This paper proposes a multi-level hierarchical model for the Tokay gecko (Gekko gecko) adhesive system and analyses the digital behaviour of the G. gecko under macro/meso-level scale. The model describes the structures of G. gecko’s adhesive system from the nano-level spatulae to the sub-millimetre-level lamella. The G. gecko’s seta is modelled using inextensible fibril based on Euler’s elastica theorem. Considering the side contact of the spatular pads of the seta on the flat and rigid substrate, the directional adhesion behaviour of the seta has been investigated. The lamella-induced attachment and detachment have been modelled to simulate the active digital hyperextension (DH) and the digital gripping (DG) phenomena. The results suggest that a tiny angular displacement within 0.25° of the lamellar proximal end is necessary in which a fast transition from attachment to detachment or vice versa is induced. The active DH helps release the torque to induce setal non-sliding detachment, while the DG helps apply torque to make the setal adhesion stable. The lamella plays a key role in saving energy during detachment to adapt to its habitat and provides another adhesive function which differs from the friction-dependent setal adhesion system controlled by the dynamic of G. gecko’s body.
1. Introduction

The Tokay gecko (*Gekko gecko*) is known for its extraordinary climbing ability [1–6]. The strong adhesion is mainly due to the van der Waals force enhanced by the hierarchical adhesive system from the nanoscale to the macroscale. The gecko can also perform a fast transition from attachment to detachment or vice versa in around 50 ms [5]. Extensive studies have been carried out to understand the strong adhesion and easy detaching mechanism of the gecko’s adhesion system in order to fabricate biomimetic dry adhesives. These bioinspired materials have potential applications in wall-climbing robots [7–9], adhesive medical skin patches [10], adhesive clamps [11], etc.

Theoretical work has focused on modelling of the gecko’s adhesive system. Several classical models of contact mechanics have been borrowed in the study of the gecko’s seta adhesion mechanism. The JKR (Johnson, Kendall and Roberts) model [12] was used to predict the contact force between the gecko’s setal spatulae and the substrate [4]. However, the model does not include the elastic deformation of the setal structures, which leads to overestimation of the tip-end adhesive strength [5]. A simplified linear flexible cantilever model considering the elastic bending deformation of the setal shaft was proposed [13]. The model treats the contact between the spatula and the surface as a constant spring or a fixed joint. In fact, the spatular pull-off force is directional and friction-dependent. The Kendall’s peeling model for adhesive strip tape [14] was employed to study the adhesion of the gecko’s spatular pad [15]. The model considers both the extensional deformation and the directional contact of the spatular pad. However, it neglects the bending deformation. Since the gecko’s seta material is rather ‘harder’ than some polymer-based adhesives and thus has a larger bending inertia, the bending deformation should be considered. The side contact model based on Euler’s elastica theorem has been adopted to address the problem for the side contact between a single fibril and the smooth rigid surface [16–19]. The model takes into account the bending deformation and the contact length in adhesion and proves to be effective in solving the anisotropic adhesive problem. As the structures of *G. gecko*’s adhesive system are from the nano-level of fine spatulae to the sub-millimetre level of the lamella, it is hierarchical. However, none of above models is hierarchy-based.

Several hierarchical models have been established to explain the gecko’s mechanical behaviour. Schargott [20] proposed a hierarchical model of the seta using linear beam array considering the multi-scale interaction, and evaluated the effect of surface roughness on the adhesive force. Persson [21] estimated the influence of the surface roughness on the effective adhesive energy of the setal array using a similar linear beam array model. However, they simplified the contact mechanism and treated the fine spatula as a spring fixed on the substrate. Arzt et al.’s study [22] focused on the contact area between the tip-end of the spatula and developed a hierarchical model based on the JKR theory. Their model can explain why the gecko needs up to 1000 spatulae at the setal termination, but it did not consider the friction effect. Tian et al. [23], Chen et al. [24] and Pesika et al. [25] used the peel-zone model to analyse the influence of the peeling angle on the adhesive force. They suggested that the peeling angle of the spatula can be adjusted by the digital gripping (DG) and digital hyperextension (DH) of the gecko. The adhesive force can even be adjusted within several orders of magnitude. In the above peeling models, elastic deformation has been considered along with the friction. However, the adhesion of the seta was obtained by simply calculating the adhesion of a single spatula then multiplying it by the total spatular number. The interaction between the seta and the spatulae, especially the torque transferred between the seta and the spatulae, was not well treated. Gao et al. [5] and Sauer [26] used the finite-element method (FEM) to model the setal system. The results could roughly predict the setal adhesion behaviour, but the computation was much more complex than the analytical models.

Besides theoretical studies on the gecko’s adhesive behaviour, several experiments have been carried out to investigate the gecko’s adhesive system at different scales. Autumn et al. [27] measured the critical normal force of the gecko’s multi-scale adhesive system with respect to the friction and proposed a frictional adhesion model. Zhao et al. [28] measured the coupling between
the adhesion and friction of the seta using a displacement-controlled method. Their findings suggested that the friction could enhance adhesion along the gripping-in direction and reduce the adhesion along the releasing direction. Further, Autumn et al. [27] proposed that the critical adhesion was proportional to the friction. Gravish et al. [6] investigated the effective adhesive energy of a single seta by dragging it in different directions until it detached. They found that when the dragging angle is less than $110^\circ$ the seta slides laterally during detachment, which leads to energy dissipation. Otherwise, no sliding occurs in the detachment and the seta releases elastic energy.

The above work has addressed well the issues in the gecko’s adhesion under static/quasi-static conditions. However, the previous models failed to explain the frictional adhesion feature, which was observed in the real gecko’s movement. Furthermore, the gecko detaches with digits peeled from the distalmost end to the proximal (named active DH), and attaches with digits gripped towards the surface (named DG) while acting repeatedly on inverted surfaces. This behaviour cannot be fully understood based on previous models. Argument exists in that if the gecko can lower the pull-off force by lowering the friction and vice versa, why are the active DH and DG needed? Therefore, it is necessary to understand the mechanical behaviour of the gecko’s adhesive system from the dynamic scenario of the gecko’s movement.

In this paper, we built up a hierarchical model of the $G. \text{gecko}'$s adhesive system including a single lamella, a single row of setae growing on the lamella, and spatulae terminating each seta. We investigated the directional adhesion of the adhesive system using Euler’s inextensible elastica theorem. With the force-controlled model, the macroscopic behaviour of the gecko’s digit was theoretically investigated based on multi-scale analysis.

2. Theoretical analyses of the seta

(a) Geometric model of the setal system

The $G. \text{gecko}'$s adhesive system covers structures from centimetre level to nanometre level. A centimetre-scaled digit contains about 20 sub-millimetre-scaled lamellae, which are supported by the soft toe skin (figure 1a). The micrometre-scaled setae incline about $45^\circ$ with respect to the lamella and are generally $30$–$130 \mu m$ long, with a diameter of about $5 \mu m$ (figure 1b). The setae align on the lamella with number of $14400 mm^{-2}$ (density of $D = 14400 \mathrm{mm}^{-2}$). The setae branch into hundreds of inclined spatulae with dimensions at the $1$–$100 \text{nm}$ scale at its tip-end, and each spatula consists of a shaft and a pad (figure 1c). The inclined and thin plate-like spatular pads contact the substrate to provide adhesion (figure 1d). The setal tip-ending surface holding the spatulae is also naturally tilted from the stalk cross section [2,15,23,29–31].

Based on observation of the $G. \text{gecko}'$s toe structures, we built up a hierarchical model for the $G. \text{gecko}'$s setal system from the seta to the spatulae using the inextensible Euler’s elastica theorem as illustrated in figure 2. The related geometric parameters of the hierarchical model were selected or measured from [23,31]. The seta and the spatular shafts are modelled as cylinders, and the spatular pads are treated as thin plates, with bending inertia $I_i$ ($i = 1, 2, 3$), respectively. The material of the setal system is $\beta$-keratin with Young’s modulus $E = 2.6 \text{GPa}$ [23]. The parameters of the setal model used in theoretical analysis are listed in table 1. The tilt angle of the setal distal ending surface is $\alpha_t$ with respect to the stalk centreline. The rotation or bending of the lamella creating a rotation of the setal proximal end is defined as $\alpha_s$, $\alpha_i$ ($i = 1, 2, 3$) is positive in the clockwise direction with respect to the upper level centreline, while $\alpha_s$ is positive when the lamellar structure rotates in the counterclockwise direction. For simplification, all the setae are treated as straight cylinders. The cross-sectional areas of the spatular pads are assumed to be constant along the longitudinal directions.

(b) Mechanical model of the setal system

During the attachment, the gecko’s toe contact force is produced by the setae mainly in the $x$–$y$ plane, as shown in figure 3; therefore, the mechanical model of the setal system is considered as a
Figure 1. (a) The digits and lamellae of the G. gecko's hind limb. (b) The setae growing on the lamella. (c) The terminal branches of the setae with the spatulae. (d) The spatula with a tilting pad at the end. ‘P’ stands for the proximal end of the digit and ‘D’ stands for the distalmost end. Figures (b)–(d) are reprinted from [29]. Copyright © 2003 American Institute of Physics. (Online version in colour.)

Figure 2. Geometric model of the G. gecko's setal system. (a) The slanted seta growing on the lamella. (b) The zoomed-in spatular shaft and spatular pad. \( w \) is the width of the spatular pad and is not shown in the figure.

two-dimensional model. The side contact between the spatular pads and the rigid smooth surface and the deformation of the setae are also shown in figure 3.

The potential energy of a single setal system can be expressed as

\[
\Pi = \Pi_1 + N(\Pi_2 + \Pi_3),
\]

where \( \Pi_i \) denotes the potential energy of the seta \( (i = 1) \), the spatular shaft \( (i = 2) \), and the spatular pad \( (i = 3) \), respectively. \( N \) is number of the spatulae. \( \Pi_i \) is the sum of the bending energy, the
Figure 3. Mechanical model of the setal system. (a) The seta is deformed when external load is applied and (b) side contact occurs between the spatular pad and the rigid surface, with adhering length $l_{\text{adhere}}$.

Figure 4. Schematic of the elastic rod-like spatula in side contact with a flat and rigid substrate.

Table 1. Parameters of the setal model.

<table>
<thead>
<tr>
<th>natural inclination angles</th>
<th>dimensions</th>
<th>bending inertias</th>
</tr>
</thead>
<tbody>
<tr>
<td>term</td>
<td>value (radian)</td>
<td>term</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>$\pi/4$</td>
<td>$l_1 \times d_1$</td>
</tr>
<tr>
<td>$\alpha_2$</td>
<td>$-\pi/3$</td>
<td>$l_2 \times d_2$</td>
</tr>
<tr>
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<td>$0, \pi/6, \pi/4, \pi/3$</td>
<td>$l_3 \times w \times b$</td>
</tr>
<tr>
<td>$\alpha_t$</td>
<td>$\pi/10$</td>
<td></td>
</tr>
</tbody>
</table>

potential of the external load and the surface energy of the setal system. Figure 4 shows the schematic of a spatula in side contact with a flat and rigid substrate. The potential energy of the elastic rod-like spatula with a uniform, flat and ribbon-like cross section in the side contact configuration under external load can be described by the following equation [19]:

$$
\Pi = \int_0^{l-\gamma} \left( \frac{K}{2} \left( \frac{d\theta}{d\xi} \right)^2 + n \cdot r' \right) \, d\xi + \int_{l-\gamma}^{l} \left[ -n \cdot E_1 - \omega \right] \, d\xi,
$$

where $K$ is the flexural rigidity of an elastic rod, $l$ is the length of an elastic rod, $\gamma$ is the adhesive length, $\omega$ is the adhesive energy per unit length and $(\xi, \theta)$ is the convected coordinate. A Cartesian basis $(E_1, E_2)$ is added with a fixed origin $O$, defining the force vector $n = f_1 E_1 + f_2 E_2$ and position vector $r = x E_1 + y E_2$. $r' = -\sin \theta E_1 + \cos \theta E_2$ is the unit tangential vector. Three terms are defined
including $U_b = \int_0^{l-y} (K/2)(d\theta/d\xi)^2 d\xi$, the bending energy; $U_p = \int_0^{l-y} (n \cdot r) d\xi + \int_{l-y}^l (-n \cdot E_1) d\xi$, the potential of the external load; and $U_s = -\int_{l-y}^l \omega d\xi$, the surface energy. In addition, an adhesion boundary condition exists $(D/2)(d\theta/d\xi)_{\xi=(l-y)} = \omega$, provided that the shear force is distributed along the adhesive length. Therefore, we have the following equation to describe each term of the rod-like spatular potential:

$$U_{p3} = \int_{\theta_{\text{adhere}}}^{\theta_{\text{adhere}+l}} \frac{1}{2} EI_3 \left( \frac{\partial \theta_3}{\partial s} \right)^2 ds$$

and

$$U_{p3} = -\frac{F_t}{N} \left( l_{\text{adhere}} + \int_{\theta_{\text{adhere}}}^{\theta_{\text{adhere}+l}} \sin \theta_3 ds \right) + \frac{F_n}{N} \int_{\theta_{\text{adhere}}}^{\theta_{\text{adhere}+l}} \sin \theta_3 ds,$$

and $U_s = -l_{\text{adhere}} \omega$. $\omega = \epsilon w = 0.01 \text{ J m}^{-2} \times 0.2 \mu \text{m} = 2 \times 10^{-9} \text{ J m}^{-1}$ [5]. $\epsilon$ is the binding energy per unit area due to the van der Waals force. The terms of $\Pi_1$ and $\Pi_2$ can be obtained similarly.

To simplify the calculations of the hierarchy, the external load is assumed to be uniformly applied to the spatulae. This assumption was verified by Chen et al. [24], through calculating the critical diameter of the seta. The stress is uniformly distributed when the diameter of the seta $d_1$ is less than the critical value.

Applying the variation method to $\Pi_i$ $(i = 1, 2, 3)$, we have the following equilibrium equations for the seta, the spatular shaft and the spatular pad, respectively:

$$EI_1 \frac{\partial^2 \theta_1}{\partial s^2} + F_n \sin \theta_1 + F_t \cos \theta_1 = 0, \quad s \in [0, l_1],$$

$$EI_2 \frac{\partial^2 \theta_2}{\partial s^2} + \frac{F_n}{N} \sin \theta_2 + \frac{F_t}{N} \cos \theta_2 = 0, \quad s \in [l_1, l_1 + l_2]$$

and

$$EI_3 \frac{\partial^2 \theta_3}{\partial s^2} + \frac{F_n}{N} \sin \theta_3 + \frac{F_t}{N} \cos \theta_3 = 0, \quad s \in [l_1 + l_2, l_1 + l_2 + l_3 - l_{\text{adhere}}].$$

By integrating both sides of (2.3a–c), we have

$$\frac{1}{2} EI_1 \left( \frac{\partial \theta_1}{\partial s} \right)^2 + F_n \sin \theta_1 - F_n \cos \theta_1 - M_1 = 0,$$

$$\frac{1}{2} EI_2 \left( \frac{\partial \theta_2}{\partial s} \right)^2 + \frac{F_n}{N} \sin \theta_2 - \frac{F_n}{N} \cos \theta_2 - M_2 = 0$$

and

$$\frac{1}{2} EI_3 \left( \frac{\partial \theta_3}{\partial s} \right)^2 + \frac{F_n}{N} \sin \theta_3 - \frac{F_n}{N} \cos \theta_3 - M_3 = 0,$$

where $M_i$ is independent of $s$, with geometric boundary conditions

$$\theta_1|_{s=0} = \alpha_1 - \alpha_s,$$

$$\theta_2|_{s=l_1} = \theta_1|_{s=l_1} + \alpha_2,$$

$$\theta_3|_{s=l_1+l_2} = \theta_2|_{s=l_1+l_2} + \alpha_3$$

and

$$\theta_3|_{s=l_1+l_2+l_3-l_{\text{adhere}}} = \frac{\pi}{2}$$

physical boundary conditions based on Newton’s law

$$EI_1 \left( \frac{\partial \theta_1}{\partial s} \right)_{s=l_1} = NEI_2 \left( \frac{\partial \theta_2}{\partial s} \right)_{s=l_1}$$

and

$$EI_2 \left( \frac{\partial \theta_2}{\partial s} \right)_{s=l_1+l_2} = EI_3 \left( \frac{\partial \theta_3}{\partial s} \right)_{s=l_1+l_2}.$$
and adhesive boundary condition

\[
\frac{1}{2} EI_3 \left( \frac{\partial \theta_3}{\partial s} \right)^2 = \omega, s = l_1 + l_2 + l_3 - l_{\text{adhere}}.
\]  

(2.7)

Substituting equations (2.5d) and (2.7) into (2.3c), we have \( M_3 = F_t/N + \omega \), which gives

\[
\frac{1}{2} EI_3 \left( \frac{\partial \theta_3}{\partial s} \right)^2 + \frac{F_t}{N} \sin \theta_3 - \frac{F_n}{N} \cos \theta_3 - \left( \frac{F_t}{N} + \omega \right) = 0, \quad s \in [l_1 + l_2, l_1 + l_2 + l_3 - l_{\text{adhere}}].
\]

Noticing \( \partial \theta_3 / \partial s > 0 \), we have

\[
\frac{d \theta_3}{\sqrt{F_t/N + \omega + F/N - (2F/N) \sin^2 (\theta_3/2 + \pi/4 - \phi/2)}} = \frac{\sqrt{2}}{EI_3} ds.
\]  

(2.8)

Integrating (2.8) in \([l_1 + l_2, l_1 + l_2 + l_3 - l_{\text{adhere}}] \), we have

\[
l_{\text{adhere}} = l_3 - \frac{F(m_3, \pi/2 - \phi/2) - F(m_3, \theta_{3|s=l_1+l_2}/2 + \pi/4 - \phi/2)}{\sqrt{(F_t/N + \omega + F/N)/2EI_3}},
\]  

(2.9)

where \( F(m, \psi) = \int_0^\psi dt/\sqrt{1 - m \sin^2 t}, \quad F = \sqrt{F_t^2 + F_n^2}, \quad \phi = \tan^{-1} (F_n/F_t), \) and \( m_3 = (2F/N)/(F_t/N + \omega + F/N) \).

The following condition is necessary to equation (2.9) have real solutions [18]:

\[
\frac{F_t}{N} > F_{t,\text{cri}} = \begin{cases} 
1/2 & F_n^2/N^2 \omega = -\omega, \\
\frac{kF_n}{N} - \frac{1}{2}(k^2 + 1)\omega, & F_n/N > k\omega, \\
\frac{F_n}{N} & F_n/N < k\omega,
\end{cases}
\]  

(2.10)

where \( k = \tan((3/4)\pi - (1/2)\theta_{3|s=l_1+l_2}) \). If (2.10) is not satisfied, the side contact does not exist.

A simplification has been made that the spatulae serve as non-frictional revolute joints, as the total moment due to the bending of the \( N \) spatular shafts is negligible in this study. Provided a shear load and a normal load, \( l_{\text{adhere}} \) is obtained, and the adhesive state can be judged using the following criteria:

(i) \( l_{\text{adhere}} = 0 \) in equation (2.9);

(ii) no \( \theta_{2|s=l_1+l_2} \) exists that satisfies both inequality (2.10) and equations (2.4a,b).

Criterion (i) means that the seta detaches when the spatulae gradually and completely peel off the substrate. Criterion (ii) means that the seta detaches immediately when no stable adhesion can be achieved, even when part of the spatular pad is still in contact with the substrate, which is called the jumping-off side contact.

(c) The directional adhesive behaviour of the seta

Using the criteria above, we calculated the normal pull-off force \( F_n = -F_{n,\text{cri}}(F_t) \) as a function of the shear load \( F_t \in [0, 130 \mu N] \), with \( \alpha_3 = 0 \) to obtain the critical lines for different \( \alpha_3 = 0, \pi/6, \pi/4, \pi/3 \) (shown in figure 5). The experimental result of the normal pull-off force is also drawn in the figure for comparison [27]. In the region above each critical line, the seta will detach from the substrate, while underneath the lines the seta will remain attached. When the spatular pad’s directional angle with respect to spatular shaft \( \alpha_3 \) is \( \pi/4 \), the theoretical results are very close to the experimental data. This demonstrates that the proposed directional adhesion model can capture the directional adhesive characteristics of the seta. The calculated critical lines for different \( \alpha_3 \) share an almost identical curve before they split into the jumping-off side contact regimes. This means that, in the non-jumping-off side contact regime, the inclination angle of the spatular pad has less effect on the directional adhesion behaviour of the seta. He et al. [18] studied the directional adhesion behaviour of a single fibril in side contact with the substrate,
and found that the critical line varies with the inclination angle of the fibril through the whole regime. The spatular pad’s angles of the gecko’s seta are varied within a certain range during climbing. However, the gecko’s directional adhesion behaviour differs little from seta to seta, digit to digit, and individual to individual. In this study, we have verified that the hierarchy of the setal system plays an important role in ensuring the gecko’s climbing stability. Previous studies also have shown that the hierarchy of the setal system could enlarge the pull-off force of seta [22].

To determine the maximum of the setal adhesion, we chose $\alpha_3 = \pi/4$ and calculated the ‘saturation line’, where the external load causes a complete attachment of the seta. The curve along with the corresponding ‘critical line’ is shown in figure 6. Above the critical line is the region where the seta detaches, while below the line is the setal attachment region. Below the saturation line is the region where the spatular pads are completely attached to the surface ($l_{\text{adhere}} = l_3$ in figure 3). The two lines intersect at the point where the normal pull-off force reaches its maximum value. At this point, further increasing friction force $F_t$ will not increase the normal pull-off force because the jumping-off side contact occurs even when the spatular pads are fully engaged with the surface and the adhesion state is extremely unstable. The range of the directional adhesive force of the gecko’s seta has been measured by Autumn et al. [27]. Tian et al. [23] and Chen et al. [24] theoretically analysed the influence of the spatular peeling angle on the pull-off force of a single spatula and obtained the maximum and minimum adhesive forces at corresponding friction forces for the gecko’s seta. The setal adhesive critical line shown in figure 5 does not intersect the point (0, 0), which differs from Autumn et al.’s experimental measurement. This error may originate from the theoretical assumption that the external load is uniformly distributed on the spatulae, for which the seta can produce a certain adhesion without friction. In reality, when friction is low, the seta cannot keep its tip-end balanced. As a result, the seta tends to bend outward against the surface, and a ‘pitch outward’ trend occurs at the setal tip-ending surface holding the spatulae. This effect may cause either early attachment of some spatulae or weakened binding between the spatular pads and the surface, both of which decrease the apparent adhesion of the seta, called a ‘partial release’ [26].

For comparisons, we list our results with different inclination angle of the spatular pad in table 2 along with previous work of [23,24,27]. In the table, the number of spatulae $N$ is taken as 1000 to obtain the theoretical results. From the table, we can see that, when $\alpha_3 = \pi/4$, the proposed model exhibits the closest maximum and minimum adhesive forces to those of the experimental results, which are shown in bold numbers. Comparing with Tian et al.’s theoretical
work, the proposed results are much smaller for the maximum and minimum adhesive forces. Chen et al.’s theoretical results are close to ours for the minimum adhesive force, but only 33% for the maximum force. There are several reasons for the differences between our results and those in other theoretical work. First, Tian et al. and Chen et al.’s work only modelled a single spatula and obtained the adhesive force for one seta by multiplying by the number of spatulae. Second, Tian et al.’s model did not consider the coupling effect between the spatular deformation and the van der Waals force. Our model included the relationship of the spatular bending and the surface energy caused by the intermolecular force. The predicted adhesive forces averaged on each single spatula are close to the measured data [27] but much smaller than those of previous theoretical work [23]. Our model also considered the torques transferred between the multi-scale structures from the seta to the spatulae. The proposed method achieved similar results to those of Chen et al.’s work at low friction where the torque is lower, but were significantly different at high friction as the torque is higher. In addition, the ‘saturation line’ has been taken into account in the model, which can predict the phenomenon where the adhesion is saturated as the friction increases.

Table 2. Comparisons of adhesive forces of the gecko’s seta.

<table>
<thead>
<tr>
<th></th>
<th>max. adhesive force</th>
<th>at friction force</th>
<th>min. adhesive force</th>
<th>at friction force</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn et al. [27]</td>
<td>24.0</td>
<td>40.0</td>
<td>0.6</td>
<td>1.0</td>
</tr>
<tr>
<td>Chen et al. [24]</td>
<td>10.0</td>
<td>17.3</td>
<td>2.0</td>
<td>0</td>
</tr>
<tr>
<td>Tian et al. [23]</td>
<td>70.0</td>
<td>400.0</td>
<td>16.0</td>
<td>0</td>
</tr>
<tr>
<td>$\alpha_3$</td>
<td>our proposed model ((\mu N))</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>n.a.</td>
<td>n.a.</td>
<td>1.5</td>
<td>0</td>
</tr>
<tr>
<td>$\pi/6$</td>
<td>58.8</td>
<td>124.3</td>
<td>1.9</td>
<td>0</td>
</tr>
<tr>
<td>$\pi/4$</td>
<td>29.2</td>
<td>52.6</td>
<td>2.1</td>
<td>0</td>
</tr>
<tr>
<td>$\pi/3$</td>
<td>93.2</td>
<td>70.0</td>
<td>2.3</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 6. The critical line (solid) and saturation line (dashed) of the setal directional adhesion with $\alpha_5 = 0$ and $\alpha_3 = \pi/4$. (Online version in colour.)
In order to see how the rotation of the setal proximal end affects the normal pull-off force, the critical loads for different $\alpha_s$ within a narrow range from $-15^\circ$ to $15^\circ$ were calculated and the results are plotted in figure 7. The figure shows that the influence of $\alpha_s$ on the pull-off force is not apparent, which means that the rotation of the seta does not affect the directional adhesion so much, as has also been observed by Autumn et al. [3].

(d) Energy analyses of the seta

Energy is involved in the attachment and detachment changes of the seta. As indicated by Majidi et al. [19], the stability of the fibril side contact can be evaluated by the second derivative potential energy $\Pi$ of the seta to the adhesive detaching length $a$ ($a = l_3 - l_{adhere}$). As shown in figure 8a for potential energy functions of different $F_t = 0, 5, 10, 15 \mu N$, the contour line of $d^2\Pi/da^2 = 0$ is explicit in figure 8a, named the ‘stable adhesion line’. Note that $d^2\Pi/da^2 > 0$ on the right-hand side of the contour line, representing the seta stable adhesion. For $F_t = 15 \mu N$, the curve is cut off at $a = 0.10 \mu m$, owing to the jump-off side contact after that value. The range of $F_t$ from 0 to $15 \mu N$ covers the dynamic threshold that each seta produces for a gecko, according to the work of Wang et al. [32], and thus is large enough to predict the gecko’s mechanical behaviour in most dynamic scenarios.
Figure 9. Curves of the seta under deformation. (a) Dragging and pressing along the natural path of the seta to preload the seta. Coloured dashed lines represent the seta of saturated adhesion and coloured solid lines represent those of stable adhesion. (b) Releasing by pulling against the natural path of the setae. (Online version in colour.)

We also draw the sum of the setal bending energy and surface energy $U (U = U_b + N(U_{b2} + U_{b3} + U_s))$ with respect to $a$ for different $F_t$ in figure 8b. This function reflects the energy consumption during the attaching and detaching procedures of the seta. As shown in figure 8b, when the adhesion is saturated ($a = 0$), $U$ is above $9.0 \times 10^{-11} \text{J}$. The state of saturated adhesion ($a = 0$) is not stable and requires almost 10 times higher energy than the stable adhesion. When $a$ increases, meaning the setal detachment, $U$ decreases sharply. Energy, most of which is elastic energy, is released because of detachment, despite some local occurrence of energy consumption within certain regimes when friction is less than $5 \mu \text{N}$. To achieve stable adhesion, the gecko only needs to bend the seta using a certain amount of work, which is almost unrelated to the friction changes. This means that the friction-dependent body locomotion would not affect attachment of the seta.

To illustrate the setal deformation, we draw the deformed curve of the seta in stable adhesion and saturated adhesion shown in figure 9a. We also show the seta at the pulled-out critical state with different friction conditions in figure 9b. As the figure shows, the attachment is accompanied by a dragging and pressing movement along the natural path of the seta, whereas the detachment requires releasing in the opposite direction. The terminating position where the seta reaches the stable adhesion line does not vary too much for various frictions. However, when the seta is in the saturation state, the friction force affects the seta deformation significantly. Comparing with the seta at the stable line in figure 9a, b shows that, when the seta is at the critical line, the larger the friction is, the earlier detachment occurs. This means that the gecko needs to take a longer route of detaching for a smaller pull-off force. In this route, the torque transferred from the seta to the spatulae reduces along with the decreasing bending. This phenomenon suggests that an adequate amount of torque prevents the external force from directly pulling the seta off, which ensures stable adhesion. Any attempt to pull off the seta without torque reduction will result in self-lock of the seta. Further pulling of the seta would result in friction exceeding the upper limit and sliding occurs. These results are in agreement with Gravish et al.’s work [6].

(e) The orientation of the setal stalk under various loading conditions

The setal shaft angle, which was reported by Autumn et al. in [3,27] as the ‘setal angle at detachment’, features the setal directional adhesion at the critical state. At the attached state,
the aligned angle between the spatulae and the substrate is another important parameter for the attachment of the seta to the surface. The two angles are related to the orientation of the setal stalk. As figure 10 illustrates, we studied the setal shaft angle with the substrate defined as $\alpha$ at the critical adhesion state. Moreover, we investigated the inclination angle between the setal distal ending surface holding the spatulae and the substrate defined as $\beta$ at the critical, stable and saturated adhesion state, respectively. The spatular uniform force production is assumed when $\beta$ is close to zero and the surface is parallel to the substrate.

In figure 11a, we plot $\alpha$ with respect to the critical adhesion, using different $\alpha_3 = 0, \pi/6, \pi/4, \pi/3$. This figure simulates Autumn et al.’s experiment in observing the setal angle at detachment, which is a function of the ‘perpendicular force at detachment’. As the figure shows, the angle curves almost coincide before the jumping-off side contact occurs. With $\alpha_3 = \pi/4$, the angle falls into the experimental range when $-F_{n, cri} > 6 \mu N$, covering the perpendicular forces of all the data points measured by the force-controlled experimental method, and those of most of the data points by the angle-controlled method. Large error occurs below $-F_{n, cri} = 5 \mu N$, mainly due to the ‘partial release’ mechanism that was neglected in our theoretical analysis. With $\alpha_3 = 0, \pi/6$, the curves only cross the experimental range with much less coverage of the critical adhesion. The curve even falls in no experimental range with $\alpha_3 = \pi/3$. This result supports the choosing of $\alpha_3 = \pi/4$ to capture the real gecko’s setal adhesion.

In figure 11b, we plot the changes of $\beta$ along with the friction in the three adhesion states as mentioned in §2d. As can be seen, when shifting from the free state to the stable adhesion state, $\beta$ increases from $-27^\circ$ (the natural inclination angle) to around $-10^\circ$, meaning that more spatulae will contact the substrate. Moreover, the parallel line ($\beta = 0$) is between the saturation line and the stable line. This means that, with more dragging and pressing towards the saturated adhesion, the seta is able to obtain uniform adhesion for each spatula at an intermediate point. For the saturation line, $\beta$ is as high as $25^\circ$ at $F_t = 0$, meaning that the spatulae tend to ‘project away’ and preloading cannot provide complete contact at low friction, as has been observed by Autumn et al. [3]. The saturated adhesion condition is thus not applicable at low friction. When shifting inversely to the critical line for detachment, $\beta$ decreases and the so-called ‘pitch outward’ occurs. $\beta$ reaches $-43^\circ$ at $F_t = 0$. The large $\beta$ angle suggests that the ‘pitch outward’ would cause ‘partial release’ of the seta. It may be a cause of our model prediction overestimating the critical adhesion at low friction when comparing with Autumn et al.’s experimental data. The two lines get closer to each other as $F_t$ increases and finally intersect at the maximum adhesion point around $\beta = -14^\circ$. The decreasing $\beta$ angle indicates that the shear dragging is necessary for uniform force distribution by each spatula in addition to producing higher critical adhesion.
3. The analyses of the digital behaviour

(a) The lamella-induced directional adhesion

In §2, we introduced an independent setal model, while at the meso-level directional adhesion is induced by the lamella from the toe to the setae. Considering the work of Tian et al. [11], and by observing the scanning electron microscopy (SEM) picture of the lamella structure (figure 12), we built up the sub-millimetre-scale lamellar model shown in figure 13a. The lamella is modelled as a cantilever supported by the digital skin, whose thickness is $h = 0.1$ mm. To simplify the calculation, the width is taken as $1/\sqrt{D} = 8.3$ μm, which just holds one single row of aligned setae. In the longitudinal direction the hairy zone’s (adhesive zone where setae grow) length is $c = 0.3$ mm, which contains approximately $M = 35$ setae, and the non-hairy (non-adhesive zone where no setae grow) length $l_0 = c/6$. As figure 13b shows, the setae are supposed to be uniformly pressed and dragged, and bending occurs in the non-adhesive part of the lamella. The convected coordinate is $(s, \theta_0)$. We here neglected the bending within the adhesive part of the lamella to simplify the calculation. The rotation of the lamella is also neglected. Thus, the potential energy of the lamella can be expressed as

$$\Pi_0 = U_{b0} + U_{p0}, \quad (3.1)$$

where

$$U_{b0} = \frac{1}{2} EI_0 \left( \frac{\partial \theta_0}{\partial s} \right)^2 ds, \quad (3.2)$$

and

$$U_{p0} = -MF_t \int_{\theta_0(s=0)}^{\theta_0(s=l_0)} \sin \theta_0 ds + MF_n \int_{\theta_0(s=0)}^{\theta_0(s=l_0)} \cos \theta_0 ds, \quad (3.3)$$

and $l_0 = h^3/12\sqrt{D}$ is the bending inertia of the lamella.

Using integrating and variation, we have

$$\frac{1}{2} EI_0 \left( \frac{\partial \theta_0}{\partial s} \right)^2 + MF_t \sin \theta_0 - MF_n \cos \theta_0 - M_0 = 0, \quad (3.4)$$

with geometric boundary condition

$$\theta_0|_{s=0} = \alpha_0 \quad (3.5)$$
Figure 12. SEM image of the cross section of a gecko’s lamella.

Figure 13. (a) The cantilever-like lamella model. (b) The bent lamella.

and

$$\theta_{0|s=l_0} = \frac{\pi}{2},$$  \hspace{0.5cm} (3.6)

and physical boundary condition

$$EI_0 \left( \frac{\partial \theta_0}{\partial s} \right)_{|s=l_0} = T,$$  \hspace{0.5cm} (3.7)

where $T$ is the torque caused by the reaction force at the contact points of the setae. Unlike the boundary condition of the spatular pad, the lamella does not contact the surface directly.
As previously mentioned, the spatulae can only serve as non-frictional revolute joints. Therefore, the torque is produced in the non-adhesive part rather than within the adhesive part of the lamella. Using the above results, we have

\[ T = MF_t \left( y_c + \frac{h}{2} \right) + MF_n \left( x_c + \frac{c}{2} \right), \]  

(3.8)

where \( x_c, y_c \) are the coordinates of the proximal end of the seta shown in figure 13.

Using a similar method, we have the following equations that describe the bending of the lamella in the directional adhesion:

\[ \int_{\theta|s=l_0}^{\theta|s=0} dt_0 = \frac{M_0 + MF_t \sin \theta|s=l_0 - MF_n \cos \theta|s=l_0}{\sqrt{1 - m_0 \sin^2 \theta|s=l_0}}, \]  

(3.9)

where

\[ M_0 = \frac{T^2}{2EI_0} + MF_t \sin \theta|s=l_0 - MF_n \cos \theta|s=l_0, \]  

(3.10)

and

\[ m_0 = \frac{2MF}{M_0 + MF}. \]  

(3.11)

As we have already obtained the directional adhesion of a single seta, the results can be integrated into the analysis for \( G. gecko \)'s lamella model to describe the attachment and detachment of the digit. We will discuss this in the following section.

(b) Analyses of the active digital hyperextension and digital gripping

The gecko’s digit produces forces mostly in the longitudinal directions. Contact force applies mainly in the fore–aft and up–down directions between the digit and the surface, which is similar to the function of a strip tape [32]. However, the gecko’s digit is hard to model as a tape, because it contains complex structures, including bones, tendons, tissues, blood, etc. Moreover, Autumn et al.’s study showed that the Kendall’s strip tape model for the digit does not match the frictional adhesion in experiment [27].

The lamella is a connector between the digit and the setae [11]. It can be directly controlled by the digit and its structure is much simpler than that of the whole digit. Therefore, to fit the real directional adhesion situation, we used the single lamella model to study the digital attachment and detachment. In the study, we used the functions of \( F_n = F_{n,cri}(F_t) \) for the critical situation, \( F_n = F_{n,stab}(F_t) \) for stable adhesion and \( F_n = F_{n,satu}(F_t) \) for saturated adhesion as shown in §2. By substituting these functions into (3.9), the proximal inclination of the lamella \( \alpha_0 \) can be calculated with a given external load.

In figure 14, we plot the bending angle of the lamella \( \Delta = \theta_0 - \theta|s=l_0 \) with respect to the friction force. For \( \Delta > 0 \), the lamella is ‘bent outwards’; otherwise, the lamella is ‘bent inwards’. We can see from the figure that for the critical state the lamella is bent outwards. The magnitude of \( \Delta \) does not rise sharply below \( F_t = 25 \mu N \) and its maximum is under 0.15°. The saturated adhesion line is below the critical line before reaching the intersecting point which represents the maximum adhesion capacity of a single seta. The stable adhesion line lies between them and is cut off at \( F_t = 15 \mu N \), due to the jumping-off side contact behaviour.

Figure 14 shows the \( G. gecko \)'s digital behaviour in the dynamic scenario. In the preloading and sustaining phases of the digit, the gecko needs to contact the surface first, then increase the adhesion and keep the load within the critical line. Therefore, friction is needed as well as the bending of the lamella. The magnitude of the bending angle depends on the external load and how stable the gecko needs to be. However, as the stable line is always below the critical line, the transition from the critical state to the stable state requires decreasing the bending angle of the lamella \( \Delta \), from outwards to inwards. On steep surfaces where gravity acts directly to pull the gecko off with little friction presented, the gecko needs to increase the friction by applying diagonal dragging to the feet towards the centreline of the body [33], and simultaneously grips
the digit to bend the lamellae inwards (figure 15). Pure friction shifting may also work, but the combination of friction shifting and bending inwards will ensure the adhesion state towards the stable line. The gecko has to repeat the gripping movement to regain local adhesion for each lamella.

In the floating phase, detachment from stable adhesion requires a reverse transition towards the critical line. Therefore, the active DH, which makes $\Delta$ increase and the lamella bend outwards, is needed (figure 15). Similarly, the combination of friction shifting and bending outwards will ensure approaching the critical line. For friction below 25 $\mu$N, $\Delta$ varies from $-0.10^\circ$ to $0.05^\circ$ when transitioning from the saturation line to the critical line. In the whole regime, $\Delta$ varies from $-0.10^\circ$ to $0.15^\circ$. In fact, the tiny bending angles are necessary for the stable adhesion and the non-sliding detachment, as they help apply the locking torque and release the locking torque of the seta accordingly. Furthermore, for the tiny angles the gecko is capable of quickly shifting from attachment to detachment, because the gecko does not need to completely adjust the friction force to zero before detaching. As previously mentioned, during the non-sliding detachment, elastic energy is released in the setal-level system. Therefore, the active DH provides an energy-saving way of detachment. In figure 16, we give the effective adhesive energy $W_{ad}$ of the lamella.
in detachment, neglecting the elastic energy return from the setae. Within $F_t = 25 \mu N$, the energy consumption is of the same order of magnitude at $10^{-3} \text{ J m}^{-2}$, whereas from $F_t = 25$ to $50 \mu N$ it increases from approximately $10^{-3} \text{ J m}^{-2}$ to approximately $10^{-2} \text{ J m}^{-2}$, covering two orders of magnitude.

If there were no lamella and the setae grew directly on the digital skin, the effective adhesive energy can be estimated using the plate deformation energy formula [21],

$$W_{ad} = \frac{E d_{\text{skin}}^3 u_1^2}{D_{\text{skin}}^2},$$

where $d_{\text{skin}}$ is the thickness of the digital skin, $u_1$ is the deformation and $D_{\text{skin}}^2$ is the area of the digital skin. As $u_1 = F_{n,\text{cri}}/K_{\text{eff}}$ ($K_{\text{eff}}$ is the effective stiffness of the digital skin), higher $F_{n,\text{cri}}$ will result in higher energy consumption. In this case, the gecko has to decrease the friction as much as possible for less energy consumption. Therefore, the lamellar structure is necessary to decouple the adhesive system from the dynamic system of the whole body.

4. Discussion

(a) The active digital hyperextension and the passive digital hyperextension

For some non-adhesive lizards, they use a different way of DH to detach, which means that they detach the proximal end of the toe prior to the distalmost end [1]. This is called passive DH. This phenomenon has rarely been observed in G. gecko, which uses its adhesive toe-pad to climb. In our model, if considering the passive DH, the gecko would tend to bend the lamella more inwards (figure 17), resulting in a torque increase to the seta and enhancing the stability of the setal adhesion. Therefore, in the passive DH, the gecko has to overcome the enhanced adhesion force and expend more energy to bend the lamella. The effective adhesive energy of the toe would increase. As a result of the long time evolution, the gecko takes advantage of active DH over passive DH, and, in this way, adapts to its habitat.

(b) The effects of the bending and rotation of the lamella

In the study, we assume that the row of setae are uniformly pressed and dragged when the lamella bends inwards, and simultaneously pulled out when the lamella bends outwards. However, it is possible that when detaching the lamella peels like a tape and the setae detach gradually.
during the peeling. When the lamella is pressed and dragged, the bending within the adhesive zone would alter the distribution of the load. To reveal this effect, we took account of the local deformation of the lamella induced by a single seta and used FEM to calculate the maximum bending angle between adjacent setal back within the adhesive zone. The results showed that the bending of the lamella is no more than $0.035^\circ$, which has little effect on the distribution force in the adhesive zone.

In addition, the rotation of the lamella was not considered in the proposed model. In the real situation, the lamella within the adhesive zone is not rigid as this could affect the distribution of the contact force. Considering the repulsive force acting between the lateral surface of the seta, we calculated the critical condition where the repulsive force occurs between the distalmost end fibrils. We found that $0 < \alpha_s < 0.3^\circ$. Therefore, the rotation is small enough to be negligible.

5. Summary and conclusion

In this paper, a hierarchical seta model was built, in which the side contact mechanism was taken into account to simulate the gecko’s directional adhesion. We established and solved a series of variation equations to obtain the critical line and saturation line with respect to the adhesive conditions. We also considered the effect of tiny proximal rotations in the analysis. The results show that the model can capture the directional adhesion feature of the gecko’s seta. This feature would not be affected by tiny rotations of the setal proximal end. Energy terms including the potential and bending energy with surface energy were calculated as a function of detaching length $a$. This proves that adhesion is stable when the seta returns energy in non-sliding detachment. The setal shaft’s curve and proximal end trajectory at different adhesion states were derived. The results demonstrate that a dragging and pressing movement is necessary for the attachment and an inverse movement is required for easy detachment.

By inspecting the bending of the lamella during the digital motion, the digital behaviour was studied to explain why the G. gecko always detaches via active DH and attaches via DG. A tiny transition from around $-0.10^\circ$ to $0.15^\circ$ is required for detachment, while an inverse transition is needed for attachment. The results further verify the necessity of the active DH and DG for easy detachment and stable adhesion in the directional adhesion configuration. A decoupled relationship between the effective adhesive energy induced by the lamellar proximal rotation and the friction below $25 \mu N$ is indicated. The meso-level analyses suggest that the lamella plays a key role in controlling adhesion and achieving fast, energy-saving detachment. This mechanism differs from the friction-dependent setal adhesion system which is controlled by the dynamic of G. gecko’s body.
Data accessibility. This work does not have any experimental data. The analysis is based on a series of energy variation equations and does not require or rely on any supporting data. The computation was carried out using Matlab R2014b of the MathWorks company.

Authors’ contributions. X. Wu investigated the technical background, carried out the computation work, interpreted the simulation results and drafted the manuscript; X. Wang helped interpret the simulation results, draft the manuscript and revise the manuscript; T.M. conceived of the study, designed the study, coordinated the study and helped revise the manuscript; S.S. helped investigate the technical background. All authors gave final approval for publication.

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