 4a) reveals large mm interossei dorsales that completely roof the m. extensor digitorum brevis. The interossei muscles arise not only from the lateral and medial faces of the metapodials, as they do in *Euleptes*, but also from a ligamentous band at the proximal end of the tarsus/carpus, rendering them relatively more extensive and voluminous than those of *Euleptes*. The manual interossei muscles of Tarentola are slightly less extensive proximally than are their pedal homologues. The tendinous raphe formed by the union of the preaxial and postaxial interosseal muscles of each digit is offset preaxially (Fig. 4a), the postaxial slip in each digit being the more strongly developed. Distally lateral tendinous sheets arise from the dorsal surface of the mm. interossei dorsales and spread to insert on the dorsal marginal scales subtending the scansorial plates (Fig. 4a). The midline tendon of the interossei continues distally, inserting on the proximal aspect of the dorsal surface of the ungual phalanx, with the muscles continuing fleshily almost to this point (Fig. 4a). The m. extensor digitorum brevis of each digit lies deep to the interosseal muscles (Fig. 4a), and at the metapodial-phalangeal joint gives rise to a stout motor tendon that continues along the dorsal mid-line of the phalanges to insert dorsally on the proximal end of the penultimate phalanx (Fig. 4a).

Ventrally the plantar aponeurosis of *Tarentola* sends a branch to the metapodial-phalangeal joint capsule of each digit, as in *Haemodracon* and *Euleptes* (Fig. 3c). A tendinous branch of the m. flexor digitorum longus courses mid-ventrally along each digit, inserting on the flexor process of the ungual phalanx of the heavily clawed digits (III and IV), and in the equivalent location on the minutely clawed or clawless remaining digits. Slips of the m. flexor digitorum brevis (data not shown) serve the more proximal phalanges, as they do in *Haemodracon* and *Euleptes*, and likewise have no direct relationship with the claw or adhesive pads.

As in *Gekko* (Russell, 1975), a robust pair of lateral digital tendons is present in each digit (Fig. 4b). These arise in the



Figure 4 (a) Dissection of the dorsal aspect of digit IV, left pes of *Tarentola gigas.* (b) Dissection of the lateral digital tendon system of *Gekko gecko* in dorsal view. The vertical dashed line demarcates the point at which the toepad begins to expand from the narrower base of the digit. Abbreviations as for Figure 3 except: ctsid, connective tissue sheet of the mm. interossei dorsales; ph4, fourth phalanx; tid, tendinous mid-line raphe of the mm. interossei dorsales.

same manner as those described for *Gekko* (Russell, 1975) and are associated with the metapodial–phalangeal joint capsules at the base of each digit. They are controlled by a complex network of muscular and tendinous connections within the tarsal/ carpal region, deep within the pes/manus. At the point where the pad expands (Fig. 4b), the lateral digital tendons send branches to the proximal border of each scansorial plate in turn (Fig. 4b; see also Russell, 1986 fig. 5), these merging with the dense connective tissue of the stratum compactum of the dermis of the ventral scansor surfaces (Russell, 1986).

Prasinite surface structure

Scanning electron microscopy (Fig. 5a,b) reveals that the powdery material released from the prasinite surface (Fig. 1e) consists of crystalline and other particles of various sizes, the smallest being less than 1 μ m in their largest dimension. Prasinite consists of an agglomeration of small to very small fragments (Fig. 5a), the surficial ones of which weather rapidly and are easily shed (Figs 1e and 5b). Adhesive tape peels (Fig. 5c) reveal the ease with which particles are removed, their crystalline nature and the great variety of their shapes and sizes.

Discussion

When compared to the situation in *Tarentola* (Fig. 4), there are major differences in muscular and tendinous inputs to the claws and adhesive plates of *Euleptes* (and *Haemodracon*)



Figure 5 Features of the surface of prasinite from Giraglia Island. (a) Scanning electron micrograph of the intact surface showing the array of randomly oriented components of the exfoliating debris. A hierarchy of particle shapes and sizes is evident, with many having their largest dimension between 0.5 and 5.0 μ m. (b) SEM of the dust removed from the prasinite rock surface by pressing the adhesive tape on the SEM stub onto it. Released particles exhibit the same size and shape hierarchy as depicted in (a). (c) Light microscopic image of an adhesive tape peel of the surface debris of prasinite indicating the range of size and form of the particles released. Scale bars in all three panels represent 20 μ m broken into 1 μ m sectors, as indicated by the black and white bands.

(Fig. 3). In Euleptes, the distal end of the paired adhesive pads and the claw are served by a divided m. extensor digitorum brevis tendon. The mm. interossei dorsales (via the lateral digital tendons) join with the lateral slips of the m. extensor digitorum brevis in raising the distal and lateral borders of the pads, but have no attachment to the phalanges. On the flexor surface the m. flexor digitorum longus of each digit serves the claw and the proximal ends of the leaf-like plates via a divided tendon. This arrangement permits the claws and adhesive pads to be controlled independently, consistent with the observations of Delaugerre et al. (2014). The claws can thus be engaged with the substratum in combination with the adhesive plates (Fig. 2c,d), or can be engaged when the adhesive plates are not adpressed to the substratum (Fig. 2a,b). Therefore, when conditions favouring adhesive contact are absent (as on the prasinite rock surface – Fig. 2c,d), the claws alone can be used to provide traction and assist in locomotion on inclined surfaces.

In *Tarentola*, scansor and claw release are controlled by the much more prominently developed mm. interossei dorsales, the

contraction of which results in hyperextension of the entire pad-bearing portion of the digits (Russell, 1975; Russell & Higham, 2009). Geckos with basal pads, including Tarentola (Russell & Higham, 2009), are known to operate their digits in two functional modes. On horizontal surfaces, the pad-bearing portions of the digits are maintained in a permanently hyperextended configuration, with the digit bases alone making contact with the locomotor substratum (Russell & Higham, 2009; Collins, Russell & Higham, 2015; Birn-Jeffery & Higham, 2016). On inclines (Russell & Higham, 2009), the adhesive pads are recruited and make contact with the substratum, effecting adhesive contact with surfaces that permit this. Thus, in geckos with basal pads, the claws and adhesive plates are no longer independently controllable, as a result of full digit hyperextension (as opposed to hyperextension of the scansors alone by medial curling in the leaf-pad situation). Recruitment of basal adhesive pads into the locomotor cycle is reflexively driven in association with perception of movement on inclined substrata (Russell & Higham, 2009).

On the dusty prasinite surfaces typical of the rocky outcrops of Giraglia Island, *E. europaea* is able to hold its adhesive pads free of the substratum (Delaugerre *et al.*, 2014) and deploy its claws (Fig. 2a,b), permitting attachment to, and movement upon, the rough but friable terrain, in both horizontal and inclined orientations. Contrastingly, *T. mauritanica* retains its pads in the hyperextended state on horizontal surfaces, inducing slippage (Delaugerre *et al.*, 2014) in the same manner as observed on low friction surfaces in laboratory situations (Russell & Higham, 2009). On inclines, *Tarentola* reflexively lowers its adhesive pads onto the surface, where they quickly lose their ability to effect adhesion because the setae pick up small particles (Fig. 5a,c) released from the prasinite substratum, fouling the adhesive system within a few strides (Delaugerre *et al.*, 2014).

In laboratory situations in which surface particles (microspheres) have been induced to adhere to the setae of freely moving, basally padded geckos (Hansen & Autumn, 2005; Hu et al., 2012), the setae are able to shed these onto cleaner regions of the locomotor surface within a few strides. This occurs because of an energetic disequilibrium, with the adhesive forces attracting the particles to the substrate being stronger than those attracting them to the setal spatulae. Digital hyperextension promotes the shedding of such particles (Xu et al., 2015; Niewiarowski et al., 2016). On naturally occurring surfaces, such as prasinite, that are uniformly 'dirty' and unconsolidated, the ability to shed particles from the setal tips is compromised (Johnson & Russell, 2009), resulting in the setae becoming saturated with particles sufficiently small to bond with them. The surface of the prasinite rock (Fig. 5a) exhibits a wide array of particle sizes, from those similar in diameter to the spatulate setal tips of geckos (0.1-0.2 µm) to those that would bridge across the terminal branches of many setae. The 'dirty' nature of the entire locomotor surface countermands the effects of setal self-cleaning (a phenomenon that is likely exapted from the more general hydrophobic, selfcleaning nature of the spinulate gekkotan outer epidermal surface - Hiller, 2009; Watson et al., 2015). Euleptes and Tarentola thus illustrate variation in the microhabitat-related ability

to avoid adhesive fouling exhibited by the two pad configurations.

Cole et al. (2005) found that H. frenatus, a basally padded taxon, was unable to invade the small powdery tuff rocky outcrop (0.05 ha) on Flat Island, north of Mauritius. This is the only location on Flat Island in which the padless gekkotan Nactus cf. coindemirensis has been able to resist extirpation by the invading H. frenatus. While Nactus employs its claws to gain traction on this powdery rock. Hemidactylus is unable to employ its claws alone to generate traction. Its adhesive pads become fouled by released particulate matter (Cole et al., 2005). Hemidactylus frenatus employs the same digital hyperextension cycle during locomotion (Autumn et al., 2006) as Tarentola, thus rendering it unable to avoid fouling of its adhesive system (see above). The adhesive capabilities of Hemidactylus declined more than 11-fold on the tuff rock compared to its clinging abilities on the trunks of Casuarina trees, and by over eight times compared to its abilities to cling to non-powdery basalt (Cole et al., 2005). Although Nactus lacks adhesive pads, it negotiates the powdery rocks using its claws, in a similar manner to Euleptes on Giraglia.

Our observations of the locomotor abilities of *E. europaea* and *T. mauritanica* on Giraglia provide insights about the existence of two fundamentally different configurations of the adhesive system in the Gekkota. They indicate why terminal, leaf-like pads may be particularly advantageous in certain rupicolous situations, where the ability to engage the adhesive pads may be sporadic. Such leaf-like plates allow the digits to operate adhesively on inclined surfaces when circumstances permit, but the configuration of the digits also permits attachment by the claws alone when circumstances are not conducive to adhesion, the digits in this circumstance operating in a manner similar to those of the primitively padless gecko *Nactus*.

Our knowledge of the microscopic nature of surfaces that geckos habitually move on is scanty (Niewiarowski et al., 2016). It is evident that many species of basally padded geckos also exploit rocky surfaces. The nature of such surfaces has been documented for the many rock types upon which members of the genus Rhoptropus are found (Russell & Johnson, 2014), none of which were noticeably powdery (Russell, pers. obs.). Thus, the particular features of surfaces are likely to be critical to our understanding of the relative effectiveness of different pad configurations in given situations. We predict that further cases of exclusion from surfaces as a result of incompatibility of digit configuration and substratum structure will be revealed as the finer details of distribution and habitat occupancy of geckos are examined. Closer attention to the nature of substrata (Niewiarowski et al., 2016) will enhance our understanding of the distribution of pad-bearing rupicolous geckos.

Russell (1976) discussed the multiple pathways (Bock, 1959) along which the gekkotan adhesive system has evolved, and noted that only when competitive interactions between taxa displaying different configurations occur can their potential adaptive advantages be contemplated. Giraglia Island (and Flat Island, Mauritius) presents sufficiently restricted microcosms to allow small-scale local circumstance to illuminate potential functional differences. In the almost 70 years that

T. mauritanica has been present on Giraglia, it has remained confined to the one (artificial) surface that its adhesive system can negotiate. On Flat Island, the aggressive colonizer *H. frenatus* has been precluded from totally extirpating the endemic gecko *Nactus cf. coindemirensis*, because of its inability to colonize surfaces that result in the fouling of its adhesive pads. The configuration of the adhesive pad is seemingly critical in determining what sorts of microhabitats can be occupied.

The possibility has to be allowed, of course, that the selfcleaning ability (Xu *et al.*, 2015; Niewiarowski *et al.*, 2016) of the setae of *E. europaea* is superior to that of *T. mauritanica*, thus permitting locomotion on the prasinite surface. This remains to be tested, but we suggest that this is an unlikely explanation because of the ubiquity of dust on the prasinite surface, precluding a suitable acceptor surface onto which particles can be shed. Furthermore, the friable surface would have to be able to support the weight of the gecko without shearing in the absence of claw-assisted traction. Future investigation of prasinite-contaminated setae should be able to shed light on this, as should comparison of the structure of the setae of these two species and measurement of the adhesive and frictional forces that they can generate when pristine and when contaminated.

Studies investigating setal self-cleaning in natural environments could be profitably conducted on saxicolous taxa occupying a variety of rock types that might exhibit different levels of surface contamination due to loose particulate matter. The genus *Rhoptropus*, which lacks functional claws and whose species exploit a broad array of rock types (Johnson & Russell, 2009), is a promising taxon for future exploration of this topic. Nano-scale examination of the rock surfaces employed by leaf-toed taxa would also be instructive, especially in the context of detailed observations on the co-occupancy or avoidance of such substrata by broadly sympatric basally padded taxa.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Species of geckos examined for this study.