Cats use hollow papillae to wick saliva into fur

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The cat tongue is covered in sharp, rear-facing spines called papillae, the precise function of which is a mystery. In this combined experimental and theoretical study, we use high-speed film, grooming force measurements, and computed tomography (CT) scanning to elucidate the mechanism by which papillae are used to groom fur. We examine the tongues of six species of cats from domestic cat to lion, spanning 30-fold in body weight. The papillae of these cats each feature a hollow cavity at the tip that spontaneously wicks saliva from the mouth and then releases it onto hairs. The unique shape of the cat’s papillae may inspire ways to clean complex hairy surfaces. We demonstrate one such application with the tongue-inspired grooming (TIGR) brush, which incorporates 3D-printed cat papillae into a silicone substrate. The TIGR brush experiences lower grooming forces than a normal hairbrush and is easier to clean.

Cats have sweat glands only on their paws (15). Thus, it has long been hypothesized that grooming helps cats thermoregulate. Indeed, many other animals lick themselves to keep cool. Rats do so (16), and kangaroos even possess thin-skinned regions on their elbows (17) that are used especially for this purpose. The dairy industry sprays water on their cows to keep them cool, a common practice used to increase dairy yield (18). It has been speculated for two decades (8, 9). In our study, we show that the papillae in fact scoop shaped, enabling it to use surface tension forces to wick saliva. Surface tension is exploited by animals to drink, walk, climb, and jump (10–12). Cats use surface tension to pull up water during lapping (13), while dogs use their tongues like ladles to drink (14).

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Significance

Grooming and cleaning are part of a multibillion dollar industry from carpet cleaning to human hair care to pet grooming. Advancements in this field focus primarily on novel cleaning fluids, with less focus on brush development. This study focuses on the cat, one of nature’s most fastidious groomers. We discover structures on the cat tongue, hollow spines that we call cavo papillae, shared across six species of cats. The papillae wick saliva deep into recesses of the fur, and the flexible base of the papilla permits hairs to be easily removed from the tongue. These multifunctional spines may provide inspiration to soft robotics and biologically inspired technologies for sorting, cleaning, and depositing fluids into fur and arrays of flexible filaments.

Author contributions: A.C.N. and D.L.H. designed research, performed research, analyzed data, and wrote the paper.

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Next, we identified the largest cavo papilla from the center of the distal region in all six cat tongues. For the domestic cat tongue, this papilla is shown by the red circle in Fig. 2C. Before papilla removal, papilla height \( h_{\text{papilla}} \) was measured from the tissue surface to the tip of the papilla. The taller the papillae, the easier it can penetrate the fur during grooming, as shown in Fig. 3B. Despite the six species of cats spanning over 30-fold in body weight, their tongue papillae have constant height: \( h_{\text{papilla}} = 2.3 \pm 0.2 \text{ mm} \) \( (n = 6) \), as shown in Fig. 2D. A constant papilla height is suggestive of the papillae’s key role during grooming.

We measured the hardness of a domestic cat papilla and a freshly excised cat tongue from a domestic cat postmortem. The Young’s modulus of a domestic cat papilla is 1.66–1.94 GPa (three tests done on a single cat papilla), similar to human fingernails \( (21) \) and five orders of magnitude stiffer than the cat tongue tissue \( (9.1 \pm 3.7 \text{ kPa}; n = 2) \). We used these values in selecting materials for our cat tongue mimic as shown in a later section.

We cleaned a papilla from each of the six cat species and scanned them using micro-CT to generate the 3D models shown in Fig. 2B. A papilla’s unique features are made visible by the transparent view of the papilla in SI Appendix, Fig. S4. A cat papilla has two hollow regions: a cavity at the base for tissue attachment and a U-shaped cavity at the tip for wicking saliva. We report the papillae measurements for six cat species in SI Appendix, Table S3.

We conducted wicking experiments by contacting a drop of food coloring with the tip of domestic cat and tiger papillae. The fluid spontaneously rose into the U-shaped cavity in 0.1 s, as shown by the image sequence in Fig. 2E. Fig. 2F shows the time course of the front of this fluid into the papillae, where \( z \) is the distance from the papilla tip. The rapid rate of fluid rise is consistent with Washburn’s Law for wicking into a half-pipe \( (22) \). This wicking acts like a lock and key for the saliva: after it is wicked into the papillae, the fluid is quite stable, even if the papilla is turned upside down. To remove the saliva, the cat simply contacts its tongue with fur, as shown in Fig. 4.

While fluid rises quickly in the papilla, the combined fluid in all of the papillae is small compared with that available on the tongue surface. For the domestic cat, each papilla captures 0.014 \( \mu \text{L} \) of saliva for a total of 4.1 \( \mu \text{L} \) across 290 papillae or a 10th of an eyedropper drop. We dipped a severed cat tongue in water, allowing excess fluid to drip off, and found that the fluid in the papillae cavities accounts for 5% of total fluid on the top of the tongue. While it is not a large volume, we will show that the papillae penetration into fur allows saliva to reach areas that the tongue surface cannot.

**Papillae Height Dictates a Cat’s Groomability.** To characterize fur across cats, we measured by hand the hair radius \( r_{\text{hair}} \) and hair length \( L_{\text{hair}} \) of nine species of cats (Materials and Methods). Additionally, fur density \( \rho_{\text{fur}} \) and length values were gathered from the literature \( (23–25) \), giving us a total of 19 species of cats, the fur properties of which are given in SI Appendix, Table S4. To fully clean their fur coat, cats must distribute saliva to the hair roots. To determine if papillae are long enough to penetrate the fur coat and reach the skin, we consider a cat compressing its own fur, as shown in Fig. 3A. The cat fur coat has two layers: the topcoat and the undercoat. The topcoat consists of thick guard hairs, which are used to protect the undercoat from the environment. Although hidden from sight, the undercoat primarily consists of thin down hairs, which can outnumber guard hairs 24 to 1 and are used for thermoregulation \( (6) \). Given their predominance in giving cat fur its shape, we only consider down hairs in our analysis.

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**Fig. 1.** Kinematics of cat grooming. (A) A domestic cat grooms its fur. (B) Close-up view of its tongue showing the anisotropic papillae, which point to the left toward the throat. (C) The four phases of cat grooming. (D and E) Thermal images of a cat grooming its leg. White colors are hottest and dark blue colors are coolest as shown by the legend on the right. During the groom (D), fur is separated by the motion of the tongue, exposing the skin. Heat from the tongue and the skin are indicated by the white color. After the groom (E), evaporation causes a temperature drop of 17°C as shown by the dark purple.
American short-hair domestic cat compresses its fur from 37 to 1.2 mm, a tiger compresses its fur from 30 to 0.6 mm, and a Persian domestic cat compresses its fur from 81 to 2.6 mm. Fig. 3C shows the relationship between compressed fur height and papillae height for 20 cats. For six cats, the papillae height was measured directly; for the remaining 14 cats, a tongue sample was not available, and therefore, we used the average cat papillae height of $h_{\text{papillae}} = 2.3 \pm 0.2$ mm. Two distinct regimes are evident depending on the height of the compressed fur.

We compare cat furs using the fur’s porosity $\epsilon$, the fraction of air in a given volume:

$$\epsilon = \frac{V_{\text{air}}}{V_{\text{total}}} \tag{1}$$

where $V_{\text{air}}$ is the volume of air in a given volume of fur $V_{\text{total}}$. A cat’s uncompressed fur is composed of mostly air, with porosity values $\epsilon$ approaching 1 (0.97 for domestic cat, 0.98 for tiger, 0.99 for snow leopard). Like a down jacket, this large air fraction provides the cat excellent insulation from the elements. As the tongue presses down on the fur during grooming, air evacuates, decreasing fur porosity as shown in Fig. 3B. The minimum compression height can be calculated considering the geometry of the hairs, as shown in SI Appendix. Our calculations show the
fur. If a cat’s papillae can penetrate through its compressed fur and touch the skin ($h_{papillae} \geq h_{fur}$), the cat can successfully groom itself. The caracal, cheetah, and leopard are the most “groomable” cats due to their short, sparse fur. Even the snow leopard, known for its plush fur, can easily groom itself. Its fur is long but sparse, and therefore, its compressed fur has a height of only 0.6 mm, which is easily penetrated by its papillae.

Conversely, if the papillae cannot reach the skin ($h_{papillae} < h_{fur}$), much of its fur cannot be accessed, making the cat “ungroomable.” Long-haired domestic breeds, such as Persian domestic cats, are notorious for their matted fur if not cared for properly. According to Veterinary Centers of America (VCA) animal hospitals, Persian cat owners should comb their cat daily and give it baths monthly to redistribute the fur’s natural oils (26). Consistent with these care instructions, two Persian breeds and give it baths monthly to redistribute the fur’s natural oils. According to Veterinary Centers of America (VCA) animal hospitals, Persian cat owners should comb their cat daily and give it baths monthly to redistribute the fur’s natural oils.

Saliva Evaporation Can Help Cats Thermoregulate. An animal’s basal metabolic rate (BMR) reflects the amount of energy expended per unit time when the animal is at rest. This energy is necessarily expended as heat, and to avoid overheating, animals must find ways to transfer this heat to their surroundings. For domestic cats, the BMR is well predicted by an intraspecies allometric scaling (27, 28) of $BMR = 293M^{2/3}$, where $M$ is body mass in kilograms and BMR is in kilojoules per day. Based on this scaling, a domestic cat of mass of 2.2 kg must expel heat at a rate of 5.7 W to not overheat.

In an ideal scenario, all saliva held by the papillae would be deposited with each lick. This deposited saliva has the potential to cool the animal at a rate of

$$\dot{Q} = \dot{m}L_v,$$

where $\dot{m}$ is the amount of saliva deposited per unit time and $L_v$ is the latent heat of vaporization of water at a body temperature. For the average cat body temperature of 39°C, the latent heat of vaporization of water is $L_v = 575 \text{cal/g}$ (5). A domestic cat sleeps on average 14 h/d and grooms 24% of its awake time (29); therefore, a cat grooms 2.4 h/d. Based on the measured lick frequency of 1.4 licks per second and maximum total papillae cavity fluid of 4 μL, the domestic cat can deposit 48 g of saliva per day with its 290 papillae, where we assume the papillae are fully refilled in the mouth after every lick. If we consider saliva transfer by only the papillae distributing saliva close to the skin surface, we find that cooling rate $\dot{Q}$ can reach a maximum of 1.3 W, nearly 25% of the needed heat release. The remaining 75% of heat would be transferred by conduction, convection, and
radiation from the hairs, paws, and ears. The tongue tissue also wets hairs for added evaporation. Using a thermal camera, we see that saliva deposited on fur can generate a temperature difference of up to 17° C between skin and topcoat and increase the cooling rate even further (Fig. 1C). In the next section, we consider the mechanical benefits conveyed by the papilla’s flexible attachment to the tongue.

The Tongue-Inspired Grooming Brush. We designed and built the tongue-inspired grooming (TIGR) brush to measure the forces involved in grooming. Fig. 5A shows a cutaway view of the cat tongue, highlighting the streamlining of the papillae. Fig. 5B shows our device, which was built at 400% scale of the domestic cat tongue by using 3D models of the domestic cat papillae. Note that the flexible substrate allows both the tongue and the brush to conform to curved surfaces.

We pulsed the TIGR brush and a human hairbrush through faux nylon fur using our grooming machine. The time course of the forces observed is shown in Fig. 5 C and D, where the colors represent the successive grooms (starting with red and proceeding in order of the colors of the rainbow). During the first three trials of both brushes, grooming force peaked at 0.6–1 N. This is likely due to the brushes encountering tangles within the fur. If a papilla catches on a tangle, it can rotate outward to achieve a height of 9 mm, which increases the applied torque on the tangle (as shown in Fig. 5E). In a real cat tongue, the deformation of the soft tissue causes a papilla to increase exponentially in resistive torque as it rotates outward (30). After just four trials, the cat tongue mimic reached a steady-state grooming force of 0.2 N, less than one-half the steady-state force of the human hairbrush.

We surmise that the decreased forces were due to the streamlined posture of the papillae: if a papilla did not encounter a tangle, it remained at a height of 4 mm. After multiple grooms, both cat and human hairbrushes accumulated hairs. Because the human hairbrush’s bristles are imbedded into a stiff matrix, hairs must be removed with an implement, such as tweezers. The cat tongue brush is much easier to clean, because the papillae are streamlined. We found that a swiping motion along the papillae direction removed nearly all of the trapped fur in a single matted roll, as shown in Movie S4. In cats, hair removal from the tongue might be accomplished by rhythmic motion of the rugillae, the wavy patterns on the roof of the mouth.

Discussion
In this study, we highlighted one function of the papillae, but it is possible that there may be others. Previous studies suggest that papillae shape may help the cat with gripping food during eating (30). The sharp tip may help with tissue deformation and penetration into meat. It may also play a role in stimulating the cat’s own skin during grooming.

As shown in SI Appendix, Table S3, the longest papillae in our study were those of the lion at 2.7 mm or 35% longer than those of a domestic cat. This lion was female, but it is possible that male lions also have longer papillae to groom and wet their manes. In 1871, Charles Darwin (31) first postulated that male lions grow a thick mane around their neck for protection against fights with other males. Since then, it has been shown that the mane acts as a status symbol yet comes with a cost. Male lions endure higher heat stress than the manelss females, especially those with the darkest, most desirable manes (32). Grooming the mane may provide additional cooling effects to the burdened male lions.

Cat owners in the United States are numerous: nearly 35% of households own a cat, despite nearly 6 million Americans being allergic to cats (33). Cat allergies have been linked with the protein Fel d 1, which is highly concentrated within cat saliva, dermis oils, and anal glands. Previous research has shown high concentrations of Fel d 1 in the fur (34, 35). Our study on saliva-filled papillae may shed light on how the protein is spread and how the protein can be selectively cleaned from the cat. Current solutions to ameliorate cat allergies include allergy shots, pills for the pet owner (36), or a daily bath for the cat, painful for both pet and owner (33). Our TIGR brush might be used to distribute cleaning solutions or medications right onto the cat skin, and provide an alternate solution to cat allergies.

Conclusion
The cat tongue is a multifunctional tool, capable of distributing saliva to clean and cool the fur layer. In our study, we found that six species of cats, from domestic cats to lions, possess cavol pupillae with hollow cavities that spontaneously wick water. These papillae are necessary to apply saliva to the base of their hairs. Without these papillae, saliva on the tongue’s surface would only wet the top layer of fur, leaving fur underneath untouched. We used theory and experiments with a grooming machine to show how the papillae transfer water to cat fur. While the saliva in the papillae cavities only accounts for 5% of the total fluid on the top of the tongue, saliva deposition near the cat’s skin can provide up to 25% of the needed cooling for a cat’s thermoregulation. Our study culminates with a biologically inspired brush that applies lower force during grooming and is easier to clean than a standard human hairbrush.

Materials and Methods
High-Speed Videography, Kinematics, and Forces During Grooming. Using a Phantom Miro M110 high-speed camera at 500 frames per second, we filmed an adult short-haired domestic cat grooming its back fur. We also observed seven additional cat species grooming on YouTube videos. Tongue motion in all videos was tracked using Tracker software; kinematic data are tabulated in...
We designed and constructed a “grooming machine” that is able to pull a tongue across a sample of fur and measure respective grooming forces (SI Appendix, Fig. S2). An encoded motor (12V 25D-mm gear motor from Pololu.com), controlled by an Arduino microcontroller, drives a rack and pinion horizontally. The frame was constructed of 80/20 T-slotted aluminum. To measure grooming forces, we used an AMTI HE6x6 force plate, with 2.2-N capacity in the x and y directions and 4.4-N capacity in the z direction (into the plate).

Measurement of Fluid Transferred from Cat Grooming. Using the grooming machine, we simulated a grooming lick by pulling a severed, wetted cat tongue through a sample of cat fur at grooming speed $v_{\text{groom}}$ and grooming force of 0.1 N. We measured the change in weight of the wetted tongue to determine fluid transferred to the fur, accounting for evaporation.

Ethics. This study was approved by the Office of Research Integrity Assurance and conducted in accordance with all protocols filed under the Georgia Tech Institutional Animal Care and Use Committee. All tongue tissue samples were donated post mortem.

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