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## Drying dynamics of pellet feces†

Benjamin Magondu,<sup>†</sup> Alexander B. Lee,<sup>‡</sup> Andrew Schulz,<sup>a</sup>  
 Gabriel Cervantes Buchelli,<sup>a</sup> Michelle Meng,<sup>a</sup> Candice Kaminski,<sup>b</sup> Patricia J. Yang,<sup>d</sup>  
 Scott Carver<sup>†</sup> and David L. Hu<sup>†</sup> <sup>\*ab</sup>

Pellet feces are generated by a number of animals important to science or agriculture, including mice, rats, goats, and wombats. Understanding the factors that lead to fecal shape may provide a better understanding of animal health and diet. In this combined experimental and theoretical study, we test the hypothesis that pellet feces are formed by drying processes in the intestine. Inspirational to our work is the formation of hexagonal columnar jointings in cooling lava beds, in which the width  $L$  of the hexagon scales as  $L \sim J^{-1}$  where  $J$  is the heat flux from the bed. Across 22 species of mammals, we report a transition from cylindrical to pellet feces if fecal water content drops below 0.65. Using a mathematical model that accounts for water intake rate and intestinal dimensions, we show pellet feces length  $L$  scales as  $L \sim J^{-2.08}$  where  $J$  is the flux of water absorbed by the intestines. We build a mimic of the mammalian intestine using a corn starch cake drying in an open trough, finding that corn starch pellet length scales with water flux<sup>-0.46</sup>. The range of exponents does not permit us to conclude that formation of columnar jointings is similar to the formation of pellet feces. Nevertheless, the methods and physical picture shown here may be of use to physicians and veterinarians interested in using feces length as a marker of intestinal health.

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## 1. Introduction

The goal of this study is to investigate the origins of pellet feces shape. We define a piece of pellet feces as one whose length is no more than twice its diameter. Pellet feces are produced by laboratory rats and mice, domesticated animals such as horses and goats, and free-ranging species such as wombats and ibex (Fig. 1). Understanding the factors that influence feces shape may inspire non-invasive metrics to evaluate digestive health.

The diverse shapes of feces have long played a role in species identification.<sup>1</sup> However, the mechanism that leads to the diversity of shapes remains poorly understood. In 2020, we studied the bare-nosed wombat *Vombatus ursinus*,<sup>2</sup> an Australian marsupial

that produces cube-shaped feces (Fig. 1a). We hypothesized that this peculiar shape evolved as an anti-rolling mechanism that enabled feces to better aggregate when laid on top of rocks and stumps. Aggregation allows the feces to act as a physical and chemical marker of the wombats' home range. We presented a mathematical model that showed that the feces' unique cross-sectional shape is created by repeated peristaltic contractions of an intestine with non-uniform stiffness. While our model showed that square cross sections can be created through this process, we did not study the factors that led to the formation of shape as measured along the axis of the intestine. In the current study, we hypothesize that the drying process of feces within the intestines gives rise to regularly spaced cracks which determine the length of pelleted feces in a number of mammals, including the wombat.

The physical process of digestion is just beginning to receive the attention of fluid mechanics.<sup>3</sup> Chewing mixes saliva into food, creating a soft bolus. Swallowing is aided by lubrication of saliva along the esophagus. The stomach mixes the bolus with gastric juices, producing chyme, an acidic mixture that is sent to the small intestine. The small and large intestines continue digestion and absorption of water. At first, the liquid-like chyme completely fills the intestines like toothpaste in a tube. The physical processes that ultimately determine the shape of feces are peristalsis and absorption of water from the intestinal wall, which solidifies the chyme. Liquids fill the shape of their containers, and flow in response to applied stress (force per unit area).

<sup>a</sup> School of Mechanical Engineering, Georgia Institute of Technology,  
801 Ferst Drive, MRDC 1308, Atlanta, GA 30332, USA. E-mail: [hu@me.gatech.edu](mailto:hu@me.gatech.edu);  
Tel: +1-(404)-894-0573

<sup>b</sup> School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332,  
USA

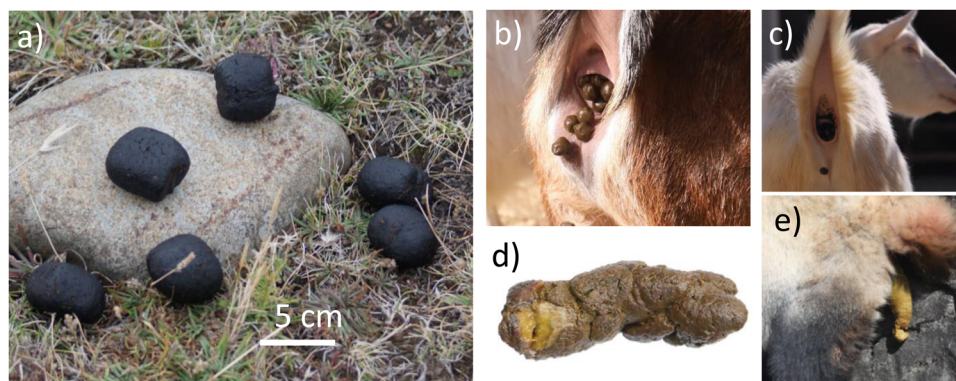
<sup>c</sup> Wallace H. Coulter Department of Biomedical Engineering,  
Georgia Institute of Technology, Atlanta, GA 30332, USA

<sup>d</sup> Department of Power Mechanical Engineering, National Tsing Hua University,  
Hsinchu, Taiwan

<sup>e</sup> Department of Biological Science, University of Tasmania, Hobart,  
Tasmania 7005, Australia

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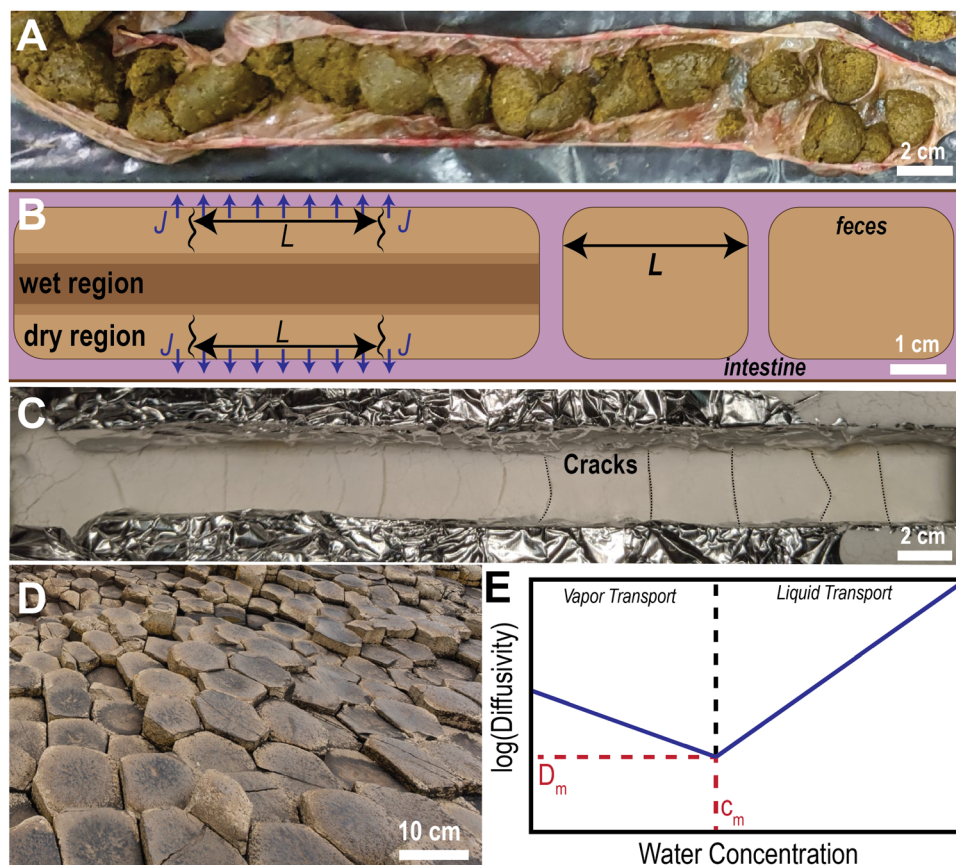
‡ Equal contributions.



**Fig. 1** The range of mammalian feces studied. (a) The cubic feces of the bare-nosed wombat atop a rock which the wombat uses as a latrine. The feces' flat faces keep them atop the rock without rolling down. These piles of cubic feces act as markers at the edges of the wombat's home range. Pellet feces from (b) a Nubian goat and (c) a Nigerian dwarf goat. Cylindrical feces from (d) a dog and (e) a panda.

In contrast, solid materials deform elastically under low stress, deform plastically under high stress, and ultimately fail at their maximum stresses. As the feces dry, they become more solid-like and susceptible to cracks. We hypothesize that the length of the pellet feces is determined by a cracking process long known to geophysics.

Geologists have long observed columnar jointings, which are naturally forming  $n$ -sided rock columns, where  $n$  can range from 3 to 7.<sup>4,5</sup> One of the most well-known examples is Giant's Causeway in Northern Island, an area featuring 40 000 hexagonal rock columns that resulted from an ancient volcanic fissure that slowly cooled (Fig. 2D). Such unique rock formations have



**Fig. 2** Crack formation in wombat feces, corn starch, and volcanic fissures. (A) Dissections of the distal region of a wombat's intestine showing the regular 2 cm crack spacing. (B) Schematic of feces queue in an intestine, showing the distribution of water content. Dark regions indicate wet regions and light regions indicate dry. As feces approaches the end of the intestine, it breaks into pieces. (C) Cornstarch drying experiments in narrow troughs show cracks at roughly constant intervals. (D) Giant's Causeway, a location in Ireland, containing the polygonal formations referred to as basalt columns. Image courtesy of Pixabay.<sup>53</sup> (E) The relationship between diffusivity and water concentration for porous materials.

inspired smaller-scale model systems in the laboratory based on drying corn starch. When lava cools, it shrinks, similar to a cake pulling away from a pan. Similarly, under the right conditions, drying corn starch cakes shrink, cracking into hexagonal columns. Such drying experiments are usually conducted in wide pans to imitate the wide exposed surface areas in geological settings. In this study, we performed experiments in one-dimensional troughs to simulate the conditions inside a mammal's intestine. We use corn starch as a model material for feces because of its qualitatively similar behavior to feces: when cornstarch cakes dry, segmentation and secondary cracking occur similar to human stools.<sup>6–10</sup> Feces cracking may also be influenced by peristalsis, a possibility that we address in the discussion section. For now, we neglect these forces and consider the drying-induced fracture alone.

By cutting away the corn starch as it dries, previous workers have obtained a good physical picture of the drying process, at least in planar settings. Planar cornstarch cakes do not dry homogeneously, but rather dry from the top down: a dry layer forms atop a deeper wet layer as shown in Fig. 2B and C. As the top layer continues to lose moisture, it contracts while the underlying wet layer maintains its volume. This mismatch in volume leads to increasing strain energy in the dry outer layer which is eventually relieved by a regular pattern of cracks. In short, shrinkage in the dry layer leads to cracking. Physically, the varying wetness in each of the layers are caused by a concentration-dependent diffusivity  $D(c)$  where  $c$  is the local water concentration.

When the corn starch cake is in a liquid state, its water concentration is at a maximum. Liquid water fills the pores, and diffusion decreases with decreasing water concentration. This trend is shown in Fig. 2E, which relates water concentration to diffusivity. As the water concentration decreases to a certain level, liquid can no longer span all of the pores, and the molecules begin to diffuse as vapor. Thus, diffusion increases with decreasing concentration.<sup>11</sup> At a critical water concentration  $c_m$  between these two regimes, diffusivity is at a minimum  $D_m$ . This minimum diffusivity  $D_m$  maintains a sharp transition between the dry outer layer in the vapor transport regime, and the wet inner layer in the liquid transport regime. This trend for diffusivity has been shown for corn starch cakes, a model system for large-scale geological systems.<sup>12,13</sup>

In this study, we use the corn starch model system (50 percent water, 50 percent corn starch by weight) as a model for mammalian feces. There is already qualitative evidence that feces crack similarly to corn starch cakes. Cracking in feces has long been observed, for example, in the Bristol stool chart, a medical tool for characterizing feces into seven types. Type three is designated as “a sausage shape with cracks in the surface,” which supports the idea that cracks occur in feces when sufficiently dry.<sup>14</sup> As the feces dries further, the surface cracks permeate deeper, as described by Bristol stool type two, “sausage-shaped but lumpy.” With further dryness, the cracks completely break the feces apart, as described by Bristol stool type one, “separate hard lumps, like nuts.” In our study, we go

beyond these qualitative terms to reproduce feces shape at varying levels of dryness using our corn starch model system.

Important to this study is a relationship we call the columnar-jointing hypothesis, which is an inverse relationship between the distance between cracks  $L$  and the rate of moisture flux  $J$ . Moisture flux  $J$  is defined as the ratio of the liquid volumetric flow rate and the cross sectional area through which it flows. The resulting flux  $J$  thus has units of length/time. The columnar-jointing hypothesis was first shown empirically,<sup>15</sup> and then reaffirmed through dimensional analysis:<sup>16</sup>

$$L \sim J^b \quad (1)$$

where  $b$  is the exponent that depends on geometry and the associated physics of heat or moisture transfer. Goehring<sup>12</sup> found  $b = -1$  for corn starch cakes and assumed that this exponent holds for planar media with constant Peclet number, where the Peclet number is a dimensionless group relating the advective transport rate to the diffusive transport rate. We hypothesize that the relationship eqn (1) holds for both mammals that create pellet feces and our one-dimensional corn starch cake drying experiments. Specifically, we expect that higher flux of water out of the feces leads to pellets of shorter length. One of the contributions of this paper is reporting the pellet length and water content for pellet feces, two variables that we will relate according to eqn (1). While we previously reported the length of cylindrical feces,<sup>17</sup> we now add pellet feces dimensions to give a more complete view of feces shape.

The columnar jointing hypothesis has not yet been proven theoretically, but the basic argument is worth noting here. Diffusion naturally redistributes moisture to make it more uniform throughout the porous solid. Thus, differences between the dry and wet layers are only achieved if water leaves the system at a sufficiently high rate so as to overcome the redistributing effects of diffusion. Higher rates of moisture flux  $J$  lead to greater discrepancy in water concentration in the outer layer relative to the inner, and thus greater stress build up in the outer layer. This higher stress in turn leads to the formation of more cracks per unit length, and thus smaller crack spacing  $L$ . The columnar jointing hypothesis was previously found to hold for planar corn starch cakes. In our study, we will test the hypothesis for the case of drying cylindrical feces in elastic intestinal walls. Such an experiment is difficult due to the requirement that the drying process must occur on the circumference of the intestine. We thus elected for a simpler experiment using rigid troughs where one exposed side evaporated the water.

In this study, we propose a mechanism for the formation of pellet feces in mammals. We begin in Section 2 with our experimental methods for measuring pellet feces of mammals and crack formation in drying corn starch cakes. In Section 3, we present the results of our experimental studies. We proceed in Section 4 to discuss the implications of this work and directions for future work. In Section 5 we close with our conclusions.



## 2. Methods

We report the detailed procedures for measuring length and water content of pellet feces, water content of wombat feces, and the flux-crack relationship in drying corn starch cakes.

### 2.1. Fecal length and water content measurement

We measured feces length and water content using feces collected from Zoo Atlanta and The Georgia Institute of Technology's animal care facility. Three to five pellets were collected from each individual and then brought to our laboratory. The length was defined as the greatest distance between opposite edges of the pellet. The width was defined as the maximum distance perpendicular to the length. Additional pellet lengths were found through literature research, with many data points coming from Scats and Tracks of North America.<sup>18</sup>

For water content measurements, mammals were observed for a defecation event. After the event, feces were collected immediately to prevent evaporation. A sample was placed in a plastic ziplock bag and weighed using a digital kitchen scale. The weight of the empty plastic bag was then subtracted. The feces was heated in an oven at 350° degrees F and baked for 10–15 hours to ensure all water was fully evaporated. Water content  $w$  was measured by weighing the sample to find  $m_{\text{wet}}$ , then baking the sample to dehydrate it, and re-weighing it again to find  $m_{\text{dry}}$ . The water content was then defined as

$$w = \frac{m_{\text{wet}} - m_{\text{dry}}}{m_{\text{wet}}} \quad (2)$$

Water content of fresh wombat feces was obtained from a humanely euthanized wombat that was the victim of a vehicle collision. The wombat was an adult male (>2 years old) dissected in 2019. Feces were removed from the distal colon.

### 2.2. Drying cornstarch experiments

Using a protocol adapted from Goehring,<sup>16</sup> we performed controlled drying experiments to mimic the drying of feces in the intestine. Here, the cornstarch slurry represents intestinal chyme, and the wooden trough represents the surrounding intestine. The drying and water flux measurement apparatus is shown in Fig. 4A. We made 600 g of cornstarch slurry containing equal parts (by weight) of cornstarch and water. The slurry was placed into a glass Pyrex dish (7.5 cm height  $\times$  15 cm inner width  $\times$  21 cm inner length). It was mixed for 5–10 minutes or until the slurry had no visible clumps. Then five spacers (3.5 cm  $\times$  1.5 cm  $\times$  19 cm) were inserted into the solution with edge-to-edge spacing of 1 cm. The spacers were constructed of wood covered in aluminum foil to make them waterproof. In order to maintain stability when placing the spacers, a small weight (55 g) was added to hold the spacers in place. When the spacers settled to the bottom, the weight was removed. An Exo-Terra™120 v 100 w intense basking lamp light with a 15 cm diameter lamp shade was placed at a fixed height above the dish. The height of the lamp, from 13 cm to 40 cm, was adjusted manually to achieve the different drying fluxes for each experiment.

Four drying experiments of 60–72 hour duration were conducted, with the dish mass recorded manually every 5–15 hours using a Kitchen Gurus digital food scale. The drying process was filmed with a Sony HDR-XR200V Digital HD video camera recorder to determine when crack formation occurred. At the end of the experiment, we photographed the crack structure and measured the crack spacing manually in MATLAB. The final images of each experiment can be seen in Fig. S1 of the ESI.† To determine the flux  $J$ , the time course of the mass of the dish was fit to a power law. Then a line was fit to the power law during the time segment when primary cracks were first observed, in this case the duration between 10 and 17 hours.

From the slope of the line,  $\frac{dm}{dt}$ , the flux was calculated  $J = \frac{dm}{dt}/(\rho A)$  where  $\rho$  is the density of water and  $A$  is the planar surface area of the dish.

## 3. Mathematical modeling

According to the columnar jointing hypothesis, the spacing  $L$  of the cracks in feces should be inversely proportional to the flux of water  $J$  into the intestines, such that  $L \sim 1/J$ . This idea holds for planar settings, whose cracks intersect to form polygons of a length scale inversely proportional to the flux of water evaporating from the surface.<sup>13,15</sup> However, the idea has not yet been tested in one-dimensional settings similar to that of intestines. In this derivation, we used animal diet data to infer a relationship between water flux and fecal crack spacing.

The columnar jointing hypothesis states that  $L \sim 1/J$ . We tested this hypothesis using previously measured relationships for scat length, feces mass, and water exchange across mammal sizes. As we will report in the Results section in eqn (13), pellet length  $L$  scales with animal body mass  $M$  according to  $L_p = 4.65M^{0.25}$  where  $M$  is body mass (kg). If the columnar jointing hypothesis is true, we expect  $J \sim 1/L \sim M^{-0.25}$ . In the following calculation of water flux  $J$ , we shall see if this is the case.

We use previous literature measurements from over 43 species of mammals to calculate a scaling law for the average flux  $J$  of water through the intestinal wall. To maintain equilibrium, we require that all water intake is either absorbed through the intestines or excreted in feces. This relationship may be written:

$$\dot{m}_{w,\text{in}} = \dot{m}_{w,\text{intestine}} + \dot{m}_{w,\text{out}} \quad (3)$$

where  $\dot{m}_{w,\text{in}}$  is the water intake rate (mass/time),  $\dot{m}_{w,\text{intestine}}$  is the water flux through intestinal walls, and  $\dot{m}_{w,\text{out}}$  is the water ejected through feces. Note that the water flux through the intestinal wall will in turn be ejected from the body through urine, sweat, or evaporation, but tracking that pathway is not necessary to understand feces shape.

The water intake  $\dot{m}_{w,\text{in}} = \dot{m}_{\text{in}} - \dot{m}_{\text{dry}}$  may be written as the difference between the total mass intake  $\dot{m}_{\text{in}}$  and the dry mass intake  $\dot{m}_{\text{dry}}$ . The total mass intake (kg per day)<sup>19</sup> and the dry mass intake (kg per day)<sup>20</sup> were previously reported as

$$\dot{m}_{\text{in}} = 0.097M^{0.97} (N = 41) \quad (4)$$

$$\dot{m}_{\text{dry}} = 0.0004M^{0.75} (N = 41) \quad (5)$$

The excreted water  $\dot{m}_{\text{w,out}} = w\dot{m}_{\text{out}}$  may be written as the product of the water content  $w$  (unitless) and the rate of defecation (mass/time). A previous compilation<sup>18,19</sup> of defecation rate showed

$$\dot{m}_{\text{out}} = 0.01M^{0.83} \quad (6)$$

Based on our literature search and our own measurements, we found water content of feces to be independent of body mass (see Table S2 in ESI†). Therefore, we set a conservative maximum water content for pelleted feces of

$$w = 0.65 \quad (7)$$

Now that we have scaling for the mass flux of water through the intestinal walls, we may calculate the water flux  $J$  using the definition

$$J = \dot{m}_{\text{w,intestine}}/(\rho A) \quad (8)$$

where  $\rho$  is the density of water and the surface area  $A = \pi L_{\text{colon}} D_{\text{colon}}$  pertains to a cylindrical intestinal wall of length  $L_{\text{colon}}$  and diameter  $D_{\text{colon}}$ . We only consider the colon because this is where the feces transforms from a watery chyme to its final solid shape.

We collected the length (cm) and diameter (cm) of the colon for 24 different species of mammals that generate pellet feces. Body masses were found from other sources.<sup>21,22</sup> We fit these data points to power law best fits, finding

$$L_{\text{colon}} = 0.31M^{0.69} \quad (9)$$

$$D_{\text{colon}} = 0.85M^{0.35} \quad (10)$$

respectively. In all, we may write the water flux as a combination of these scalings,

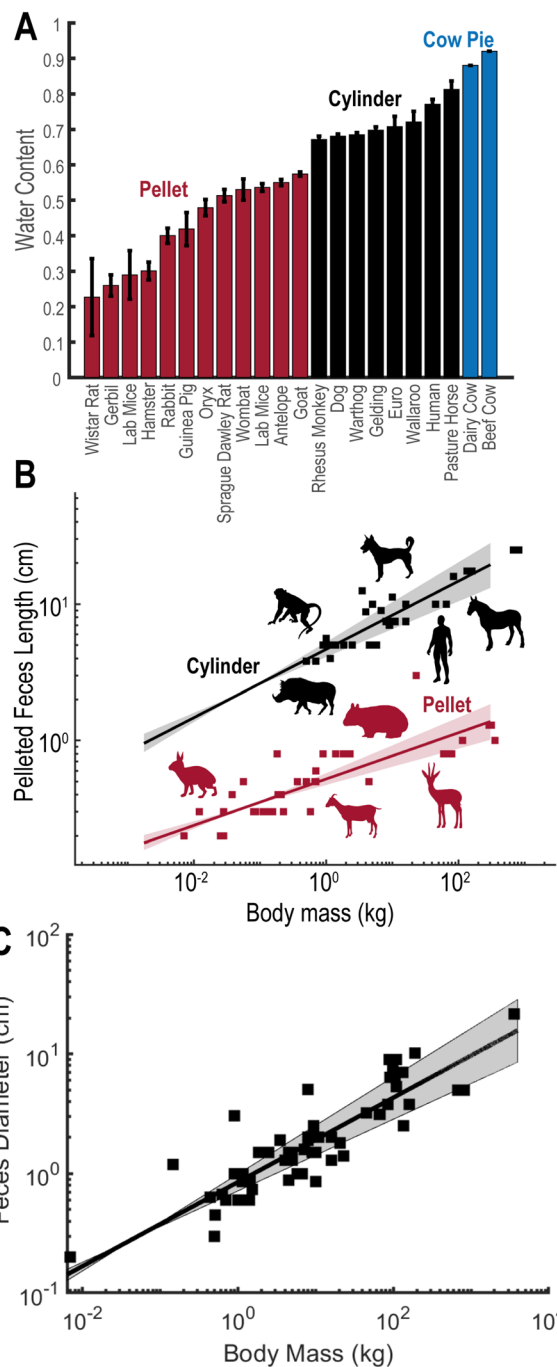
$$J = \frac{\dot{m}_{\text{in}} - \dot{m}_{\text{dry}} - w\dot{m}_{\text{out}}}{\pi \rho L_{\text{colon}} D_{\text{colon}}} \quad (11)$$

We substituted measured scalings into the above expression, eqn (11), and performed a best fit (see Fig. S3 in ESI†) to determine a single power law for the relationship between water flux and body mass,

$$J \sim M^{-0.12} \quad (12)$$

## 4. Results

We begin by characterizing the dimensions and water content of pellet feces. We report three kinds of feces in this report, pellet feces, cylindrical feces, and cowpies. A cowpie is a stool produced by cows. It is liquid-like and when poured on the ground resembles a pancake. Other mammals produce stools with circular or square cross sections. Such shapes are characterized by two dimensions, a length and width. Once a stool



**Fig. 3** (A) Water content of mammal feces, organized in order of increasing water content. The red columns indicate pelleted feces, the black columns cylindrical feces, and the blue columns cow pies. Pellets are drier than other feces, having a water content less than 0.65. Table S2 in the ESI† details each species' fecal matter water content. (B) The relationship between feces length and body mass. Red points are pellet feces and black points are cylindrical feces. (C) The relationship between pellet feces diameter and body mass. Power law best fits shown by the lines. Confidence bounds are listed in Table S4 of the ESI†. Images of animals are provided from Philopic.

lands on the ground, it can roll, bounce, and land in a random manner. Thus, we define the longest dimension of a stool as its length, and the diameter as the dimension measured

perpendicular to the length. If the length is less than twice the width, we define the stool as a pellet. If the length is longer than twice the width, we define the stool as a cylinder. For stools of square cross section, the square width was listed as the “diameter.” We collected the lengths of six pellet feces from Zoo Atlanta and ten from the literature. In addition, Fig. 3A shows the relation between body mass and feces length. Least-squares power law fits for pellet feces length and diameter are given by

$$L_p = (4.65 \pm 0.45)M^{0.25 \pm 0.04} (n = 56, R^2 = 0.89) \quad (13)$$

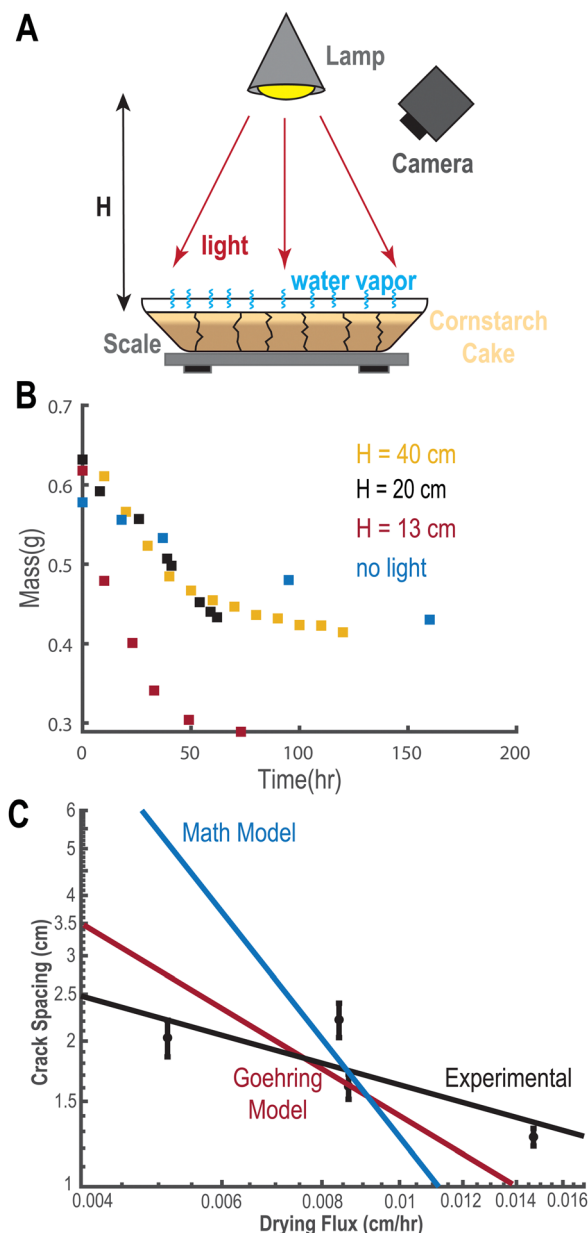
$$D_p = (0.85 \pm 0.14)M^{0.35 \pm 0.05} (n = 56, R^2 = 0.74) \quad (14)$$

where length  $L_p$  and diameter  $D_p$  are in cm and body mass  $M$  is in kg. The red points indicate pellet feces. The black points referring to cylindrical feces are given for comparison. The feces length is fairly described by a power law best fit. Fig. 3C shows the relation between body mass and feces diameter, which is more variable because of the different shapes that can occur. Given the three orders of magnitude of body mass reported, we use a common technique in scaling analysis: we neglect error bars because they appear illegible on log-log.

Our model relies on the hypothesis that pellet feces are sufficiently dry for cracks to occur. We test this hypothesis by directly measuring the water content of two species (the warthog and wombat) and collecting the fecal water content across 22 species found in physiology studies.<sup>23–43</sup> From these studies, we took the water content value from the control group that did not receive experimental interventions. Fig. 3A shows the water content of mammalian feces, arranged from lowest to highest water content. The resulting arrangement supports our hypothesis that pellet feces (the red columns) have water content  $w < 0.65$  and cylindrical feces (the black columns) have  $w > 0.65$ . Pellet-forming animals include mice, rats, moles, antelope and goats. Generally, animals such as monkeys, warthogs, horses, and humans have cylindrical feces. For reference, human feces has a water content of 0.75.<sup>44</sup> Note that the very wettest fecal states, such as the cow pie, are up to 90 percent water and thus do not have enough solid matter to form either pellets or cylinders.

Although a wombat's cubic feces is not circular in cross section like the other pellet feces, it still has a water content of 0.54, characterizing it distinctly in the pellet feces category.<sup>2</sup> Note that the wombat feces did not start out that way: chyme in the proximal colon has a high water content of 0.80. Samples appear pelleted as they approach the distal colon and have a lower water content of 0.54. As chyme flows down the intestine, water is continuously absorbed, and cracking begins to occur.

Using scaling laws, we may be even more quantitative for the flux of water  $J$  through the intestinal walls. Flux is defined as the ratio of volumetric flow rate of water to the surface area through which the water flows. Larger animals will likely consume more total mass of water per day, but they also will have greater surface area of intestine to absorb this water. By keeping track of the intestinal surface area, the water content of food eaten, and the rate of feces produced, we show in eqn (12)



**Fig. 4** Corn starch drying experiments to mimic feces in the intestine. (A) Experimental setup for drying corn starch cakes. (B) Time course of the mass of the corn starch cakes for four trials. The legend gives the distance from the lamp to the cake. (C) The relationship between corn starch pellet length and drying flux, both measured experimentally and plotted on a log-log scale. The black circles represent experimental values, and the error bars represent standard error. The black line indicates the power law best fit of the experimental data shown by eqn (16). The blue line indicates the mathematical model based on mammal water intake rates, eqn (15). The red line indicates the Goehring columnar jointing hypothesis, eqn (1) with the pre-factor optimized to best fit the experimental data.

in the Math Modeling section that the flux scales as  $J \sim M^{-0.12}$ . We now interpret this finding in light of our pellet size measurements. From our measurements in eqn (14), we have pellet feces length  $L_p \sim M^{0.25}$ . Combining eqn (12) and eqn (14), we have  $J \sim L_p^{-0.12/0.25} \sim L_p^{-0.48}$ , which we may rewrite as

$$L_p \sim J^{-2.08} \quad (15)$$

This exponent has the same sign as that of the columnar jointing hypothesis,  $J \sim L^{-1}$ , but the substantial difference in exponents suggests other mechanisms might be at play. To gain more insight into the pellet length scaling, we conduct experiments with drying corn starch cakes.

We perform four experiments of drying corn starch cakes at three different fluxes associated with different heights of the heat lamp shown in Fig. 4A. We observe the formation of primary cracks that run perpendicular to the trough walls, as shown in Fig. 2C. Secondary cracks also formed within 24 hours as shown in Supplementary Fig. S1 (ESI†). The time course of the mass of the corn starch cakes is shown in Fig. 4B. Because of the diffusion processes outlined in the introduction, mass did not decay linearly but with exponential decay. In all trials, the primary cracks formed within 10 to 17 hours of heating. We approximated the pertinent flux as the average flux during this window of time. Fig. 4C shows the relation between the flux and the crack spacing, whose power law best fit is given by

$$L = 1.6J^{-0.46} (R^2 = 0.896) \quad (16)$$

where  $L$  is in units of cm and  $J$  is in units of  $\text{cm h}^{-1}$ . The power law fits the data well. In summary, our mathematical modeling yields  $L \sim J^{-2.08}$ , experiments yield  $L \sim J^{-0.46}$ , and Goehring's hypothesis is  $L \sim J^{-1}$ . There is substantial spread between the three exponents, so it will take further work to determine if drying-induced cracking indeed influences the formation of pellet feces.

## 5. Discussion

Our mathematical modeling and experiments were designed to test the columnar jointing hypothesis in a one-dimensional intestine. Here we list a few caveats. Most data from our biological survey came from North American mammals. Animals outside North America were often outliers: for example, the Australian bare-nosed wombat has feces of width 2.5 cm and length 4 cm, longer than the feces of similarly-sized mammals. Moreover, the feces shortest dimension was in the axis of the colon, different from feces of other animals. The wombat also has an exceptionally long colon, whose large surface area causes the water flux (flow rate/surface area) to be lower than that of most mammals. The columnar jointing hypothesis states that flux and feces length are inversely proportional. Thus, a low water flux potentially explains the exceptionally long feces for wombats. To more strongly establish the trends found here, we would need one-to-one measurements of pellet length and water flux.

Other important considerations we neglected include peristaltic contractions and intestinal pressures which may apply additional forces on feces. Intestinal pressures in humans range from 2 kPa in the colon to 4 kPa in the rectum.<sup>45–49</sup> In other animals, rectal pressures have similar magnitude, from 0.1 to 10 kPa.<sup>17</sup> Peristaltic contractions are a feature inherent to digestion. Recent methods have been developed to measure the

wavelength of peristalsis *in vivo* in rats. The observed wavelength of 1 cm is comparable to the length of the rat feces, but further work is needed to show that peristalsis may influence feces shape.<sup>50</sup>

According to our biological survey of mammals, cracks occur when fecal water content drops below 0.65. Above this water content, feces are an elongated cylindrical shape. Based on trends for porous media such as corn starch, a critical water content of 0.33 signifies the transition between liquid and vapor diffusive transport.<sup>51</sup> In comparison, it is surprising that the pellet feces from a wide range of species had water contents below 0.65. Future workers may one day confirm our finding that 0.65 is the critical water content for feces by direct measurement. Goehring *et al.*, for example, performed such tests using a series of drying experiments with corn starch and collecting small samples at various distances from the surface of the corn starch cake.<sup>12</sup>

Our observation that pelleted feces form when the water content is below 0.65 is further supported by considering human feces. The Bristol Stool Chart maps qualitative descriptions of human feces to quantitative values from 1–7, with 1 indicating constipation and 7 indicating diarrhea. Of note, a Bristol number of 1 describes the feces as hard nuts that are difficult to pass. The physical description of the feces is similar to that of pelleted feces. In fact, feces characterized as a Bristol number 1 had a water content of 0.65, very similar to the threshold water content for pelleted feces found in this study, and much lower than the typical human fecal water content of 0.75.<sup>14</sup>

Future workers may consider the appearance of pelleted feces during human constipation. In many animals, water removal from feces is made possible on the molecular scale by aquaporins, a family of proteins that transports water across membranes.<sup>52</sup> It is intriguing that pelleted feces are considered normal for many animals, but are difficult to expel for humans. Future comparative studies may consider the evolutionary trade-offs of pelleted feces as well as adaptations allowing for pelleted feces to be dispelled. By understanding how pelleted feces form, we may gain a better understanding of how to prevent and treat human constipation.

## 6. Conclusion

The goal of this study was to show that pellet feces length is governed by the same principles as prismatic rock column formation. Underlying this study was the hypothesis that crack spacing is inversely proportional to flux of water. We presented a mathematical model of the flux of water through intestines using available data on intestinal geometries, defecation, and eating rates. We then mimicked feces drying within an intestine using drying corn starch cakes in troughs. The scaling laws found using theoretical and experimental methods varied significantly from each other and Goehring's hypothesis. Future work will be needed to determine whether drying dynamics occurs within pellet feces.



## Conflicts of interest

There are no conflicts to declare.

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