Self-buckling of filamentous cyanobacteria reveals gliding forces

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Filamentous cyanobacteria are one of the oldest and today still most abundant lifeforms on earth, with manifold implications in ecology and economics. These phototrophic organisms form long and flexible filaments that exhibit gliding motility in contact with solid surfaces. The underlying force generating mechanism is not yet understood. We measure their bending rigidity with micropipette force sensors, and investigate how filaments buckle after gliding onto an obstacle. Comparing Kirchhoff theory to the experiments, we derive the active forces and the friction coefficients associated with gliding from the observed critical filament length for buckling. Remarkably, we find that these two quantities are strongly correlated to each other, while dependencies on other observables are largely absent. The observed critical lengths align with the peaks of natural length distributions: small changes in active forces or length distributions may determine whether the majority of a colony undergoes buckling instabilities or not.

INTRODUCTION

Self-propelling rod-like micro-organisms are abundant in nature, holding key positions in many ecosystems. Myxobacteria [1], for instance, recently gained significant attention as a model system for pattern formation in crowded situations [2]. Here we investigate organisms from one of the oldest, yet today most widespread phylogenetic clades: Filamentous cyanobacteria. These phototrophic organisms played an important role in the paleoclimate of our planet, having generated the atmospheric oxygen [3, 4] on which animal life is based. Today, they are commonly known for their role in giant marine or limnic blooms, which may pose ecological and economical threats [3–6], but also enable bioreactor applications, for instance as a renewable energy source [3]. Many species from many genera exhibit gliding motility when in contact with solid surfaces or other filaments, but no swimming motion [7]. The mechanism behind gliding appears to be distinct from myxobacteria [8, 9], and remains debated in literature [10–18]. Understanding the collective phenomena in colonies of filamentous cyanobacteria is a key element in interpreting fossil and sediment structures [19–21], managing blooms [22, 23], or optimizing bioreactor efficiency [24]. At the base of these phenomena lie the properties of the individual filament, but neither their bending rigidity nor their propulsion forces have been investigated.

Here we quantify the bending moduli $B$ of filaments from two species, *Kamptotema animale* and *Oscillatoria lutea* (Fig. 1 A and B, respectively) by micro-three-point bending tests (Fig. 1 C) and demonstrate that the gliding force density $f$ can efficiently be quantified by making use of self-buckling (Fig. 1 D). The concept goes back to the
work of Leonhard Euler in 1780 [25-28] and is adapted to
to self-propelling filaments [29, 30]: Individuals that exceed
a certain critical length \( L_c \) buckle when they glide onto an obstacle. Buckling changes the orientation
of the head or may trigger a direction reversal, enabling
the organism to escape from traps. By recording numer-
ous collision events, we obtain a comprehensive statistics
to derive \( L_c \). Using Kirchhoff beam theory, we derive an
analytical expression for the prefactor in \( L_c \), and numer-
cally calculate the evolution of the filament shape upon buckling. This continuum-theory is in perfect agreement
with molecular dynamics simulations of self-propelled,
semi-flexible particle chains. Comparing experiment with
theory, we derive the propulsion force densities and fric-
tion coefficients of the living filaments. The correlation
between force and friction supports an adhesion-based
propulsion mechanism. The critical lengths we found are
close to the peak in the length distribution in freely grow-
ning colonies, indicating the importance of this quantity
for their self-organization.

**RESULTS**

**Bending measurements**

The bending moduli \( B \) of individual filaments of \( O.
\) lutea and \( K. \) animale were measured by microscopic
three-point bending tests [31, 32]. Filaments that glide freely across liquid-immersed micro-pillar decorated sur-
faces (SU-8 on glass) were pushed into a gap between
two pillars (base diameter \( \sim 35 \) µm, pitch \( \Delta x = 80 \) µm)
with a Micropipette Force Sensor (MFS, spring constant
9.5 nN/µm, see Fig. 1 C). Experiments were recorded
with an inverted microscope at 20× magnification and
40 fps. The deflection \( d \) of the pipette is proportional to the
load \( P \) acting on its tip, which is calibrated indepen-
dently. The base of the pipette was actuated with a con-
stant speed of \( \pm 5 \) µm/s to increase and release the force.

Pipette and filament deflections were analyzed with a
custom image analysis procedure in MATLAB (see Method-
mics and Materials and [33–35] for details).

Figure 2 A shows an exemplary force-displacement curve,
the experiment on the islets, for \( K. \) animale. The measured force-distance
relation is continuous, linear, speed-independent, and
free of hysteretic effects, allowing an analysis with stan-
dard beam theory to derive the effective bending modulus
through \( B = (\Delta x^3/48) \partial P/\partial d \). Occasionally, measure-
ments showed non-ideal force-distance relations, which
could be traced back to long filaments that were entan-
gled between pillars at some distance to the measuring
site. These measurements were not considered in the fur-
ther analysis.

FIG. 2. Micro-three-point bending tests and flexural
modulus. A, Representative force-deflection relation for \( K.
\) animale. Insets: Snapshots of the experiment. B, Box plot of the bending stiffnesses for \( N = 35 \) individuals (each tested
3–6 times) of \( K. \) animale and \( O. \) lutea. Box limits denote the
first and third quartile, whiskers the last measurement within
1.5× the inter-quartile distance away from the respective box
limit. Diamonds denote the outliers.

Each individual filament was typically tested three to
six times at different locations along its contour. The
mean and standard deviation were calculated separately
for each individual (see supplementary material for a col-
lection of individual measurements). We observed no sys-
tematic dependence of \( B \) on the length of the filament
or the position along the contour. The mean bending
rigidities of 35 individuals were then analyzed for their
median and quartiles to obtain typical population distri-
butions. Fig. 2 B shows the quartiles of the bending
stiffness in a box plot, indicating rather symmetric dis-
butions with some outliers toward larger stiffnesses.

**Buckling measurements**

The buckling behavior of \( O. \) lutea and \( K. \) animale was
observed by optical microscopy in quasi-two-dimensional
microfluidic compartments filled with liquid medium (see Fig. 1 D and Methods and Materials). The channels were
either 20 µm or 40 µm wide and ended in a tapered ob-
stacle. The height of the chambers was approximately
5 µm, only slightly larger than the diameter of the fila-
ments, such that motion and buckling was confined to the
x-y-plane. After loading cyanobacteria to the device,
microscopy images were taken at 6× or 10× magnifica-
tion with time intervals of 1 s, 10 s, or 30 s for a couple of
hours. Filaments explored the entire device and stochas-
tically entered the channels that direct them onto the
V-shaped traps (opening angle 90°). After colliding, the
filaments escaped these traps, either by reversing their
gliding direction or, if they buckled, due to the reorien-
Frequently, individual filaments were observed multiple times, finding that the previous buckling behavior is not reproduced. In total, we collected 388 collision events for *O. lutea* and 280 for *K. animale*.

The observed events were classified as buckling or non-buckling manually by visual inspection (Fig. 3 A). The length $L$ as well as the free gliding velocity $v_0$ prior to hitting the obstacle were determined by automated image processing (see Data analysis). Buckling frequencies (Fig. 3 B & C, bars) were evaluated by binning the observations into fixed intervals of the contour length $L$. Frequently, individual filaments were observed multiple times, finding that the previous buckling behavior is not readily repeated. These multiple observations of a single individual were weighted with the inverse of the number of observations of that individual, to obtain an unbiased representation of the population.

The weighted events were analyzed by a logistic regression of the buckling probability

$$ p = \text{sig}(x) = \frac{1}{1 + e^{-x}}, \quad (1) $$

with $x = (L - L_c)/\Delta L_c$. The median critical length $L_c$ and the width of its distribution $\Delta L_c$ are obtained by maximum likelihood estimation (see Logistic regression). The results are depicted as the dashed curves in Fig. 3 B and C. For *O. lutea* we find $L_c \pm \Delta L_c = (161 \pm 35) \mu m$ and for *K. animale* $(148 \pm 18) \mu m$. Median, quartiles, and 5th and 95th percentiles of the sigmoid are shown in the box plot in Fig. 3 D.

In an over-damped motion with co-linear friction, the propulsion force $f$ and the free gliding velocity $v_0$ of a filament would be directly proportional to each other, $f \sim v_0$. Thus, since $L_c \sim f^{-1/3}$, one may expect also a strong correlation between $L_c$ and $v_0$, as observed immediately before hitting the obstacle. In order to investigate such a possibility, we include $v_0$ as a second independent variable to the logistic regression, by setting $x = (L - L_c(v_0))/\Delta L_c$ in Eq. (1), with $L_c(v_0) = (\alpha v_0)^{-1/3}$, to reflect our expectation from the scaling arguments. Fig. 3 E and F show the buckling behavior as color code in terms of the filament length $L$ and the free gliding velocity $v_0$ prior to hitting the obstacle. The $L_c(v_0)$ from the maximum likelihood estimation is shown as black lines on top of the individual events, and in Fig. 3 G for both species as a function of $v_0$, together with the result from the simple logistic regression. The critical length at the mean velocity, i.e. $L_c(\bar{v})$, aligns well with the one-dimensional regression.
Within the observable range of velocities, the median critical length remains fairly constant, as compared to the rather broad distribution, indicated by the bands in Fig. 3 G. However, we were not able to observe short and fast filaments of K. animale, which might be caused by physiological limitations [7]. For neither species, filaments slower than ~0.5 μm/s were observed. Therefore the trend in Fig. 3 G should not be over-interpreted, and we conclude that the velocity has a minor influence on \( L_c \) while buckling is predominately triggered by the length of the filament.

Buckling theory and profile analysis

In the classical self-buckling theory by Euler, the critical length for a vertical column, clamped at its lower end and free to move at its upper end, of uniform bending modulus \( B \), subject to a gravitational force density \( f_g \), is given by \( L_c = (7.837 B/f_g)^{1/3} \) [28]. The buckling of our active filaments differs in two aspects: the propulsion forces are oriented tangentially instead of vertically, and the front end is supported instead of clamped. Therefore, all initial orientations of filaments with \( L < L_c \) are indifferently stable, while for \( L > L_c \), buckling induces curvature and a resultant torque on the head, leading to rotation [29].

We use classical Kirchhoff theory for a uniform beam of length \( L \) and bending modulus \( B \), subject to a force density \( \vec{b} = -f \vec{t} - \eta \vec{v} \) that is composed of an active force \( f \) acting tangentially (unit tangent vector \( \vec{t} \)) toward the head, and an effective friction (coefficient \( \eta \)) opposite and proportional to the local velocity \( \vec{v} \). We assume a vanishing twist and a planar configuration, and parametrize the beam by its orientational angle \( \phi(s) \) as a function of the contour coordinate \( s \) (see Fig. 1 D), to obtain the Kirchhoff equation [36]

\[
B \partial_s^2 \phi - \vec{n} \cdot \int_s^L ds' \left( f \vec{t}(s') + \eta \vec{v}(s') \right) = 0, \tag{2}
\]

where \( \kappa = \partial_s \phi \) is the curvature and \( \vec{n} \) is the unit normal vector. The head of the filament \( (s = 0) \) is subject to a localized force \( \vec{P} \) that balances the load integral and thereby fixes its position. The tail \( (s = L) \) is naturally force-free, and the two boundary conditions are vanishing torques at the head and tail of the filament:

\[
\kappa|_{s=0} = \kappa|_{s=L} = 0. \tag{3}
\]

The local velocity is expressed through

\[
\vec{v} = \partial_s \vec{x} = \partial_s \int_0^s ds' \vec{t}(s') = \int_0^s ds' \vec{n}(s') \partial_s \phi(s'). \tag{4}
\]

Inserting Eq. (4) into Eq. (2) and changing the order of integration, the inner integral can be evaluated to obtain

\[
B \partial_s^2 \phi - \vec{n} \cdot \left\{ \int_s^L ds' \left( f \vec{t} + \eta (L - s') \vec{n} \partial_s \phi \right) \right\} + \eta (L - s) \int_0^s ds' \vec{n} \partial_s \phi \right\} = 0. \tag{5}
\]

Eq. (5) is solved by the method of lines (see Numerics and Fitting and supplementary material).

To derive the critical self-buckling length, Eq. (5) can be linearized for two scenarios that lead to the same \( L_c \): early-time small amplitude buckling and late-time stationary rotation at small and constant curvature [29]. Here we focus on the latter, see supplementary material for the former. Scaling \( s \) by \( L \) and \( t \) by \( t_0 = L^4 \eta/B \), a single dimensionless parameter remains, the activity coefficient \( \kappa = L^3 f/B \). Seeking stationary rotor solutions \( \phi(s,t) = \phi(s) + \omega t \), rotating with angular frequency \( \omega \), Eq. (5) reduces to (in scaled units)

\[
\partial_s^2 \kappa + (1 - s) \kappa + \omega s = 0. \tag{6}
\]

This second order ordinary differential equation is subject to three boundary conditions, \( \kappa|_{s=0} = \kappa|_{s=1} = \partial_s \kappa|_{s=1} = 0 \), hence fixing \( \omega(k) \). The trivial solution \( \kappa = 0 \) with \( \omega = 0 \) is amended by a first non-trivial branch of buckled filaments at \( k \approx 30.5722 \ldots \), the root of a combination of hypergeometric functions which is given in Numerics and Fitting. Thus, in physical units, the critical length is given by \( L_c = (30.5722 \ldots B/f)^{1/3} \), which is reproduced in particle based simulations, see supplementary material.

We will now compare the evolution of theoretical profiles from Eq. (5) to the evolution of the experimental buckling contours. The latter were extracted from the micrographs with an in-house trained convolutional neural network with modified U-Net architecture [37] (see Fig. 4 A, green contour) and tracked from the moment of impact until parts other than the head made contact with the confining walls. This limitation narrows down the available data substantially because buckling frequently induced contact with the channel walls early on during the profile evolution. As the residual for fitting theoretical profiles to the experiments, we used the square distance between the experimental and theoretical profiles, integrated along the contour. The activity coefficient \( k \) and time scale \( t_0 \), together with a global rotational and two translational degrees of freedom, were then adapted to minimize the sum of the residuals over all time steps of the recorded evolution. In order to estimate the error of the fit, we applied a very coarse bootstrapping, repeating the fit 20 times with randomly chosen subsets of the time steps.

Fig. 4 A shows a representative time series of micrographs for the evolution of a buckling filament, together with the extracted contour and the fitted solution of Eq. (5). The active force \( f \) and the friction coefficient...
DISCUSSION

Remarkably, the median active forces for the two species, as derived from the logistic regression, match almost perfectly, $f \sim 1.0 \text{nN/µm}$, even though $O. \text{lutea}$ and $K. \text{animale}$ are currently associated to different genera. The logistic regression gives a good estimate for the whole population, and the distribution derived from of individual profile fits is centered around this median. This similarity indicates a potential homology of the gliding apparatus between the two species.

The comparison with Kirchhoff theory allows us to measure active forces and friction coefficients on an individual basis, going beyond the population mean. Thus it allows for a more insightful analysis, correlating, for instance, these values with length and free gliding speeds. We see no significant correlation between $L$ or $v_0$ and $f$ or $\eta$, but the observed values of $f$ and $\eta$ cover a wide range. For over-damped free gliding and a co-linear friction relation, we expect (and may derive from our theory, setting $\vec{b} = 0$) $f = \eta v$. Thus, $f/v$ provides another estimate of the friction coefficient. Importantly, the two estimates are measured in (predominantly) orthogonal directions: tangentially for free gliding friction and transversely for the buckling evolution. Thus we plot $f/v$ over $\eta$ in Fig. 4 B, finding a nearly linear trend over about two decades. This relation is remarkable in two aspects: On the one hand, it indicates that friction is indeed mainly isotropic. Therefore, we may conclude that it is governed by external friction, i.e. from lubrication forces, while the available power of the gliding apparatus is not rate limiting: the latter would greatly enhance the effective tangential friction coefficient. On the other hand, it indicates that friction and propulsion forces, despite being quite variable, correlate strongly. Thus, generating more force comes, inevitably, at the expense of added friction. This supports the argument of focal adhesion [8] as the underlying mechanism of the gliding apparatus of filamentous cyanobacteria; more contacts generate more friction. This supports the argument of focal adhesion [8] as the underlying mechanism of the gliding apparatus of filamentous cyanobacteria; more contacts generate more friction, thereby increasing friction to the same extent. Still we emphasize that many other possibilities exist.

One could, for instance, postulate a regulation of the generated forces to the experienced friction, to maintain some preferred or saturated velocity.

Finally we remark that the distribution of $L_c$, due to its dependence on $f^{-1/3}$ with a relatively small exponent, is more narrow. The median $L_c$ aligns well with the peak of natural length distributions (see supplementary material). As a consequence, small changes in $f$ (or the length distribution) determine whether the majority of the filaments in a colony is able to buckle or not. This, in turn, has dramatic consequences on the exploration behavior and the emerging patterns [38–41]: $(L/L_c)^3$ is, up to a numerical prefactor, identical to the...
flexure number [39, 42], the ratio of the Péclet number and the persistence length.

METHODS AND MATERIALS

Cell cultivation

Species Oscillatoria lutea (SAG 1459-3) and Kamp-tonema animale (SAG 1459-6) were obtained from The Culture Collection of Algae at Goettingen University and seeded in T175 culture flask with standard BG-11 nutrition solution. The culture medium was exchanged for fresh BG-11 every four weeks. Cultures were kept in an incubator with an automated 12 h day (30% light intensity (≈ 20 µE, 18°C) and 12 h night (0% light intensity, 14°C) cycle, with a continuous 2 h transition. All experiments were performed at a similar daytime to ensure comparable phases in their circadian rhythm. The night cycle began at 11 a.m. so experiments could typically be started in the morning towards the end of the bacteria’s day.

Bending measurements

Rectangular arrays of cylindrical micropillars (base diameter 35 µm and pitch of 80 µm) were fabricated using standard SU-8 photo-lithography on glass substrates. In order to make a liquid-filled chamber for the experiment, two glass slides, the bottom one exposing the pillars, were sandwiched on top of one another, separated by an O-ring cut in half. After filling the chamber with standard BG-11 nutrient solution, a small fragment from our cyanobacterial bacterial cultures is introduced into the chamber with a syringe.

As filaments glided and thereby dispersed into the pillar-decorated surface, a small region with sparsely distributed individual filaments is chosen for measurement. Then, a filament is bent between two pillars with the nozzle of the L-bent glass micropipette force sensor (spring constant 9.5 nN/µm), mounted on a closed-loop piezo actuator.

Image sequences of deflections were recorded at 20 x magnification and 40 fps with an Olympus IX-83 inverted microscope and a scientific CMOS camera (PCO Edge). The images were then analyzed with a custom-made image analysis procedure in MATLAB, to determine the deflections of the filament and the pipette simultaneously. The deflection of the micropipette is obtained by subtracting the time-dependent position of the piezo controller, which is actuating the base of the pipette, from the nozzle position in the image. The obtained data of the applied force and filament deflection results in a linear plot as shown in Fig. 2 A.

Buckling experiments

We prepared microfluidic devices according to standard procedures of SU-8 clean-room photolithography, followed by PDMS-based soft lithography [43], binding the cured PDMS imprints to rectangular glass cover slip by plasma activation (Electronic Diener Pico plasma system, 50% exposure, 30 seconds). Prior to binding, two 1 mm holes for flushing the device with BG-11 medium, and one 2 mm hole for loading cyanobacteria to the device, were punched in the PDMS, keeping the punch-outs for sealing the chip later on. Four different device architectures, each with 20 µm and 40 µm wide channels, with heights of ~ 5 µm were used.

The devices were first flushed with approximately 5 µL of conditioned BG-11 medium, through one of the small ports. Then, about 1 mm³ of blue-greenish cyanobacteria were loaded to the device through the large port. Finally, the device was sealed with the cylindrical stoppers retained from the punching, and covered by a small round cover slip to minimize evaporation from the device during the experiment.

Buckling experiments were observed by a Nikon Ti2-E inverted microscope on a passive anti-vibration table, with transmitted illumination at about 20 µE illumination intensity. Microscopy images were taken at 6x- or 10x-magnification with time intervals of either 1 s, 10 s and 30 s for a couple of hours at a resolution of 4096 x 4096 pixels with a CMOS camera (Dalsa Genie Nano XL).

Image analysis of buckling events

Regions of interest were cropped from the image sequences for each of the manually detected collision events, from 50 s before to 50 s after the collision, and analyzed further. The length of each filament was obtained by manually adding a path on top of the images in a standard image editor (GIMP). The decision whether a filament buckles or not is made manually by watching the video of each event. The velocity is determined by extracting the position of the head of a filament prior to hitting the obstacle for up to six snapshots, and taking the mean travelled distance over this period.

Profiles were extracted only for selected events in which no additional collisions of the filament with the confining walls were observed for at least ten seconds after the first contact of the head with the obstacle. First, the microscopy images were processed by an in-house trained, modified U-Net to detect their mid-lines (contours). These contour representations of the images were then vectorized into subpixel-accurate x-y-coordinates, to obtain the green contour from Fig. 4 A.
Logistic regression

We perform a logistic regression on the individual (weighted) buckling events with a maximum likelihood estimation. This classification algorithm approximates the probability distribution by a logistic function; see Eq. (1). By maximizing the log-likelihood, we find the parameters that best predict the buckling probability. The likelihood of correctly predicting the buckling \((y = 1)\) or non-buckling \((y = 0)\) behavior of a filament of known length \(L\) is given by

\[
P(y|L) = \left[ \frac{L - L_c}{\Delta L_c} \right]^y \cdot \left[ 1 - \frac{L - L_c}{\Delta L_c} \right]^{1-y},
\]

(7)

with two parameters \(L_c\) and \(\Delta L_c\) that describe the median critical length and the width of the distribution, respectively. Each individual \(i\) with length \(L_i\) is observed \(N_i\) times to determine the buckling outcomes \(y_{i,j}\). The log-likelihood for representing all the data by a logistic distribution is then given by

\[
\log \mathcal{L}(L_c, \Delta L_c) = \sum_{i,j} \frac{y_{i,j}}{N_i} \log \frac{L_i - L_c}{\Delta L_c} + \frac{1 - y_{i,j}}{N_i} \log \left[ 1 - \frac{L_i - L_c}{\Delta L_c} \right]
\]

(8)

where the weight of each observation is given by \(1/N_i\), the number of observations of individual \(i\), to yield an unbiased estimate for the subsample of the population. Maximal \(\mathcal{L}\) requires vanishing derivatives of \(\log \mathcal{L}\) with respect to the parameters \(L_c, \Delta L_c\). Here, we choose the limited-memory Broyden-Fletcher-Goldfarb-Shanno algorithm (LBFGS) [44, 45]. For the regression with two explanatory variables \(L\) and \(v_0\) i.e., \(L_c(v_0) = (\alpha v_0)^{-1/3}\), the same procedure is used, adding the derivative with respect to \(\alpha\) to the minimization criteria.

Numerics and fitting

The evolution of the contour shapes according to Eq. (5) was derived for 30 different values of \(k\), ranging from just above the critical length up to \(L/L_c \sim 9\), by a numerical solution of Eq. (5). Eq. (5) was discretized into \(n = 64\) segments, defining the discrete \(\phi_i\) on the midpoints of the intervals. Second order polynomial interpolation was then used to evaluate differential and integral terms. Time integration was performed with the method of lines, initiating with a solution to the linearized small-amplitude equation. Snapshots of the solution were stored for 64 times, ranging form small amplitude to head angles \(\phi(s = 0) \sim 90^\circ\). These profiles were linearly interpolated in \(s\) and \(t\) to obtain a continuous function for fitting to the experimental contours.

In the fitting, first the theoretical profile with the smallest mean square distance is determined, with time and \(L_c\) as free parameters. Rotation and translational degrees of freedom were also included since initial orientation and position of the filament are arbitrary. The average over these individual fit results were then used as initial parameters for a global fit, where the sum of the residuals of all time steps was minimized for a global set of the time scale \(t_0\) and the critical length \(L_c\).

To derive an analytical expression for the critical \(k\) in Eq. (6), we first solve the homogeneous equation by

\[
k_{\omega=0} = c_1 \text{Ai} \left( k^{1/3}r \right) + c_2 \text{Bi} \left( k^{1/3}r \right),
\]

(9)

with \(r = s - 1\), and give a particular solution to the inhomogeneous equation:

\[
k = k_{\omega=0} + \frac{1}{k} - r^2
\]

\[
\cdot \left( \begin{array}{c} 0F_1 \left( \frac{4}{3}; \frac{k}{9} \right) \frac{1}{3}F_2 \left( \frac{1}{3}; \frac{2}{3}; \frac{4}{3}; \frac{k}{9} \right) \\
- \frac{1}{2} 0F_1 \left( \frac{2}{3}; \frac{k}{9} \right) F_2 \left( \frac{2}{3}; \frac{4}{3}; \frac{5}{3}; \frac{k}{9} \right) \end{array} \right),
\]

(10)

where the \(F_q\) are the generalized hypergeometric functions. The parameters \(c_1\) and \(c_2\) are determined by the torque boundary conditions. Then, \(k\) is found form the remaining force boundary condition, which boils down to the roots of

\[
2k_0 F_1 \left( \frac{4}{3}; - \frac{k}{9} \right) F_2 \left( \frac{1}{3}; \frac{2}{3}; \frac{4}{3}; - \frac{k}{9} \right) + 0F_1 \left( \frac{2}{3}; - \frac{k}{9} \right) \left( 2 - k F_2 \left( \frac{2}{3}; \frac{4}{3}; \frac{k}{3} \right) \right) = 2.
\]

The smallest root is \(k \approx 30.5722\).

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