# Chapter 9
# Solutions to a Sticky Problem: Convergence of the Adhesive Systems of Geckos and Anoles (Reptilia: Squamata)

**Anthony P. Russell and Austin M. Garner**

**Abstract** The modes and mechanisms of organismal attachment are numerous and diverse. Terrestrial vertebrates, however, achieve robust and releasable attachment to both abiotic and biotic substrata in three chief ways: hook-like anchors, such as claws, permit temporary attachment to surfaces via mechanical interlocking and/or frictional interactions with surface asperities; attachment organs releasing glandular secretions (e.g., the toe pads of hylid frogs, suction cups of disc-winged bats) achieve attachment via wet adhesion and/or suction; subdigital pads of some lineages of lizards possess filamentous outgrowths that induce friction and/or adhesion via molecular interactions. Lizards are the largest organisms to employ fibrillar-based attachment, but only the adhesive subdigital pads of geckos and anoles are sufficiently adhesively competent to support forces in excess of their body mass. The adhesive systems of geckos and anoles have long been considered convergent, but beyond general statements to this effect, convergence has not been rigorously assessed. Here we review what is known of the adhesive apparatus of both gekkotan and anoline lizards within the context of two hierarchically stratified domains: (1) adhesive attachment and the structure of setae and setal fields, and (2) the higher-order anatomical specializations that control the operation of the setae. We employ this information to identify the physical and organismic drivers of convergence of fibrillar adhesive systems, thereby enabling us to assess the particular, rather than superficially general, extent of convergence of the adhesive system of geckos and anoles.

Our synopsis of gekkotan and anoline setae, setal fields, and their adhesive systems reveals numerous physical and organismic constraints, perceived as the drivers of convergent evolution, that have led to similar morphological and functional outcomes. We posit that the setae and setal fields of geckos and anoles are

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convergent structures that enhance effective attachment to diverse substrata. Setae exhibit deep homology, arising from the convergently evolved spinulate Oberhäutchen of the epidermis. Following the initial exaptation of spinules as van der Waals adhesion-promoting setae, those of geckos and anoles followed somewhat different evolutionary pathways as the setae became organized into integrated setal fields. These pathways are reflective of differences in how the biomechanical control of the setal fields, during their application and release from the substratum, is achieved. Although anoles seemingly exhibit only a single evolutionary origin of the adhesive system, that of geckos has arisen on multiple independent occasions, with a broad range of expression of anatomical configurations that characterize the functional system. A broad survey of such configurations among geckos reveals that some are morphologically (and probably behaviorally) more similar to those of anoles than are others. Our assessment of the extent of convergence of the adhesive apparatuses of geckos and anoles identifies gekkotan taxa with an adhesive apparatus that most closely resembles that of anoles and explores what is minimally necessary to promote reversible attachment via molecular interactions. Our findings should contribute not only to ongoing investigations of the functional morphology of these adhesive systems but also should be informative to those who design biomimetic fibrillar adhesives intended to operate similarly to their natural counterparts.

## 9.1   Attachment Systems of Vertebrates and the Filament-Based Adhesion of Geckos and Anoles

The ways in which organisms attach themselves to components of their environment (both biotic and abiotic) are numerous and diverse (Nachtigall, 1974), and such attachment may be permanent or temporary and releasable. If the latter, attachment may be long-term, momentary, or anywhere in between (even for a given individual under differing circumstances). Terrestrial vertebrates employ three main ways of achieving releasable attachment, and most often, but not exclusively, it is their digits (Tornier, 1899; Nachtigall, 1974; Rosenberg & Rose, 1999) that carry the attachment devices (*sensu* Vogel, 1988). Hook-like anchors, such as claws, are widespread among amniote vertebrates (Maddin et al., 2009) and rely upon frictional interlocking interactions (Garner et al., 2017). Attachment organs employing glandular secretions, such as the "suckers" of hylid frogs (Green, 1981; Barnes et al., 2006), disc-winged bats (Wimsatt & Villa-R, 1970; Riskin & Fenton, 2001), mouse lemurs, tarsiers (Nachtigall, 1974), and feathertail gliders (Rosenberg & Rose, 1999), rely chiefly upon a combination of suction and wet adhesion. Molecular bonding via filamentous outgrowths of the integument relies upon attraction between surfaces at nano-scale separation distances and occurs in few lineages of lizards (Maderson, 1970). The latter mode of attachment is accomplished in the absence of

secretions and independently of, although perhaps cooperatively with, claws (Naylor & Higham, 2019), if present. Similar fibrillar adhesives are widely distributed amongst insect and arachnid arthropods (Home, 1816; Gorb & Beutel, 2001; Federle, 2006). In some cases this occurs in combination with glandular secretions that enhance attachment (Gorb & Beutel, 2001; Federle, 2006; Gorb, 2008) whereas in others, as for lizards, attachment is achieved via dry adhesion that relies solely upon the properties of the extremely fine tips of their filaments (Federle, 2006). Dry filamentous adhesives permit exploitation of surfaces not available to taxa without them (Russell et al., 2015: Higham et al., 2017b; Pinto et al., 2018).

Organism-surface interactions using any one of the above-mentioned methods are not necessarily mutually exclusive (Riskin & Fenton, 2001; Barnes et al., 2006; Langowski et al., 2018), but the dominant attachment mode is reflected in the overall morphology of the system.

The largest organisms to employ attachment-enhancing integumentary filaments occur in certain lineages of squamate reptiles (Arzt et al., 2003; Labonte et al., 2016). Squamate scales are characteristically covered with keratinized epidermis that provides both mechanical protection and an effective barrier against water loss (Maderson et al., 1978). The β-keratin of the outer scale surfaces is stiffer and less flexible than the α-keratin that invests the hinge region between scales (Sawyer et al., 2000; Autumn et al., 2006a). The attachment filaments of squamates are derived from β-keratin (Alibardi, 2009) that is geometrically modified such that their effective elastic modulus is lessened (Autumn et al., 2006a), promoting contact with the substratum and enhancing friction, or in some cases, inducing adhesion.

The mode and magnitude of attachment in squamates is lineage dependent. Some clades of scincid lizard effect relatively weak attachment using elaborations of the outer epidermal generation (Irschick et al., 1996). The digits and tail tip of some chameleons bear friction-enhancing (but not demonstrably adhesive) seta-like filaments (Lange, 1931; Khannoon et al., 2014; Spinner et al., 2014). Filament-dependent adhesion is most evidently expressed, both morphologically and functionally, among gekkotan and anoline (dactyloid) lizards that carry their epidermal outgrowths on modified scales (Fig. 9.1)—the scansors of geckos and lamellae of anoles (Russell & Eslinger, 2017). The adhesively competent digits of geckos and anoles (Fig. 9.1) are generally regarded as being convergent (Hagey et al., 2017), but the functional and structural extent of such convergence has not previously been detailed.

## 9.2   Review of the Gekkotan and Anoline Adhesive Systems

To explore the extent of convergence of the adhesive system exhibited by geckos and anoles (Fig. 9.1), we review what is known of the system in each clade in the context of two hierarchically-stratified domains: (1) adhesive attachment and the structure of setae and setal fields, and (2) the higher-order anatomical specializations that control their operation. In so-doing, we attempt to identify what is necessary and
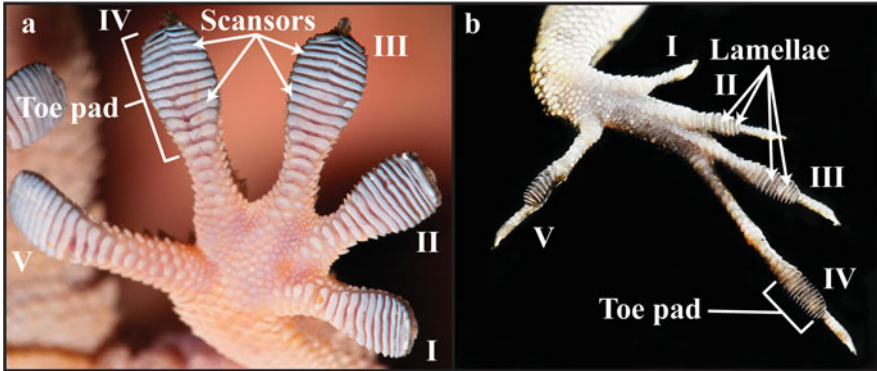
**Fig. 9.1** (**a**) Ventral view of the right pes of *Tarentola mauritanica* showing the symmetrical disposition of the digits with the toe pads arranged in a fan-like fashion and lying essentially directly adjacent to each other around a broad arc. All five digits bear a toe pad. The toe pads in this taxon extend beneath the intermediate and distal phalanges and there is no free distal portion of the digits beyond the toe pads. (**b**) Ventral view of the left pes of *Anolis sagrei* showing the staggered disposition of the toe pads, the absence of a toe pad on digit I, the free distal portions of the digits extending distal to the toe pads, and the tightly clustered bases of the first four digits, with the fifth being markedly deviant from them. Note that in both taxa the scansors/lamellae become shorter from proximal to distal along the digits. The toe pads in both taxa are elliptical, with the scansors/lamellae being widest at about the midpoint of the toe pad

sufficient for reversible, locomotor-integrated adhesion in squamates and use this to assess the extent of convergence between geckos and anoles.

### 9.2.1 Gekkotan Setae and Setal Fields

#### 9.2.1.1 Form and Variability of Gekkotan Subdigital Epidermal Outgrowths

Epidermal outgrowths of the subdigital pad surface of gekkotans vary considerably in form (Delannoy, 2005; Russell et al., 2007; Koppetsch et al., 2020). Delannoy (2005) described a morphotypic series of the epidermal outgrowths occurring on the subdigital scales of *Gekko gecko* (Fig. 9.2a): (1) true setae, outgrowths between 47.4 and 130 μm in length that are cleft into several sequential distal subdivisions, resulting in multiple branches that carry expanded, triangular, plate-like tips called spatulae, (2) seta-like outgrowths, branched fibrils with round, hook-like termini that range in length between 13.3 and 36.4 μm, (3) branched prongs with curved, rounded ends that range between 7.6 and 28.2 μm in length, and (4) hooked spines that range between 1.2 and 4.3 μm in length. The latter three may be involved in the enhancement of friction and are generally found on proximally situated lamellae, but the true setae, located on the scansors, are responsible for gekkotan adhesive attachment (Autumn et al., 2000).
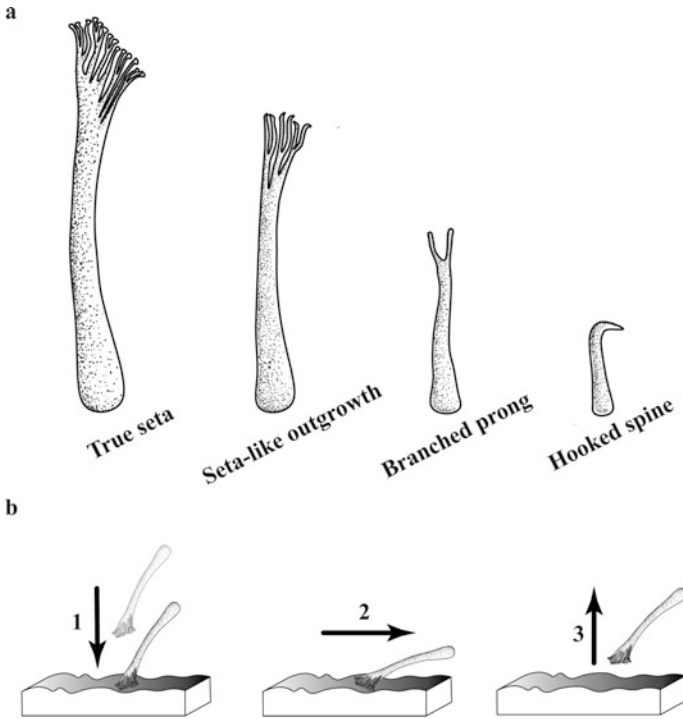
**Fig. 9.2** (**a**) The clinal series of epidermal outgrowths occurring on the subdigital scales of *Gekko gecko* [as documented by Delannoy (2005)]. True setae are multiply branched outgrowths between 47.4 and 130 μm in length that carry expanded, triangular, plate-like tips called spatulae. These are present on true scansors and are responsible for the majority of gecko attachment forces. Seta-like outgrowths are, like true setae, multiply branched filaments, but terminate in multiple rounded, hook-like tips in lieu of spatulae and are 13.3–36.4 μm in length. Branched prongs are outgrowths with curved, rounded tips and are 7.6–28.2 μm in length. Hooked spines range in length from 1.2 to 4.3 μm. Seta-like outgrowths, branched prongs, and hooked spines may enhance frictional interactions with the substratum but are not thought to contribute to the majority of gecko attachment capacity. (**b**) The attachment and detachment mechanics of isolated gekkotan setae as revealed by Autumn et al. (2000). Gekkotan setae approach a substratum at an incident angle greater than 30°. A normal (perpendicular) preload is applied to the setae, pressing its spatulae onto the surface of the substratum (1). A shear (parallel) load is then applied, reorienting the triangular-shaped faces of the spatulae to make intimate contact with the surface, promoting the induction of van der Waals intermolecular forces. The shear load also results in the depression of the setal shaft angle to below 30° (2). Setal shafts are raised beyond 30°, at which point the spatulae detach from the surface of the substratum (3)

The term "seta" has historically been reserved for the elaborations of the squamate spinulate Oberhäutchen that carry expanded, spatulate tips capable of inducing adhesion (e.g., Ruibal & Ernst, 1965; Ruibal, 1968; Williams & Peterson, 1982; Peterson, 1983a, b). A recent study (Koppetsch et al., 2020), however, introduced an alternative definition of "setae" that encompassed all filaments constituting the spinulate outer epidermal generation. This stands in opposition to the extensive

literature describing epidermal micro-ornamentation of squamates (e.g., Lange, 1931; Ruibal, 1968; Maderson, 1970; Stewart and Daniel, 1972; Peterson, 1983a, b) and makes no distinction between outgrowths that vary considerably in form and function. It essentially simply describes epidermal outgrowths as being unbranched or branched, and terminology for this is already recognized by more conventional nomenclature (e.g., branched prongs, see Fig. 9.2). We continue with the more conventional and broadly understood definition of "setae" that restricts its usage to filaments carrying expanded, spatulate tips capable of inducing adhesion (Ruibal & Ernst, 1965; Ruibal, 1968; Williams & Peterson, 1982; Peterson, 1983a, b; Autumn et al., 2002).

### 9.2.1.2 Adhesion Mechanics and Properties of Individual Gekkotan Setae

To generate reliable and reversible adhesion by means of van der Waals intermolecular forces, setal tips must be able to make and break intimate contact with the substratum (Autumn et al., 2002). Setae, in their default, unengaged state, rest at angles greater than 30° relative to the plane of the epidermal surface of the scansor, with their spatulae randomly arranged (Fig. 9.2b) (Autumn et al., 2000; Autumn & Hansen, 2006). As the setae are brought into contact with the sub-stratum's surface, a normal (perpendicular) load presses the setal tips onto the surface (Fig. 9.2b). Subsequent application of a shear (parallel) load reorients the randomly arranged spatulae so that their expanded, triangular-shaped faces are placed into intimate contact with the surface, inducing van der Waals intermolecular forces (Fig. 9.2b) (Autumn et al., 2000, 2002; Autumn & Peattie, 2002). The normal and shear forces depress the setae to angles below 30°, which theoretically increases the adhesive force potential (Kendall, 1975; Autumn et al., 2000). Setal detachment occurs when the shear load is relaxed and the setal shaft angle is increased to at least 30°, at which point spatulae detach from the surface likely resulting from stress concentrations at the trailing edge of the spatulae (Fig. 9.2b) (Autumn et al., 2000; Autumn & Peattie, 2002).

The hierarchical structure of gekkotan setae (their subdivision into branches and the carriage of multiple spatulae) has been hypothesized to improve adhesion capacity (Peattie & Full, 2007; Murphy et al., 2009; Garner et al., 2021). Contact splitting (the subdivision of an adhesive area into many smaller adhesive contacts) was initially advanced to describe the benefit that accrues from breaking down an adhesive organ into many fibrils rather than it consisting of a single contact (e.g., one soft pad). The Johnson-Kendall-Roberts (JKR) theory of elastic contact predicts that the overall adhesive pull-off force is increased relative to a single contact when contact splitting occurs (Arzt et al., 2003). The adhesive pads of gekkotans are broken up into smaller, denser setae, with these, in turn, being subdivided into smaller, denser spatulae. In light of this, some authors (Peattie & Full, 2007) have hypothesized that geckos reap the benefits of contact splitting at two levels (via subdivision of the pad and the setae). Based on the theory of contact splitting, the

subdivision of setae into multiple, smaller spatulae should increase the adhesive force potential compared to unbranched fibrils of similar dimensions (Garner et al., 2021). This prediction has been validated for synthetic fibrillar systems (e.g., Murphy et al., 2009). Structural hierarchy of setae may also reduce the potential for the formation of cracks, allowing the spatulae to detach uniformly (flaw tolerance) (Yao & Gao, 2006), and may allow for robust adhesion because for a branched fibril adhesive failure of a single tip is unlikely to impact adhesion of the entire fibril (Arzt et al., 2003; Peressadko & Gorb, 2004).

The form of gekkotan setae thus endows them with many properties that enhance their function in unpredictable and challenging environments. They are self-cleaning—when incapacitated by particulate matter (e.g., dust, sand) they can be passively cleaned by contacting a surface free of additional contaminants, whereby the energy imbalance between the substratum and the spatulae on one hand and the particle and substratum on the other, results in the shedding of the particle to the substratum (Hansen & Autumn, 2005). The efficacy of self-cleaning is actively enhanced by the disengagement of the setae from the substratum during subdigital pad peeling (mechanisms discussed later), whereupon the release of sufficient stored elastic energy propels particulate matter from the setal array (Hu et al., 2012). Structural hierarchy has also been suggested to improve adhesion to unpredictably rough and undulant substrata by increasing conformation to surface asperities (Persson, 2003; Bhushan et al., 2006; Kim & Bhushan, 2007).

### 9.2.1.3   Configuration of Gekkotan Setal Fields

Gekkotan setae are clustered in groups of four (tetrads) that form clearly distinguishable rows (proximodistally) and ranks (mediolaterally) on the scansors (Fig. 9.3a, b) (Ruibal & Ernst, 1965; Delannoy, 2005). The tetrads are uniformly spaced apart (Fig. 9.3a) with the branched distal tips (Fig. 9.3b) filling the spaces evident at their bases (Fig. 9.3b). The presence of tetrads and the organization of the setal arrays, however, varies depending upon the scansor on which they are carried (Delannoy, 2005). Many studies of the mechanics of individual setae describe setal dimensions as if they are invariant, but for any species there is seemingly no typical seta. Instead, setal characteristics (and form) vary predictably along the proximodistal axis of gekkotan subdigital pads (Fig. 9.4) (Delannoy, 2005; Russell et al., 2007; Johnson & Russell, 2009; Russell & Johnson, 2014). In general, the length of gekkotan setae increases proximodistally both within and between scansors (Fig. 9.4). Within scansors, setal basal diameter decreases proximodistally (Fig. 9.4). Such variation in setal length and basal diameter effectively results in setae with greater flexibility distally because of their higher aspect ratio. Scansor length (Fig. 9.1a) and the number of setal rows, however, decrease proximodistally (Fig. 9.4). Overall, setal density is greatest on the proximalmost scansors of the subdigital pad, but within the confines of individual scansors density increases proximodistally (except for the proximalmost scansors) (Fig. 9.4). This patterning of setal morphometrics is consistent across several genera of gekkotans and suggests that such variability is integral
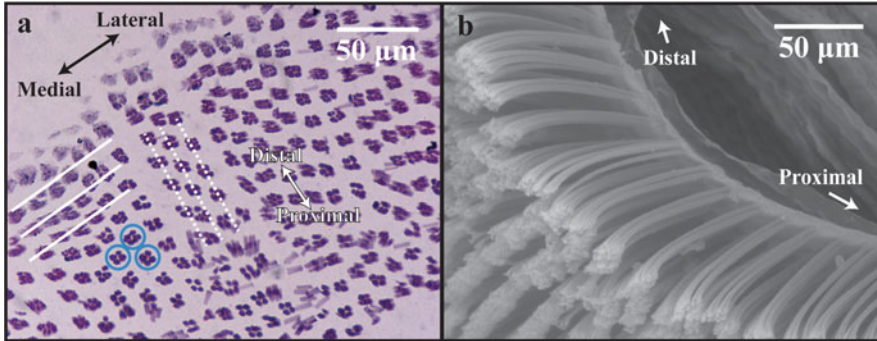
**Fig. 9.3** Arrangement of the setae on the scansors of *Gekko gecko*. (**a**) Frontal section through the setal stalks close to their bases on a distal scansor of digit III, right manus. Section cut at 10 μm and stained with haematoxylin. The setal stalks are arranged in tetrads (outlined by blue circles) and are arrayed in rows proximodistally (indicated by dashed white lines connecting tetrads) and ranks mediolaterally (indicated by solid white lines connecting tetrads). The spacing between tetrads is approximately equal proximodistally and mediolaterally. (**b**) Scanning electron micrograph of a longitudinal section through a distal scansor of digit IV, left pes. This section cuts a transect along a single row of setae and shows the increasing length of the setae from proximal to distal along the scansor. The equidistant spacing between tetrads of fibrils is evident at their bases and the branching of the setae into a plethora of spatulate tips is evident towards their free ends. Extending into the plane of the picture are distinct ranks of setae that are aligned mediolaterally across the width of the scansor
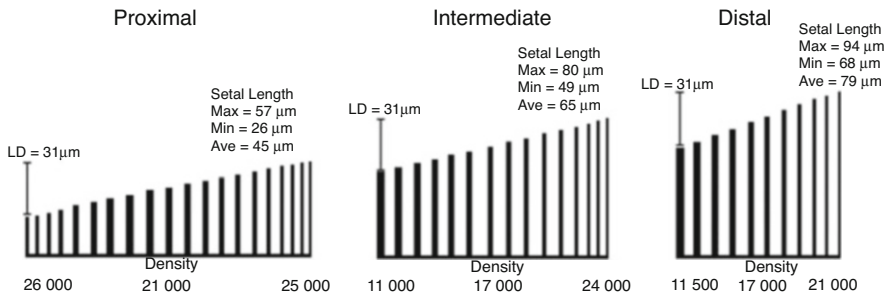


**Fig. 9.4** Proximodistal variation in setal morphometrics of *Rhoptropus* geckos [data from Johnson and Russell (2009)]. Setal length increases proximodistally within and between scansors, whereas setal base diameter decreases proximodistally within scansors. Scansor length decreases proximodistally. Setal density is greatest on the proximal scansors of the subdigital pad. Within the confines of individual scansors, setal density increases proximodistally (except for the most proximal scansors). The discrepancy between the maximum and minimum length of setae on any given scansor remains constant (LD=31 μm)

to the effective operation of the integrated setal fields (Johnson & Russell, 2009). For effective attachment and detachment of the setal arrays, interference of individual setae should be minimized and the variability in setal length (Fig. 9.4) may allow for this (Johnson & Russell, 2009).

### 9.2.1.4 Attachment and Properties of Gekkotan Setal Arrays

Arrangement of setae into setal fields leads to a number of emergent properties beyond those of individual setae. The hydrophobic nature of the phospholipid coating of gekkotan setae (Alibardi et al., 2011; Hsu et al., 2012), in addition to the surface roughness of the closely packed hierarchical fibers (Fig. 9.3b), results in superhydrophobicity (strong water-repellence) of the setal field (Fig. 9.5a) (Pesika et al., 2009). This is critical for adhesion of the subdigital pads to wet, hydrophobic substrata, since dry contact is effected through expulsion of water from the contact interface (Stark et al., 2013). This state, however, is metastable; the subdigital pad's surface can transition to a hydrophilic wetting state under some conditions (Fig. 9.5b) which can reduce adhesion by interfering with the intimate contact needed to sustain van der Waals interactions (Stark et al., 2012). Much like the self-cleaning capability of gecko setae and setal arrays, geckos taking steps on clean, dry substrata can rapidly dry their subdigital pads by shedding water to the substratum and thus regaining maximum adhesive capacity and the subdigital pad's innate superhydrophobic state (Stark et al., 2014; Garner et al., 2019b).

In many gekkotans with well-developed subdigital pads, detachment of the setal fields occurs by distoproximal hyperextension of the digits driven by contraction of the interossei dorsales muscles (Russell, 1975). Other taxa with adhesively competent digits, but with less well-elaborated toe pads, employ the ancestral lacertilian pattern of digital roll-off whereby the digits are raised proximodistally onto their tips (Russell et al., 2015; Higham et al., 2017a, b; Russell & Gamble, 2019) and hyperextended in this fashion. Peeling of the subdigital pad, either distoproximally or proximodistally, is thought to raise the setal shaft angles to above 30°, resulting in
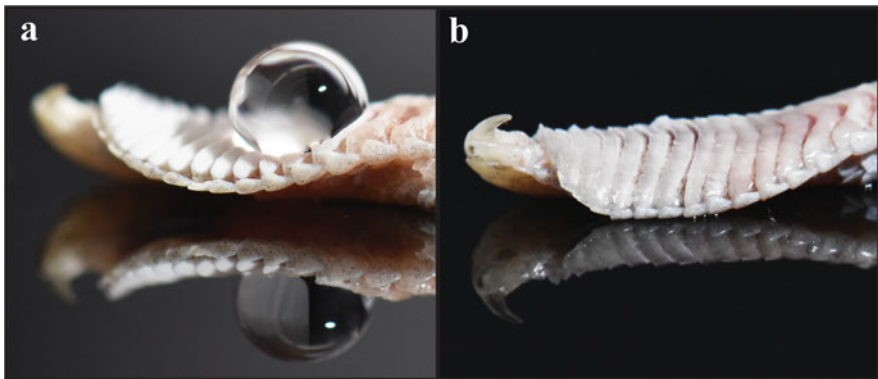


**Fig. 9.5** (**a**) The superhydrophobicity (strong water-repellence) of *Gekko gecko* setal arrays. This property allows geckos to adhere underwater or to wet surfaces when the substratum is hydrophobic (Stark et al., 2013). Water contact angles of pristine setal arrays are generally greater than that observed in the image; water droplets often roll-off the setal arrays immediately after placement (this subdigital pad was only partially wetted to permit the water droplet to remain in place). (**b**) The superhydrophobic nature of gekkotan setal arrays is a meta-stable state; setal arrays can transition to a hydrophilic wetting state under certain circumstances (Stark et al., 2012)

the release of the spatulae from the substratum (Autumn et al., 2000; Autumn & Peattie, 2002). Step-like variation in setal length (Figs. 9.3b and 9.4) permits all the setae on a single scansor to reach the critical detachment angle simultaneously, resulting in the instantaneous release of the entire scansor (Johnson & Russell, 2009). Contraction of the digital flexor muscles results in proximodistal unfurling of the subdigital pad onto the substratum's surface, driving the setae and their spatulae into contact (Fig. 9.2b) (Russell, 1975) and contributing the normal and shear displacements critical for spatular attachment (Autumn & Peattie, 2002; Russell, 2002).

Most studies of the attachment capabilities of the gekkotan adhesive system (and that of *Anolis*) have been conducted using relatively smooth substrata (e.g., glass, acrylic) (Niewiarowski et al., 2016). Real-world substrata utilized by free-ranging gekkotans, however, likely vary in surface roughness across multiple length scales (Higham et al., 2019; Niewiarowski et al., 2019). Studies of uniform, elastic materials in contact with rough substrata reveal a dependence of adhesion on the material properties of the adhesive (e.g., elastic modulus); pressure-sensitive adhesives with low elastic modulus are capable of better deforming to accommodate to surface asperities, increasing the apparent contact area and subsequent adhesive force (Fuller & Tabor, 1975). Although gekkotan setae are composed of β-keratin, which has a bulk elastic modulus of about 1–3 GPa (Autumn et al., 2006a), the high aspect ratio of the fibrils (Fig. 9.4) results in a lowering of the effective elastic modulus (Autumn et al., 2006a) to that falling within the range of pressure-sensitive adhesives (e.g., Sylgard 184, polydimethylsiloxane; Khanafer et al., 2008; Bartlett et al., 2012). The low effective elastic modulus of gekkotan setal arrays, and the presence of structural hierarchy, promote the ability to conform to rough substrata (Persson, 2003). Furthermore, the patterning of setal length along the proximodistal axis of gekkotan subdigital pads (Fig. 9.4) provides the potential for allowing adhesion to be maintained on substrata that vary unpredictably in surface roughness (Johnson & Russell, 2009).

The results of studies detailing the form and function of gekkotan setae and setal arrays furnishes information that allows us to assess the extent of convergence exhibited independently by their anoline counterparts. Since these structures depend upon governance mechanisms to be effective, however, we must also consider the structure of the adhesive system that carries them to fully appreciate the level of fidelity of convergence.

## 9.2.2 The Gekkotan Adhesive System

### 9.2.2.1 General Characteristics

Although often subsumed under the simplified umbrella term "toe pads" (Fig. 9.1a) (Liu et al., 2015; Hagey et al., 2017; Harrington & Reeder, 2017), there are many variants of the anatomical composition of the adhesive apparatus among geckos

(Russell & Gamble, 2019: Table 1). The functional adaptive complex (Russell, 1976) constituting adhesive toe pads has arisen independently on multiple occasions within the Gekkota (Gamble et al., 2012, 2017; Russell & Delaugerre, 2017; Russell & Gamble, 2019). The attributes of the adhesion mechanics of setae (see above) have thus been integrated with anatomical systems of varying configuration that control their application and release.

The structure of the gekkotan adhesive apparatus has been most extensively studied for the Tokay gecko (*Gekko gecko*) (Russell, 1975). Russell (2002) documented many of the hierarchically integrated mechanical units (*sensu* Gans, 1969) of its digital adhesive apparatus and discussed how these are coordinated to bring about effective substratum contact and release of the setal arrays. Lauff et al. (1993) provided information about cutaneous sensilla on the Tokay's digits, thereby indicating how sensory feedback is inculcated into the operation of the adhesive apparatus.

Russell and Gamble (2019) mapped 34 digital characters and their states onto a well-supported, time-calibrated phylogeny of the Gekkota, and analyzed combinations of features that characterize the hierarchical structure of the adhesive system across all gekkotan families (except for the limbless pygopodids). Complimentarily, Russell et al. (2015) and Higham et al. (2017b) investigated evolutionary transitions from adhesively non-competent to adhesively competent digits in geckos, indicating that such a shift requires only relatively minor alterations of epidermal filament form, scale structure, digit proportions, and phalangeal morphology (Fig. 9.6a–c). These studies established that many of the features characterizing the structurally more complex adhesive pads of geckos, such as *Gekko gecko*, are not necessary for the establishment of adhesive competency. Occurrences of incipient toe pads (Russell, 1976; Gamble et al., 2012; Russell & Gamble, 2019) in various gekkotan taxa corroborate the hypothesis that the transition to adhesive competency has occurred independently many times within the Gekkota and provides the necessary information for establishing the assembly rules (Zweers, 1979; Haefner, 1988) minimally necessary and sufficient for the deployment of reversible adhesion in geckos. Such data also provide us with the context for determining to what degree the independently-evolved adhesive system of *Anolis* has converged upon that of geckos.

### 9.2.2.2  Selection of an Appropriate Gekkotan Model for Comparison with Anolis

Russell and Gamble (2019: Table 1) detailed modifications of skeletal, compliance-related, tendinous and muscular features associated with the gekkotan adhesive system. These were shown to be numerous for the Tokay gecko (*Gekko gecko*) and its relatives. Contrastingly, Russell and Gamble (2019: Table 1) noted that the incipient adhesive pads of *Gonatodes humeralis* (Fig. 9.6a–c; Russell et al., 2015; Higham et al., 2017b) express few such anatomical modifications, these being mostly associated with the phalanges. Compared to its congeners, *G. humeralis*
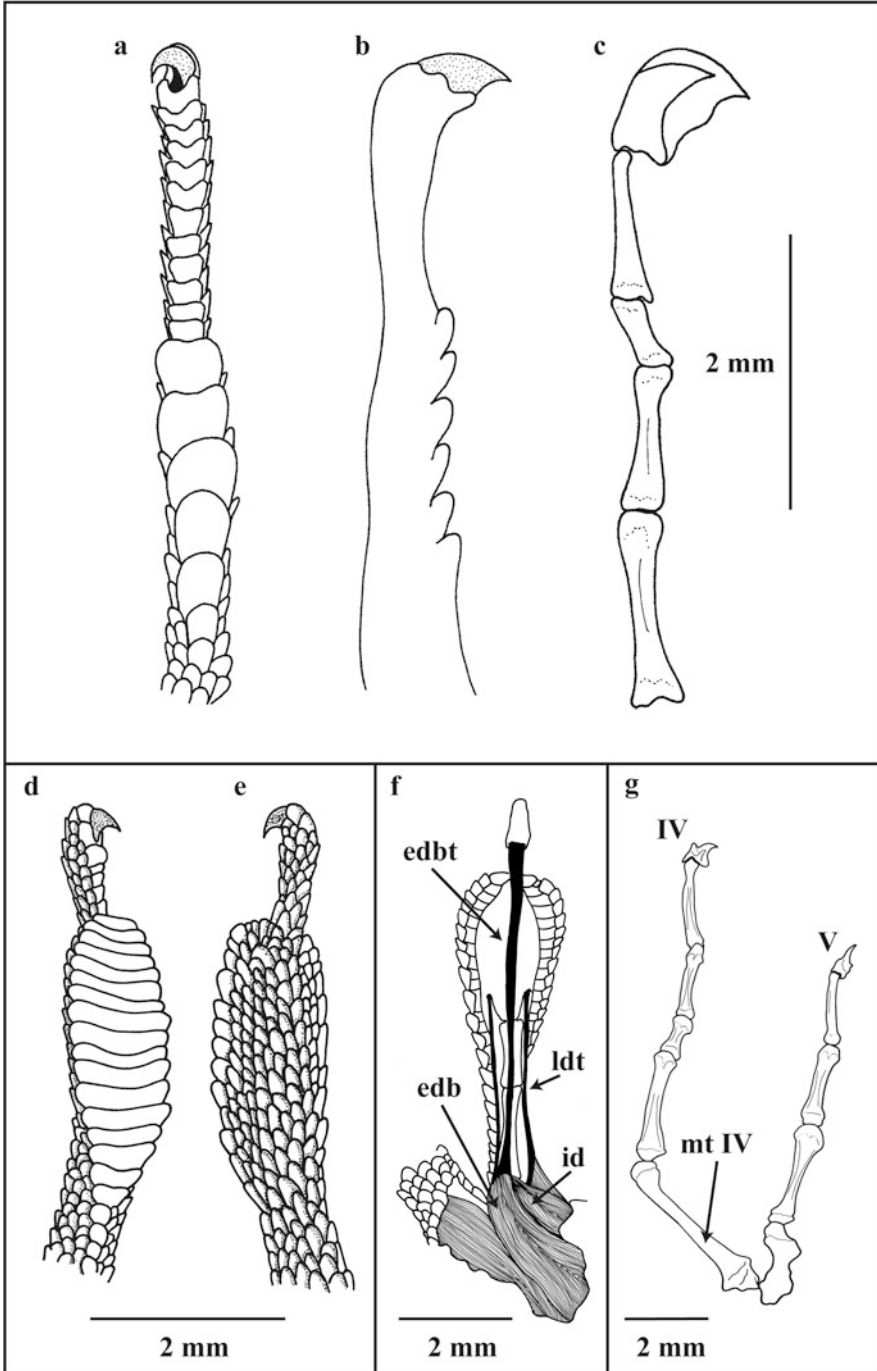
**Fig. 9.6** (**a**) Ventral aspect of digit IV, right pes (Natural History Museum, London BMNH 1971.1047); (**b**) lateral profile of digit IV, left pes (BMNH 1971.1049); and (**c**) lateral view of the skeleton of digit IV, right pes (BMNH 1971.1049) of the sphaerodactylid gekkotan *Gonatodes*

exhibits additional subtle changes of digit proportions, phalangeal orientation, patterns of scalation and epidermal micro-ornamentation, with setae being present in the region of the incipient toe pads (Russell et al., 2015). Collectively the modified features of *G. humeralis* enable adhesion-based locomotion on smooth, low-friction vertical surfaces (Higham et al., 2017a, b) while using ancestral (Brinkman, 1980; Rewcastle, 1980, 1983) locomotor digital kinematics. Its adhesively-competent digits are detached by proximal-to-distal digital hyperextension, rather than the distal-to-proximal hyperextension pattern typically associated with gekkotan adhesive release (Autumn, 2006).

*Gonatodes humeralis*, although adhesively competent, lacks conspicuously obvious subdigital toe pads (Fig. 9.6a, b) and lacks lateral digital tendons (Russell, 1986), features that are clearly evident in *Anolis* (Russell & Gamble, 2019: Table 1). Among basally-padded geckos (Russell & Gamble, 2019: Table 1) the least complex manifestation of visibly recognizable toe pads is encountered in the *Aristelliger* lineage of the Sphaerodactylidae (Fig. 9.6d–g). Beyond the changes documented above for *G. humeralis*, *Aristelliger* possesses an arcuate penultimate phalanx that carries the distal part of the digit beyond and above the toe pad and provides the ungual phalanx and claw with a steep angle of attack relative to the substratum (Fig. 9.6d–g). *Aristelliger* has a subphalangeal cushioning structure in the form of a central vascular sinus and reticular networks that permeate the proximal regions of the scansors (Russell, 1981). It also has prominent lateral digital tendons (Russell, 1986) (Fig. 9.6f) that merge directly with the stratum compactum of the dermis of the scansors. The bellies of the dorsal interossei muscles do not extend beyond the metapodial-phalangeal joint capsules (Fig. 9.6f), and their insertion tendon does not extend along the digit in the fashion seen in *Gekko* and many other pad-bearing geckos (Fig. 9.7). *Aristelliger* thus appears to lack a mechanism for distal-to-proximal digital hyperextension (Russell, 2002). Setal structure in *Aristelliger* (Ruibal & Ernst, 1965) is relatively simple by gecko standards. Compared to the *Luperosaurus-Gekko* lineage (Russell & Gamble, 2019: Table 1), which includes *Gekko gecko* (Fig. 9.7a), anatomical modifications associated with the operation of

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**Fig. 9.6** (continued) *humeralis*. These panels show the enlarged plates (**a** and **b**) beneath the intermediate region of the digit that bear adhesively-competent setae and the modified phalangeal structure (**c**) related to a flattening of the proximal region of the digit associated with the location of the adhesively-competent enlarged scales. (**d**–**g**) Subdigital pad structure in the sphaerodactylid gekkotan genus *Aristelliger*. (**d**) and (**e**) The ventral and dorsal aspects, respectively, of digit IV, left pes of *Aristelliger lar* showing the expanded subdigital adhesive pad occupying the basal region of the digit and the free distal portion, bearing the terminal claw, extending beyond the toe pad. (**f**) Dorsal view of digit IV left pes of *Aristelliger lar* dissected to reveal the extent of the musculature and tendons associated with the control of the adhesive apparatus. (**g**) Dorsal view of the skeleton of digits IV and V of the right pes of *Aristelliger praesignis* (drawn from an Alizarin-stained preparation) showing the elongate proximal phalanges, the modified intermediate phalanges associated with the toe pads, and the penultimate and ungual phalanges supporting the free distal portion of the digit that extends beyond the toe pad. *edb* extensor digitorum brevis muscle, *edbt* tendon of the extensor digitorum brevis muscle, *id* interossei dorsalis muscle, *ldt* lateral digital tendon, *mt IV and V* fourth and fifth metatarsals, *IV and V* digits IV and V
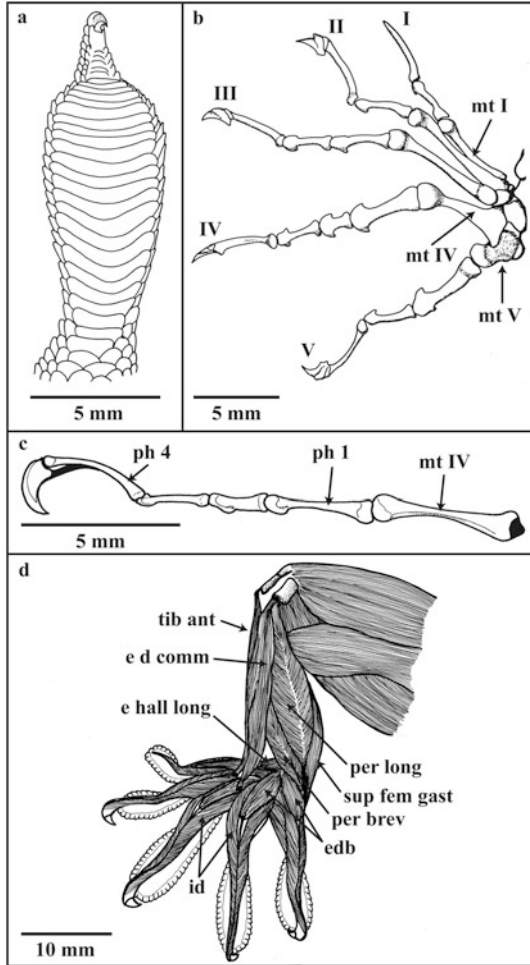
**Fig. 9.7** Digit structure in the gekkonid gekkotan genus *Gekko*. (**a**) Ventral aspect of digit IV, right pes of *Gekko smithii* (Natural History Museum, London BMNH 91.8.29.23) showing the extensive toe pad that encroaches far distally along the digit. (**b**) Dorsal aspect of the skeleton of the right pes of *Gekko gecko* (drawn from an Alizarin-stained preparation) showing the modified, short, depressed phalanges associated with the more proximal parts of the toe pads and the elongated penultimate phalanges of digits II–V that are enveloped within the confines of the toe pads, with only the ungual phalanges extending beyond the pad (see panel **d**). Note the unusual phalangeal structure of digit I, in which the ungual phalanx does not carry a claw but is instead elongated to support the toe pad on this digit. (**c**) Medial aspect of the articulated skeleton of digit IV, right pes of *Gekko gecko* (BMNH 1910.4.26.14A) showing the depressed and shortened intermediate phalanges and the strongly arched penultimate phalanx (ph4). (**d**) Superficial musculature of the left crus and pes of *Gekko gecko* showing the incursion of muscle bellies along the length of the digits as far distally as the ungual phalanx. *edb* extensor digitorum brevis muscle, *e d comm* extensor digitorum communis muscle, *e hall long* extensor hallucis longus muscle, *id* interossei dorsalis muscle, *mt I, IV, V* first, fourth and fifth metatarsals, *per brev* peroneus brevis muscle, *per long* peroneus longus muscle, *ph1, ph4* first and fourth phalanges, *sup fem gast* superficial femoral gastrocnemius muscle, *tib ant* tibialis anterior muscle, *I, V* digits I and V

the toe pads are much less extensive in *Aristelliger*. The digital patterns expressed by *Gonatodes humeralis*, *Aristelliger*, and *Gekko*, together with other expressions of anatomical modification documented by Russell and Gamble (2019: Table 1) provide comparative information appropriate for assessing the extent of anatomical convergence between the variously expressed adhesive system of geckos and that of anoles.

### 9.2.3 Anoline Setae and Setal Fields

#### 9.2.3.1 Anoline Setal Form and Variability

Not surprisingly, the epidermal outgrowths of the subdigital pads of *Anolis* also vary considerably in form. Peterson and Williams (1981) described a morphotypic series of epidermal outgrowths of *Anolis* (Fig. 9.8a), which ultimately led to similar observations in gekkotans by Delannoy (2005). Five morphotypes were identified by Peterson and Williams (1981): (1) true setae, outgrowths 10–30 µm in length with expanded, spatulate tips, (2) seta-prong intermediates, outgrowths 5–20 µm in length with flattened tips, (3) prongs, outgrowths 5–20 µm in length terminating in blunt tips with a slight taper, (4) spikes, outgrowths 5–15 µm in length with straight or recurved, pointed tips, and (5) spines, outgrowths up to 5 µm in length with recurved, pointed tips. All lamellae (scales bearing true setae) of *Anolis* with well-developed subdigital pads are thought to display a proximodistal clinal gradation of all 5 morphotypes (from spines to setae) on each lamella. As in gekkotans, it is the true setae and their spatulae that are responsible for the majority of adhesive force capacity in *Anolis*.

#### 9.2.3.2 Anoline Setal Field Configuration

Table 9.1 (reproduced from Garner et al., 2019a) summarizes what was known about the morphometrics of exemplar anoline setae up to 2019. Although these data have been of crucial comparative value for describing and comparing the fibrillar adhesive outgrowths of squamates, they are drawn from single exemplar setae and therefore do not indicate whether the inter- and intraspecific variability of setal morphometrics of gekkotans (Delannoy, 2005; Russell et al., 2007; Johnson & Russell, 2009; Russell & Johnson, 2014) are also evident in anoles. Garner et al. (2021) explored this possibility by examining the morphometrics of the setal arrays of the Cuban knight anole (*Anolis equestris*), a dactyloid of similar size to *Gekko gecko*. That study revealed that the setae of *A. equestris* increase in length and decrease in basal diameter proximodistally along regions (proximal, intermediate, distal) of the subdigital pad (Fig. 9.8b). Within a single lamella, however, setal length is greatest in the intermediate region, whereas setal basal diameter decreases proximodistally (Fig. 9.8b). The length of lamellae decreases proximodistally along regions of the
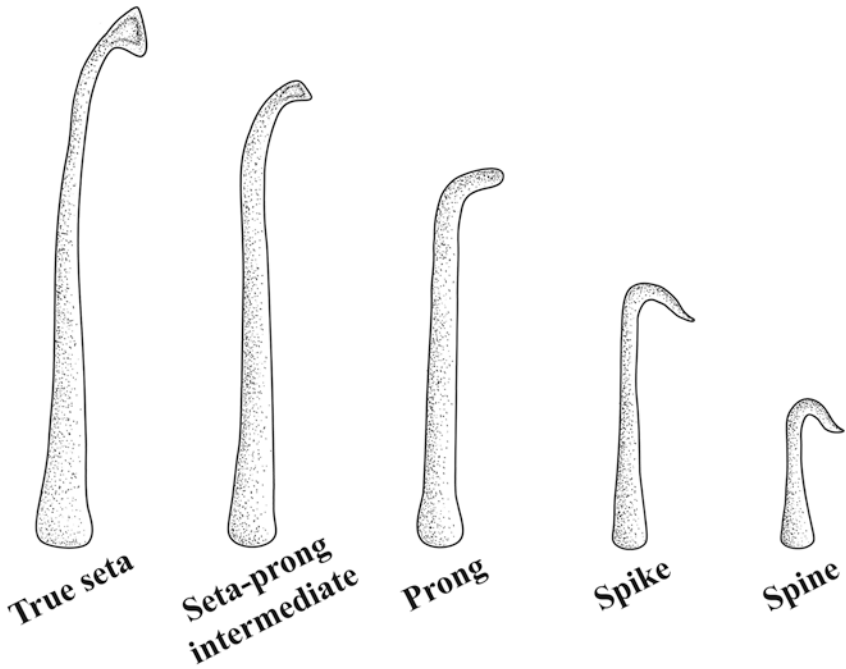
**Fig. 9.8** (**a**) Clinal series of the epidermal outgrowths present on the subdigital pad of anoline lizards (as described by Peterson and Williams, 1981). True setae are outgrowths 10–30 μm in length that carry a single, expanded spatulate tip. Seta-prong intermediates are outgrowths 5–20 μm in length with flattened tips. Prongs terminate in a blunt tip with a slight taper and are 5–20 μm in length. Spikes possess straight or recurved, pointed tips and are 5–15 μm in length. Spines are outgrowths up to 5 μm in length with pointed recurved tips. (**b**) Trends of setal morphometrics along subdigital pad regions and lamellar zones of *Anolis equestris* (as reported by Garner et al., 2021). Setal length increases and setal base diameter decreases proximodistally along pad regions. Setal length is maximal in the intermediate zones of lamellae. Setal base diameter decreases proximodistally along lamellar zones. Lamella length decreases proximodistally

**Table 9.1** A summary of the known average setal morphometrics of anoline lizards (Garner et al., 2019a)

| Species | Density (setae/$\mu m^2$) | Length ($\mu m$) | Diameter ($\mu m$) | Tip width ($\mu m$) | Tip area ($\mu m^2$) | Sources |
|---|---|---|---|---|---|---|
| *Anolis chameleontides* | 1 | 18.4–18.6 | 0.56–0.58 | – | 0.206–0.377 | (1) |
| *Anolis porcus* | 1 | 22.3 | 0.53 | – | 0.264 | (1) |
| *Anolis barbouri* | 0.5–0.6 | 5.0–8.4 | 0.47–0.56 | – | 0.6–1.472 | (1) |
| *Anolis heterodermus* | 1.2 | 13.7–14.8 | 0.41–0.46 | – | 0.214–0.308 | (1) |
| *Anolis cuvieri* | 0.9–1.4 | 22.4–27.2 | 0.51–0.65 | – | 0.184–0.253 | (1) |
| *Anolis cuvieri*** | 1 | 22.4 | 0.51 | 0.729 | 0.229 | (2) |
| *Anolis sheplani* | 1.1–1.2 | 11.8–12.6 | 0.39–0.41 | – | 0.220–0.279 | (1) |
| *Anolis occultus* | 1.4 | 11 | 0.49 | – | 0.237 | (1) |
| *Anolis* sp. n. near *eulaemus* | 1 | 20.4 | 0.57 | – | 0.593 | (1) |
| *Anolis valencienni* | 1.1–1.4 | 15.3–17.2 | 0.40–0.47 | – | 0.171–0.209 | (1) |
| *Anolis carolinensis* | 0.83 | 21 | 0.5 | 0.87 | – | (3,4) |
| *Anolis equestris* | 0.7 | 30 | – | – | – | (3,4) |
| *Anolis lineatopus* | 0.51 | – | – | 1 | – | (3,4) |
| *Anolis sagrei* | 1.7 | 20 | – | 0.75 | – | (3,4) |
| *Anolis homolechis* | – | 20 | – | – | – | (3) |
| *Anolis annectens*** | 1.0–2.0 | 20 | 0.48 | 0.73 | 0.211 | (5) |

Note that only 15 species are represented by these data and that the complete set of setal characters have only been reported for two of these species (denoted by **). Sources: (1) Peterson (1983b), (2) Williams and Peterson (1982), (3) Ruibal and Ernst (1965), (4) Peattie and Full (2007), and (5) Peterson and Williams (1981). Table reproduced from Garner et al. (2019a). Going out on a limb: how investigation of the anoline adhesive system can enhance our understanding of fibrillary adhesion. *Integr Comp Biol*, 59, 61–69 by permission of the Society for Integrative and Comparative Biology

subdigital pad (Fig. 9.1b). Setal density remains relatively consistent along the entire subdigital pad and along regions (proximal, intermediate, distal) of individual lamellae. Garner et al. (2021) also estimated the effective elastic modulus ($E_{eff}$) of the setal arrays of *A. equestris* and found that in most regions of the setal fields this falls below 2 MPa, suggesting that anoline setal fields can deform to surfaces to maximize contact area and adhesion

### 9.2.3.3 Attachment Mechanics and Functional Morphology of Anoline Setae and Setal Arrays: What We Do and Don't Know

Currently the attachment mechanics of anoline setae and setal arrays remain relatively understudied when compared to those of gekkotans (Garner et al., 2019a). Given the similarity of setal form and material properties, however, the setae of *Anolis* and gekkotans presumably require similar loading conditions (normal load followed by shear load), because measurements of whole animal adhesive performance of geckos and anoles indicate that the adhesive systems of each can be engaged in the same manner (Irschick et al., 1996). The means by which setal loading and unloading occurs in anoles, however, differs from that typically attributed to geckos. Russell and Bels (2001) examined the kinematics of *Anolis sagrei* running on an inclined acrylic surface and found that subdigital pad placement and retraction occurs proximodistally (as opposed to the distoproximal pattern of some geckos), with the digits rolling off onto their distal tips, a pattern typical of the digital kinematics of lizards in general (Brinkman, 1980; Rewcastle, 1980, 1983). This pattern of release of the setae is consistent with the notion that the step-like patterning of setal length in setal arrays assists in the effective detachment of the adhesive apparatus. The patterning of setal length and subdigital pad peeling of *Anolis* (Garner et al., 2021) are effectively identical to those taken to be characteristic of geckos (Johnson & Russell, 2009), but are expressed in the opposite direction.

The measurement of the adhesive forces of single gekkotan seta by Autumn et al. (2000) resulted in a deluge of interdisciplinary research focusing on the mechanisms, mechanics, and properties of this system (Niewiarowski et al., 2016). Investigation of the adhesion mechanics of anole setae has not, however, been explored in like fashion and adhesion in these lizards has largely been explored by biologists alone (Garner et al., 2019a). Three approaches have predominated: (1) examination of gross aspects of setae and setal field morphology (Ruibal & Ernst, 1965; Peterson & Williams, 1981; Williams & Peterson, 1982; Peterson, 1983a, b; Peattie & Full, 2007); (2) investigation of adhesion of intact animals to smooth substrata (Irschick et al., 1996; Elstrott & Irschick, 2004; Bloch & Irschick, 2005; Irschick et al., 2005; Garner et al., 2017); and (3) exploration of correlations between morphology and performance of the subdigital adhesive pads as a whole (Macrini et al., 2003; Elstrott & Irschick, 2004; Irschick et al., 2005; Donihue et al., 2018). When introducing *Anolis* as a model system for the study of fibrillar adhesion, Garner et al. (2019a) acknowledged the invaluable contribution that such studies have made, but concomitantly recognised clear gaps in our knowledge of the form and function of anoline setae and setal fields.

Although anoline setae likely operate under similar principles and conditions to those of geckos, differences in their overall form and dimensions may result in differential attachment mechanics. For example, the critical angle of detachment of gekkotan setae is about 30°. Do anoline setae also detach from surfaces at such angles or does the lack of structural hierarchy and presence of greater tip sizes result in different detachment angles? Preliminary data measuring detachment of entire

anoline subdigital pads suggest that anoline setae detach at angles of less than 30° (Hagey, 2013), but more conclusive work with isolated single setae is necessary to validate this. Furthermore, the properties of anoline setae and setal arrays have not been investigated. For example, do they exhibit the same wetting and self-cleaning properties as gekkotan setal arrays? Anoline setae, like those of geckos, are clad in phospholipids (Alibardi et al., 2011), and the roughness introduced by the surface profile of the batteries of setae should enable them to be superhydrophobic. Additionally, there is no reason to suspect that anoline setal arrays are not self-cleaning, but self-cleaning performance could differ between the two groups as a result of differences in tip density and area.

There has been considerable attention paid to the investigation of gekkotan adhesive system in ecologically relevant conditions (Russell, 2002; Autumn et al., 2014; Niewiarowski et al., 2016, 2017) and such studies are increasing. This, however, is not the case for anoles, even though they are model organisms for evolutionary ecological studies (Losos, 2011). How the differences in setal form between geckos and anoles might relate to differential adhesive performance in ecologically relevant circumstances is an area ripe for future research.

### 9.2.4  The Anoline Adhesive System

The anatomical modifications associated with the expression of the adhesive system in geckos are modestly represented by *Anolis*, being confined to skeletal (phalangeal) and tendinous features (Russell & Gamble, 2019: Table 1). The toe pads of *Anolis* are visibly evident (Figs. 9.1b and 9.9a) and are located basally on the digits, ventral to the location of the digital inflection (between phalanges 2 and 3 of digit IV—Fig. 9.9a; Russell et al., 2015). The penultimate phalanx is arcuate and extends distally beyond the toe pad. The claw is thus carried some distance beyond the distal extremity of the pad (Figs. 9.1b and 9.9a).

The metapodial-phalangeal joints of *Anolis* are unicondylar (Fig. 9.9b), permitting a greater range of movement than the ginglymous joints of lizards without subdigital pads (including other iguanoids) (Russell & Bauer, 2008). Although the metacarpals are widely divergent in the manus (Fig. 9.9a), a situation widespread among lizards, the first four metatarsals of the pes are subparallel, with the pes (Fig. 9.1b) having the asymmetrical form of lizards in general rather than exhibiting the secondary symmetry evident in geckos (Fig. 9.1a; Russell et al., 1997). In both the manus and pes the structure of the phalanges and the joints between them are highly modified. This is particularly so for the phalanges associated directly with the toe pads (for example, phalanges 2 and 3 of digit IV of the manus and pes—Fig. 9.9a, b) when compared to those for lizards ancestrally lacking toe pads (Russell & Bauer, 2008). Their cross-sectional profile is depressed and widened, with a ventral excavation that conducts the tendon of the flexor digitorum longus muscle (which inserts on the ungual phalanx). In the manus digits III and IV are subequal in length (Fig. 9.1b) as a result of metacarpal III being relatively elongated and phalanx

**Fig. 9.9** (**a**) Dorsal view of the left manus of *Anolis garmani* showing the carpals, metacarpals and phalanges in grey and the arterial vessels in black. Note the pattern of arterial vessels that outline the contours of the toe pads on digits II–V. Drawn from a cleared and Alizarin-stained Microfil-injected specimen. (**b**) Phalanges of digit IV, right pes of *Anolis garmani* in dorsal (left) and ventral (right) aspects (except for the ungual phalanx, which is shown in lateral view). Note the greatly elongated first phalanx and the relatively short, somewhat depressed third phalanx that supports the majority of the toe pad (see panel a for a depiction of the location of the phalanges in relation to the toe pads). *ph1–ph5* phalanges 1–5, *I–V* digits I–V
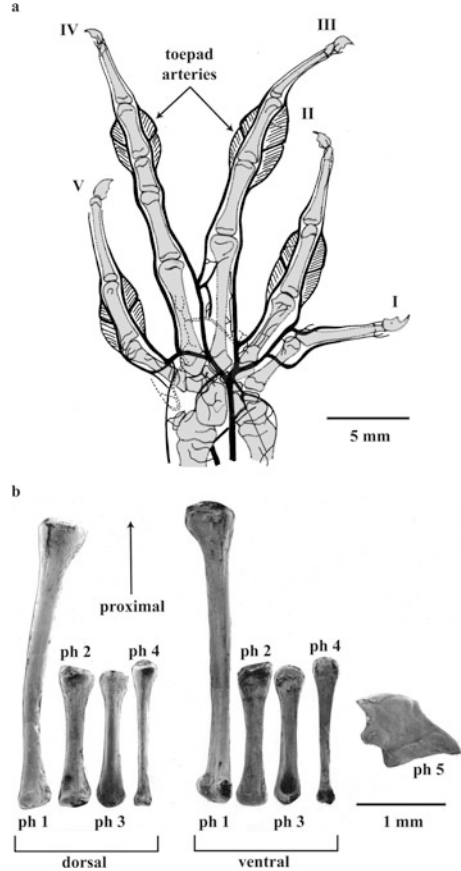


2 of digit IV being relatively short. In the pes, in contrast, phalanx I of digit IV is greatly elongated (Fig. 9.9b), resulting in the relative distal displacement of the toe pad on that digit (Fig. 9.1b). Phalanx 2 on pedal digit IV is longer than its corresponding manual phalanx. Thus, the osteology of the manus and pes of *Anolis* both deviate from the ancestral pattern (Russell & Bauer, 2008) but exhibit differences from each other reflective of the symmetrical disposition of the digits in the manus and their asymmetrical carriage in the pes. The accommodation of the toe pads and their potential to impinge upon one another due to their breadth has been accomplished differently in the manus and pes.

Associated with the toe pads of *Anolis* are lateral digital tendons (Fig. 9.10a) similar to those of geckos. These course along the lateral and medial borders of the phalanges of each digit (except the first which lacks a toe pad, due to constraints imposed by phalangeal number—Russell & Bauer, 1990) and branch to serve each lamella (Fig. 9.10a). As in geckos the dense, collagen rich connective tissue of the lateral digital tendons is continuous with the stratum compactum of the dermis of the lamellae (Fig. 9.10b) and the lamellar dermis lacks a stratum laxum. Thus, as in

**Fig. 9.10** (**a**) Medial aspect of a dissection of digit III, right pes of *Anolis garmani* showing the lateral digital tendons and their association with the lamellae. (**b**) Parasagittal section through the toe pad of digit IV, right pes of *Anolis garmani* showing the relationship of the epidermal lacunar cells to the configuration of the lamellae and their epidermal free margins that carry the setae. Section stained with Masson's trichrome, section thickness 8 μm. *efm* epidermal free margin of lamella, *fdlt* tendon of the flexor digitorum longus muscle, *lam* lamella, *lat br ldt* lateral branch of the lateral digital tendon, *ldt* lateral digital tendon, *lt* lacunar tissue, *ph1, ph3* phalanges 1 and 3, *str comp derm* stratum compactum of the dermis
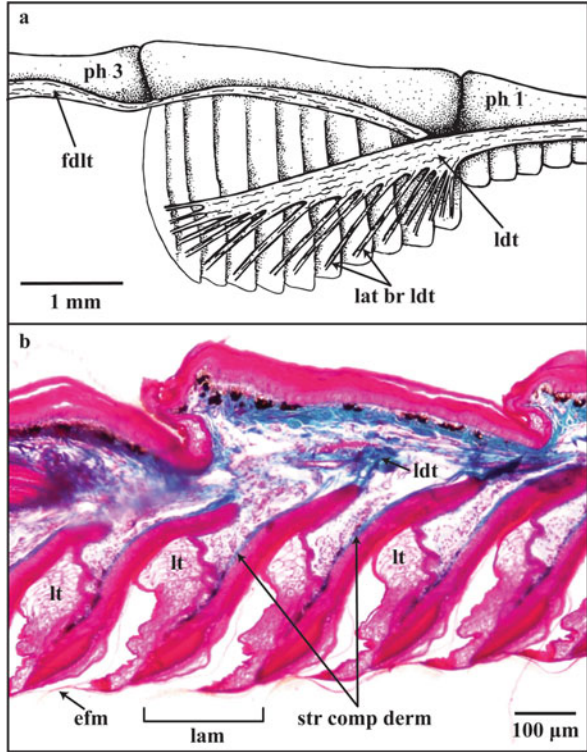


geckos (Russell, 1986) the lateral digital tendon/lamellar dermis complex furnishes a tensile skeleton that provides connectivity between the setae and skeleton at the metapodial-phalangeal joint capsules. This chain reinforces the junction between the integument and the underlying tissues and permits the tensile load imposed on the setae to be channeled to points of resistance deep within the manus and pes, and also permits active tensile loading to be imposed upon the setae via the muscles acting on the metapodial-phalangeal joint capsules. The digits of *Anolis* exhibit little in the way of muscular modifications (Fig. 9.11) akin to those exhibited by at least some gecko lineages (Russell & Gamble, 2019) (Fig. 9.7d).

The above-mentioned features of the anole adhesive system are those that Russell and Gamble (2019: Table 1) documented in their broad comparative survey of the adhesive system of geckos. Other gecko-like modifications are also present, however. Although there is no vascular-based cushioning structure (Russell, 1981) associated with the lamellae (Fig. 9.10b), there is something akin to this. *Anolis* lamellae lack a perfect resting stage of the epidermis (Lillywhite & Maderson, 1968) and the lacunar epidermal cells of the inner faces of the lamellae show precocious development in stage 1 of the shedding cycle and by stage 4 are hypertrophied (Fig. 9.10b). This expansion of lacunar cells as far distal as the base of the epidermal free margin of the lamellae results in a continuous band of such cells that lies dorsal
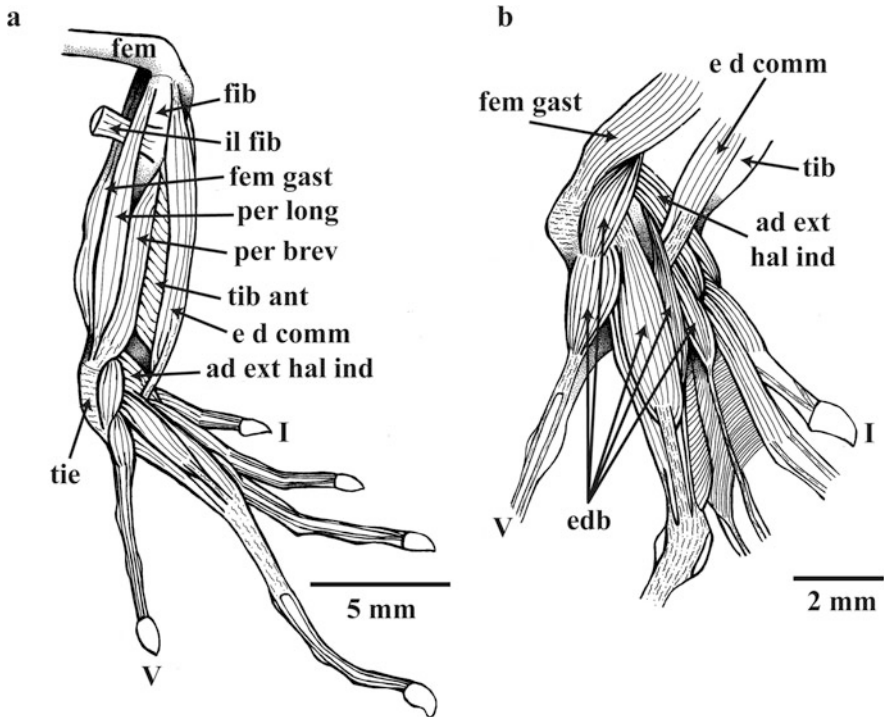
**Fig. 9.11** Musculature of the crus and pes of *Anolis garmani*. (**a**) Lateral aspect of the right crus and pes showing the superficial extensor musculature; (**b**) Superficial extensor musculature of the distal end of the right crus and adjacent pes. *ad ext hal ind* adductor et extensor hallucis et indicus muscle, *edb* extensor digitorum brevis muscle, *e d comm* extensor digitorum communis muscle, *fem* femur, *fem gast* femoral gastrocnemius muscle, *fib* fibula, *il fib* iliofibularis muscle, *per brev* peroneus brevis muscle, *per long* peroneus longus muscle, *tib* tibia, *tib ant* tibialis anterior muscle, *tie* tie tendon, *I, V* digits I and V

to the setae and overlies the entire setal field when the toe pad is flattened against the locomotor surface (Russell, 2016), suggesting that it serves to transmit pressure to the underlying setae, thereby assisting with compliance of the setal fields with the substratum (although this has yet to be biomechanically confirmed). The vascularity of the toe pads is not markedly different from that of lizards in general (Fig. 9.9a; Russell, 2016), but includes arteries that branch from the main supply to the digits and serve the borders of the pad and, by branching further, the individual lamellae (Fig. 9.9a). All of these vessels are nutritive and play no role in hydrostatic support (Russell, 1981) of the lamellar system.

### 9.2.5  Comparison of Clinging Performance in Geckos and Anoles

Only two reports compare the adhesive performance of geckos and anoles. Ruibal and Ernst (1965) observed gecko and anole adhesive locomotion on a vertical raceway and noted no obvious differences in performance. More comprehensive work by Irschick et al. (1996) corroborated this finding and found that static clinging performance of geckos and anoles is not markedly different. These results are surprising given the marked differences in morphology and anatomy of the adhesive apparatuses of the two groups.

As noted above, the structural hierarchy present in the fibrils of the gekkotan adhesive system should result in greater adhesive force production than unbranched fibrils of similar size (Peattie & Full, 2007; Murphy et al., 2009; Garner et al., 2021). Therefore, if geckos and anoles only differed in the presence of structural hierarchy of their setae, gekkotan setae should induce greater adhesive forces. Gekkotan and anoline setae and setal fields, however, differ in setal size, the number of spatulae per seta, and the number of fibrils present per unit area (Garner et al., 2021). Application of the Johnson-Kendall-Roberts (JKR) theory of elastic contact to the assessment of adhesive performance of gekkotan and anoline setal arrays, in conjunction with the comprehensive morphological data obtained about the setal fields of *Gekko gecko* (Delannoy, 2005) and *Anolis* (Garner et al., 2021), reveals that adhesive performance of gekkotan and anoline setal arrays should theoretically be similar when taking the differences in the morphology and configuration of their setae and setal fields into consideration. Anoles possibly compensate for the lack of structural hierarchy of their setae by possessing greater setal density compared to geckos. Structural hierarchy of setae may, however, be important in other aspects of the gekkotan adhesive system beyond those that directly affect adhesion (Persson, 2003; Yao & Gao, 2006; Persson, 2003). The impact of morphological and anatomical disparities on the function of gekkotan and anoline adhesive apparatuses may become more apparent in dynamic and/or more ecologically relevant circumstances.

## 9.3  Fundamental Factors Affecting the Form and Function of Fibrillar Adhesive Systems

Based on our review above, it is clear that organisms employing dry, fibrillar, molecularly-based adhesive systems are challenged by many environmental and organismic demands. These collectively influence the structure and deployment of the adhesive organs and drive them towards functionally and structurally similar outcomes (Federle, 2006). In accord with this, we compartmentalize our consideration of the drivers of convergence of the gecko and anoline adhesive system into those related to (1) the physical interactions between the filaments and the

substratum, and (2) the means by which attachment and detachment of the filaments is controlled by morphological adaptations of the organs that bear them.

### 9.3.1    Physical Constraints

Physical strictures are imposed upon fibrillar systems that chiefly rely upon van der Waals forces (Autumn et al., 2002) for attachment. To be effective in supporting the animal's body mass during station holding and locomotion (Higham et al., 2017a), the potential contact area of the fibril tips must be appropriately extensive and the separation distances minute enough to induce van der Waals interactions. Exploitable surfaces, for example, must fall within a range of asperity configurations (roughness) to enable sufficient access of the fibrillar arrays (Johnson & Russell, 2009; Russell & Johnson, 2007, 2014; Gillies et al., 2014); sufficient contact area with the surface is a function of the length of the fibrils, dimensions of their tips, and their material properties (Ruibal & Ernst, 1965; Persson, 2003; Federle, 2006). Release of the fibrils from contact with the substratum must be able to be repeatedly and rapidly accomplished without loss of adhesive capacity (which would occur if the filaments were damaged in this process).

The default state of the filaments in the unloaded, unattached state must be non-sticky (Autumn & Hansen, 2006) to avoid them attaching to each other, thereby rendering them ineffective. Furthermore, because minute, loose particles may adhere to the tips of the filaments during their operation, they must be self-cleaning (Hansen & Autumn, 2005; Hu et al., 2012), promoting the shedding of contaminants that may otherwise foul the system and result in loss of adhesive capacity (Russell & Delaugerre, 2017). Other physical environmental parameters, such as temperature, humidity and the presence of surface water, also impact the effectiveness of fibrillar adhesives (Bergmann & Irschick, 2005; Chen & Gao, 2010; Puthoff et al., 2010; Prowse et al., 2011; Stark et al., 2012, 2013, 2016; Garner et al., 2019b; Stark & Mitchell, 2019). At the most fundamental level, therefore, the organism-environment interface is the critical juncture at which selection operates to determine the configuration (Russell et al., 2007, 2015) and material properties (Greiner et al., 2009) of the adhesive system.

### 9.3.2    Structural Constraints

The organismally-related set of challenges facing molecularly-based fibrillar adhesives concern the mechanics of their operation. The surface area able to be devoted to the adhesive apparatus (Fig. 9.1) must be compatible with the configuration of the locomotor system and must be able to compensate for increases in body mass as growth occurs (Webster et al., 2009). Beyond the simple relationship of available surface area relative to volume (and hence mass), the fibrils must be arranged,

arrayed, and controlled such that sufficient contact with the substratum can be made to effect body support under the various demands of static clinging and active locomotion (Autumn et al., 2006b; Russell & Oetelaar, 2016; Higham et al., 2017a; Song et al., 2020).

The small size of the fibrils and the relatively high tensile loadings imposed upon them render them potentially easily damaged and suggest that careful control during their deployment and release is essential (Russell et al., 2019). The fibrils are products of the epidermis and the loading that they experience must be able to be transmitted to deeper layers of the integument and other parts of the locomotor system (Russell, 1986) to avoid integumentary rupture. Thus, reinforcement of the bond between the skin and underlying tissues of tetrapod vertebrates, which generally allows movement between it and the underlying subdermis (Roach, 2003), is essential.

Following the initial evolutionary establishment of adhesive effectiveness of subdigital fibrils, as determined by the physical demands outlined above, selection may further operate on structural aspects of the anatomy that carries and operates them (Russell et al., 2015). This may lead to the elaboration of more complex control and monitoring mechanisms that may add to the structural complexity (and possibly functional versatility) of the adhesive system.

## 9.4 Assessing the Fidelity of Convergence Between Gekkotan and Anoline Adhesive Systems

The hierarchical dependency outlined above has led to overall general convergence (the evolutionarily independent reoccurrence of form and function—Kuhn et al., 2020) in both the physical and structural domains pertaining to the fibrillar adhesive systems of geckos and anoles. There are, however, because of multiple transitions to adhesively-competent digits within the Gekkota, differences of expression of the structure of the adhesive system in various gecko lineages (Russell & Gamble, 2019). Thus, assessment of the convergence between anoles and geckos must take the variation within the Gekkota into account.

Both geckos and anoles have accomplished filament-based adhesion via the elaboration of epidermal outgrowths present on the surface of their integument. The spinulate Oberhäutchen of these squamates has been exapted (Gould & Vrba, 1982; Russell et al., 2015) for adhesion using intermolecular forces. Selective pressures for robust attachment to vertical and inverted substrata ultimately led to the elaboration of epidermal outgrowths (setae) capable of supporting the lizard's body mass via van der Waals intermolecular forces (Russell et al., 2015; Higham et al., 2017a, b). Several gekkotans possess adhesive structures on the ventral surface of their tail tips (Bauer, 1998), providing evidence that transitions to adhesive competence can occur in any region of the integument that makes regular and close contact with the substratum. The spinulate Oberhäutchen of the digits of

some other squamate clades, such as chameleons and some skinks, has also under-gone elaboration to support enhanced friction (or modest adhesive capacity, in the case of skinks) (Williams & Peterson, 1982; Irschick et al., 1996; Khannoon et al., 2014). Fundamentally, the adhesive setae of geckos and anoles are convergent structures that arose to support reversible attachment for static clinging and effective locomotion on heterogeneous and complex substrata via molecular interactions. Nevertheless, these two groups of squamates achieve this with structures that differ in form and, in some cases, function (Garner et al., 2021).

After the initial transformation of relatively simple fibrillar outgrowths to those that could effect robust organismal attachment via intermolecular forces, the evolu-tionary elaboration of setae and setal field configuration differed in geckos and anoles. The setae of geckos became further elaborated into multiply branched structures [even in one of the simplest manifestations, *Gonatodes humeralis* (Russell et al., 2015)] whereas those of anoles remained unbranched. Recent work has also revealed that the dimensions of the setae of *Anolis equestris* differ markedly from those of *Gekko gecko*, being between 3 and 5 times shorter and having bases between 2 and 7 times narrower (Garner et al., 2021). The differences in morphology and dimensions of setae in anoles and geckos are accompanied by differences in the manner in which the setal fields are assembled. The clinal pattern of setal length of *Anolis equestris* is similar to that of geckos but effectively opposite in direction (Garner et al., 2021), indicating that the pattern of setal length is largely driven by differences in the mechanics of subdigital pad peeling in these two clades. The majority of anoline setae are located on the epidermal free margin, a thin, flexible extension of the lamella (Ruibal & Ernst, 1965; Ernst & Ruibal, 1966; Maderson, 1970; Peterson, 1983a, b; Russell & Eslinger, 2017). An epidermal free margin may be present on the scansors of some gekkotans, but it is not as extensive (Alibardi et al., 2007). Functionally, the epidermal free margin of anoline lamellae is thought to promote conformation with the substratum to increase setal contact fraction (Russell & Eslinger, 2017), although this has not been investigated empirically. Thus, although gekkotan and anoline setae seem to operate utilizing similar princi-ples and mechanics, differences in setal form and dimensions relate to the perfor-mance and properties of the adhesive apparatus as a whole.

Geckos exhibit multiple origins of adhesively-competent digits within their ranks (Russell & Gamble, 2019) whereas anoles have originated such a system only once (Losos, 2011). The strictures imposed upon the interactions between keratinous dry fibrillar adhesives and surfaces to which they can attach determine the fundamental mechanics of their deployment. Initially the adhesive competence of setae was incorporated into pre-existing locomotor repertoires, as indicated by gekkotan taxa with incipient toe pads, such as *Gonatodes humeralis* (Russell et al., 2015; Higham et al., 2017a, b). These incipient toe pads rely upon proximodistal hyperextension of the digits for detachment of the adhesive filaments, as do those of *Anolis* (Russell & Bels, 2001). Neither *Gonatodes humeralis* nor *Anolis* (Russell & Gamble, 2019: Table 1) exhibit modifications of their digital musculature (Russell, 1975, 2002) associated with driving distoproximal digital hyperextension.
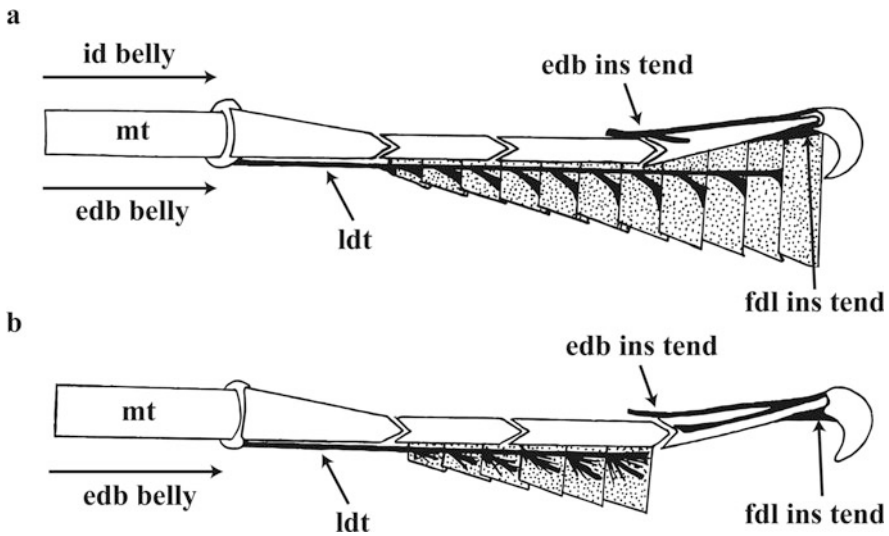
**Fig. 9.12** Diagrammatic representation of the arrangement of the major mechanical units of digit IV of the pes of the sphaerodactylid gekkotan *Aristelliger* (**a**) and *Anolis* (**b**). Both diagrams start at the left with the metatarsal (mt). Scansors and lamellae are represented by stippled overlapping plates. The extent of the bellies of the extensor digitorum brevis (edb) and interossei dorsalis (id) muscles are indicated by arrows, and the insertion of the tendons of the extensor digitorum brevis (edb ins tend) and flexor digitorum longus (fdl ins tend) muscles are indicated by arrows pointing to the respective tendons. The lateral digital tendons (ldt) and their branches that meld with the stratum compactum of the scansors and lamellae are shown. Joints modified for hyperextension are indicated by chevron shapes (>>)

The initial critical changes of the subdigital integument, phalanges and overall conformation and proportions of the digits of *Gonatodes humeralis* are quite subtle when compared to those of their congeneric non-adhesive relatives (Gamble et al., 2012; Russell et al., 2015). In contrast, *Anolis* exhibits fully expressed toe pads (Fig. 9.1b) and modifications of the intermediate phalanges (Fig. 9.9) that enhance both the pressing of the toe pads onto the substratum during attachment and their hyperextension during release. It also possesses a lateral digital tendon system that merges with the dermis of the lamellae (Fig. 9.10) and transmits tensile loading from the setae to points of resistance deeper within the autopodium (Russell, 1986). Furthermore, *Anolis* incorporates a compliance-promoting cushioning system (Fig. 9.10) into its toe pads, in the form of hypertrophied lacunar cells of the epidermis (Russell, 2016). This cushioning system is unique to *Anolis* but is analogous and positionally similar to the vascular (Russell, 1981) and adipose tissue (Russell & Bauer, 1988) compliance structures found among geckos. Based on this, the gekkotan configuration structurally most closely resembling that of *Anolis* is that of the sphaerodactylid genus *Aristelliger* (Fig. 9.12). Compared to those of *Gekko gecko*, the setae of *Aristelliger* are relatively short and slender, have a modest branching pattern and terminate in relatively broad spatulate tips (Ruibal & Ernst, 1965). Whether *Aristelliger* employs proximodistal or distoproximal digit

hyperextension during toe pad peeling is not known, but it lacks modifications of the digital musculature (Figs. 9.6f, 9.11, and 9.12a) associated with the latter (Fig. 9.7d).

## 9.5   General Conclusions Relating to Convergence of Gekkotan and Anoline Adhesive Systems

The spinulate outer epidermal generation of geckos and anoles was derived independently and served as the precursor of adhesively interactive, deeply homologous setae in each [originating multiple times in the former (Gamble et al., 2012; Russell & Gamble, 2019), but once only in the latter (Losos, 2011)]. The physical principles governing substratum adhesive attachment and release of setae have resulted in similar (but not identical) configurations in the two clades. The integration of the operational strictures governing seta-substratum interactions into the locomotor repertoires of the taxa that bear them has resulted in regimented patterning of setae within the setal fields and the development of basic mechanisms for controlling these interactions. There is no genus of gecko that shows precise convergence on the anole configuration, but at least one approaches it closely (Fig. 9.12). Physical principles have determined the way in which keratinous filamentous adhesives are able to be successfully deployed and ancestry has determined the particular form that the controlling anatomical superstructure takes (Russell & Gamble, 2019).

Recent years have witnessed a multitude of studies that have investigated the gekkotan adhesive system (Russell et al., 2019) and these provide clear evidence of how productive and enlightening interdisciplinary and transdisciplinary research can be. Such studies, however, have focused on relatively few taxa (most frequently *Gekko gecko*) and investigation and modelling has been largely based on taxa with the most complex configurations of the adhesive system. Although such research has greatly influenced the design and fabrication of biologically inspired fibrillar adhesives, recognition that there are simpler structural configurations exhibited by anoles and certain gekkotan lineages provides background for potential refinement of biomimetic applications based upon more basic structural and operational principles (Garner et al., 2019a). The common elements of convergence between anoles and geckos points to new possibilities for investigating and exploiting fibrillar adhesives. Comparison of the functional and structural aspects of the adhesive apparatus of both clades yields information about what is minimally necessary and sufficient for its effective operation and potentially simplifies approaches that can be taken in the development of biomimetic derivatives.

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