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Adhesion–stiffness competition in caterpillar crawling enhanced by non-linear elasticity and buckling

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ABSTRACT

Caterpillars move very efficiently traversing arboreal, geometrically uneven and extremely varied environments through a complex mechanism that allows highly adaptable, stable and bone-free locomotion. The gait efficiency is vital for these animals at their larval stage, since it significantly increases their survival chances in the very short period in which they have to eat, grow quickly and shed their skin multiple times for finally performing the metamorphosis, one of the most profound and fascinating transformations in nature. As demonstrated recently, the signature of the caterpillar crawling gait can be identified in the way it operates, coordinating periodic muscle contractions and substrate grip ruled by a unique competition between body elasticity and adhesion of suction-cup-like abdominal prolegs, which test shapes, anchor surfaces and recognise roughness of material substrates to adapt and orient locomotion modes and speeds. To upgrade previous mechanical models and more faithfully capture further experimentally observed caterpillar gait features, which in fact appear more pronounced in some species, we propose to incorporate large deformations, nonlinear elasticity and buckling instability of the body segments, showing how the synergy of all them makes evident additional important strategies actuated by caterpillars for enhancing their crawling gait, maximising elastic energy release, skipping intermediate states and selecting the most energetically favourable locomotion sequence. It is felt that, by deciphering how soft invertebrates exploit non-linear elasticity, adhesion and buckling to optimise and stabilise their movement, this work might contribute to better understand animal biomechanics and to design next-generation bio-inspired climbing and multi-legged soft robots.

1. Introduction

Soft robotics has increasingly turned to nature to design machines capable of navigating unstructured environments (Ci & Guo, 2025; Guo et al., 2022; Iida & Laschi, 2011; Kim & Cha, 2023; Kortman et al., 2025; Kulkarni et al., 2025; Laschi & Cianchetti, 2014; Tang et al., 2020; Trimmer, 2008; Wu et al., 2023). Soft-bodied organisms represent a successful paradigm of adaptable locomotion achieved entirely without a rigid skeleton (Calisti et al., 2017; Hochner, 2011; Kulkarni et al., 2025; Wang et al., 2017, 2024; Xavier et al., 2022). By exploiting tissue compliance, these invertebrates seamlessly traverse diverse complex terrains. Consequently, decoding and fully understanding their fundamental biomechanics is a critical prerequisite for engineering next-generation bio-inspired soft robots (Hu et al., 2018; Laschi & Cianchetti, 2014; Trivedi et al., 2008; Xavier et al., 2022).

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As a primary example of this biological blueprint, caterpillars exhibit highly efficient and adaptable crawling locomotion (Cornejo et al., 2025; Trimmer & Issberner, 2007; Trimmer et al., 2006; Van Griethuijsen & Trimmer, 2014), a remarkable trait that has long served as a valuable source of inspiration for advancements in soft and bio-inspired robotics. In previous research (Argenziano et al., 2026a, 2026b, 2026c, 2025), the fundamental mechanical principles of this locomotion modality – specifically, the competition between surface adhesion and axial stiffness – were successfully described using deliberately simplified, one-dimensional linear models. However, while commonly adopted in the literature (Argenziano et al., 2025; Schuldt et al., 2015) for describing this larva locomotion, such unidirectional approaches ultimately prove insufficient to capture the overall kinematics (Brackenbury, 1997, 1999). Specifically, they fail to account for the bending curvature of the body (Trimmer et al., 2012; Wang et al., 2009) that may characterise the actual motion of the soft invertebrate, as illustrated in Fig. 1.

This competition between adhesion and elasticity is accompanied by a distinct arching of the caterpillar body, which may be more or less pronounced depending on the animal's morphology and biological features (Hayashi & Sugiura, 2021; Johnston & Levine, 1996; Lin, 2011; Lin et al., 2009; Lin & Trimmer, 2010, 2011; Saunders et al., 2011; Van Griethuijsen & Trimmer, 2014). This deformation encompasses a combination of bending and buckling phenomena that serve a crucial purpose: not only does it accommodate the physical curvature, but it also actively assists in the proleg detachment mechanism, providing the mechanical advantage needed to overcome adhesive forces. Therefore, to faithfully capture this complex detachment process in which the adhesion–stiffness interplay is enhanced by the body arching, it is essential to move beyond linear elasticity, also including constitutive and geometric non-linearities.

To bridge this gap, the present study introduces a two-dimensional mechanical model specifically designed to rigorously account for the bending curvature of caterpillars during forward progression. This distinctive arching is typically triggered by an inelastic contraction initiated at the terminal appendage of the animal (Johnston & Levine, 1996; Simon et al., 2010; Van Griethuijsen & Trimmer, 2014; Woods Jr et al., 2008). Within our proposed approach, the segmented body of this soft invertebrate is modelled and discretised into a series of structural elements endowed with bending rigidity. Simultaneously, the axial compressibility of the body is represented through the implementation of longitudinal elastic elements that exhibit a non-linear mechanical behaviour. Following past approaches (Argenziano et al., 2026a, 2025), a Winkler-like foundation bed (Gerolymos & Gazetas, 2006; Hetényi, 1946) simulates the interaction prolegs-substrate along the horizontal direction.

To accurately reflect the hyperelastic nature and the capacity of the soft animal to experience large deformations (Argenziano et al., 2026c; Dorfmann et al., 2007; Lin et al., 2009), a specific neo-Hookean constitutive formulation (Cowin & Doty, 2007; Horgan et al., 2004; Puglisi & Saccomandi, 2016; Saccomandi et al.) is employed. Starting from the discrete multiple degrees of freedom (M-DoFs) system adopted, this research introduces a reduced-order discrete paradigmatic scheme, which is essential for the analytical evaluation of the critical inelastic displacement. More in detail, the attainment of the critical inelastic contraction localised at the terminal proleg represents *de facto* the trigger of the buckling phenomenon, causing the animal's body to suddenly snap into its characteristic arched configuration and detaching from the substrate. This theoretical framework yields closed-form critical displacements that are then prescribed to equivalent continuous structural models, which allow for the step-by-step reconstruction of the entire process of the bending curvature and crawling motion of the larva.

Consequently, this work aims to provide a comprehensive analytical and numerical tool to deeply understand the full complexity of the biomechanics of caterpillar locomotion, thus refining previous mechanical models and including the non-negligible effect of the body arching that aids the animal in lifting from the substrate. It is therefore felt that this research could provide a significant upgrade with respect to the existing literature, thus establishing a robust theoretical foundation for the advancement of next-generation soft robotics.

The paper is organised as follows: Section 2 proposes a detailed description of the mechanical model, while specific minor theoretical aspects are addressed in the Appendix; Section 3 reports the numerical results obtained by implementing the previously described model on selected samples; finally, Section 4 summarises the main findings and concluding remarks.

2. Mechanical model

2.1. Two-dimensional analysis of caterpillar locomotion

Building on previous research (Argenziano et al., 2026a, 2025), we generalise the one-dimensional (1D) mechanical model (see Fig. 2a and 2b) with a two-dimensional (2D) discrete system in order to account for the bending curvature of caterpillars during locomotion, schematically sketched in Fig. 2e. Following the same approach adopted in the above-mentioned works (Argenziano et al., 2026a, 2026c, 2025), the segmented body of the soft-invertebrate is discretised into a series of beam elements characterised by bending rigidity $E_V I$ and negligible axial stiffness, which has been instead uploaded on longitudinal springs linking each lumped DoF, as depicted in Fig. 2c. The horizontal springs represent the axial stiffness of both the body segments and their connecting joints (highlighted in brown in Fig. 2b and 2e). The set of horizontal Winkler-like springs (with constant stiffness appointed as k_2) modelling the substrate–animal interaction of the 1D model of past research has been maintained here by adding further supports that constrain the vertical displacements of the abdominal and terminal segments (see Fig. 2c). The Lagrangian Coordinates of the model are the horizontal and vertical displacements of the body subunits' centre of gravity, with the sole exception of the prescribed inelastic contraction Δ applied to the terminal proleg for triggering and maintaining the locomotion. This approach enriches the movement kinematics of the model, allowing to fully characterise the bending curvature of the animal during the crawling gait. The mechanical parameters adopted in the proposed model are derived from previous research (Argenziano et al., 2026c, 2025), to which the reader is referred for a more detailed explanation and a comprehensive physical justification.

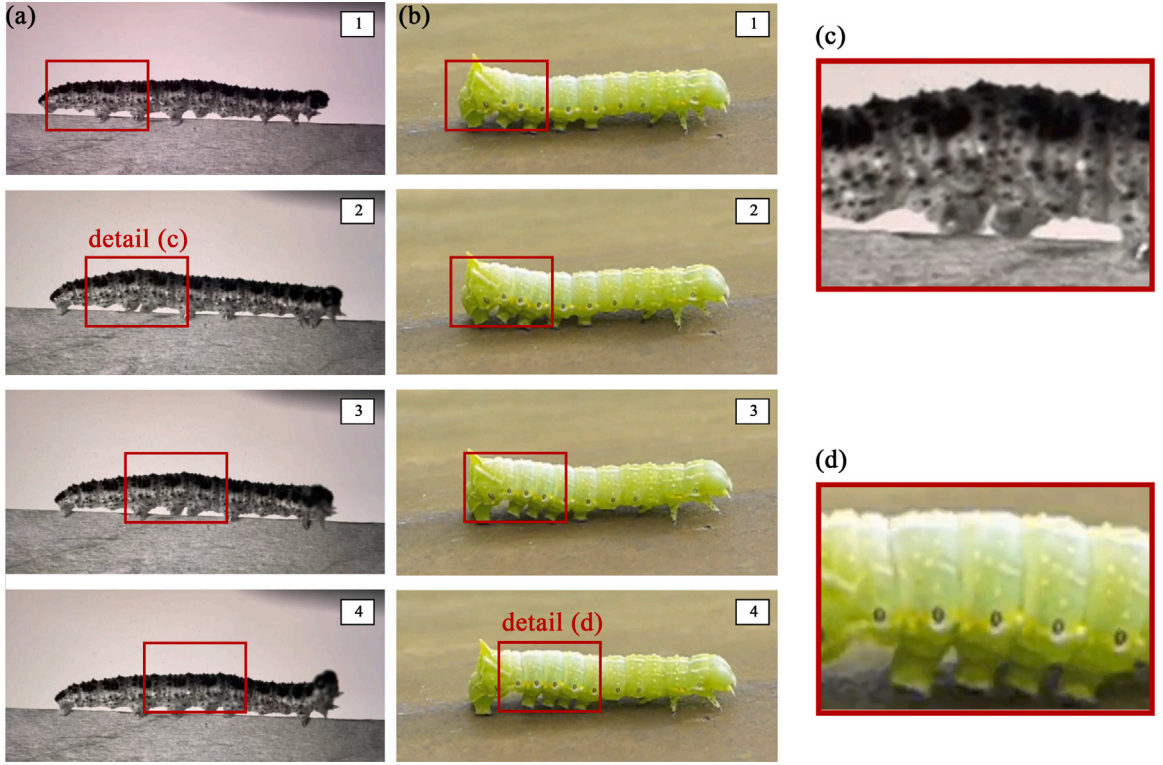


Fig. 1. Forward locomotion of caterpillars: body arching (highlighted in the red rectangles) driven by an inelastic muscle contraction initiated at the terminal proleg. Comparison between two larva species: *Pieris brassicae* on the left-hand side (part a) and *Amphipyra pyramidea* on the central side (part b). In parts (c) and (d), two in-zoom views are reported, in order to emphasise the body arching. Source: Snapshots are adapted from Argenziano et al. (2025).

To analytically evaluate the critical Δ that triggers buckling in a portion of the caterpillar body thus inducing bending curvature of the soft-invertebrate, we introduce an intentionally simplified lumped-parameter model (Fig. 2d) derived from the one shown in Fig. 2c, by condensing the mechanical properties of the elements between two consecutive prolegs into discrete components. Specifically, the total bending stiffness of the segment is lumped into a single equivalent rotational spring (k_φ or $2k_\varphi$) depending on the number of body segments separated by two consecutive anchors and the axial stiffness is split into two equal parts (k_1 or $2k_1$) that are function of the resting length of the body portions distributed along the longitudinal axis (Fig. 2d). To trace back the progressive proleg detachment, as also specified in Argenziano et al. (2025), we refer to 4 potential mechanical configurations, each one characterised by the release of once at the time of the Winkler-like constraint modelling the proleg, as depicted in Fig. 3b, c, d and e.

2.2. Closed-form solutions of a paradigmatic scheme for evaluating the buckling onset

In order to analyse the elastic instability of the caterpillar, we further simplify the discrete system reported in Fig. 2d, by assuming a minimalist paradigmatic model that can be updated and calibrated for each possible mechanical configuration (see Fig. 3). By lumping the flexural stiffness of the caterpillar's body segments into a single central rotational spring and representing axial compressibility via non-linear elastic springs, also accounting for the elastic response of the residual part through an additional spring with stiffness k_0 , the formulation effectively reduces the order of a multiple degree-of-freedom discrete system. This paradigmatic scheme can successfully capture the critical displacement at which the structure can no longer withstand axial compression and suddenly snaps into an arched configuration. Ultimately, it provides mathematically elegant and easy-to-manage expressions that can be used to trace back the curvature of the soft animal in a fully parametric way. We study the system as a function of the inelastic Δ , defining it by two Lagrangian parameters: the longitudinal stretch, λ_L (which is equal for both springs due to the rotational spring's self-equilibrium condition), and the rotation of the first spring, φ .

Within this perspective, the total potential energy of the paradigmatic system can be defined as the sum of the hyperelastic potential of the longitudinal springs Ψ_λ , the bending potential Ψ_φ of the rotational hinge, and the elastic contribution of the residual part of the system activated by the inelastic displacement Δ , as reported in what follows:

$$\Pi = 2\Psi_\lambda(\lambda_L, \lambda_T) + \Psi_\varphi(\varphi) + \frac{1}{2}k_0(\Delta + 2L(\lambda_L \cos \varphi - 1))^2, \quad (1)$$

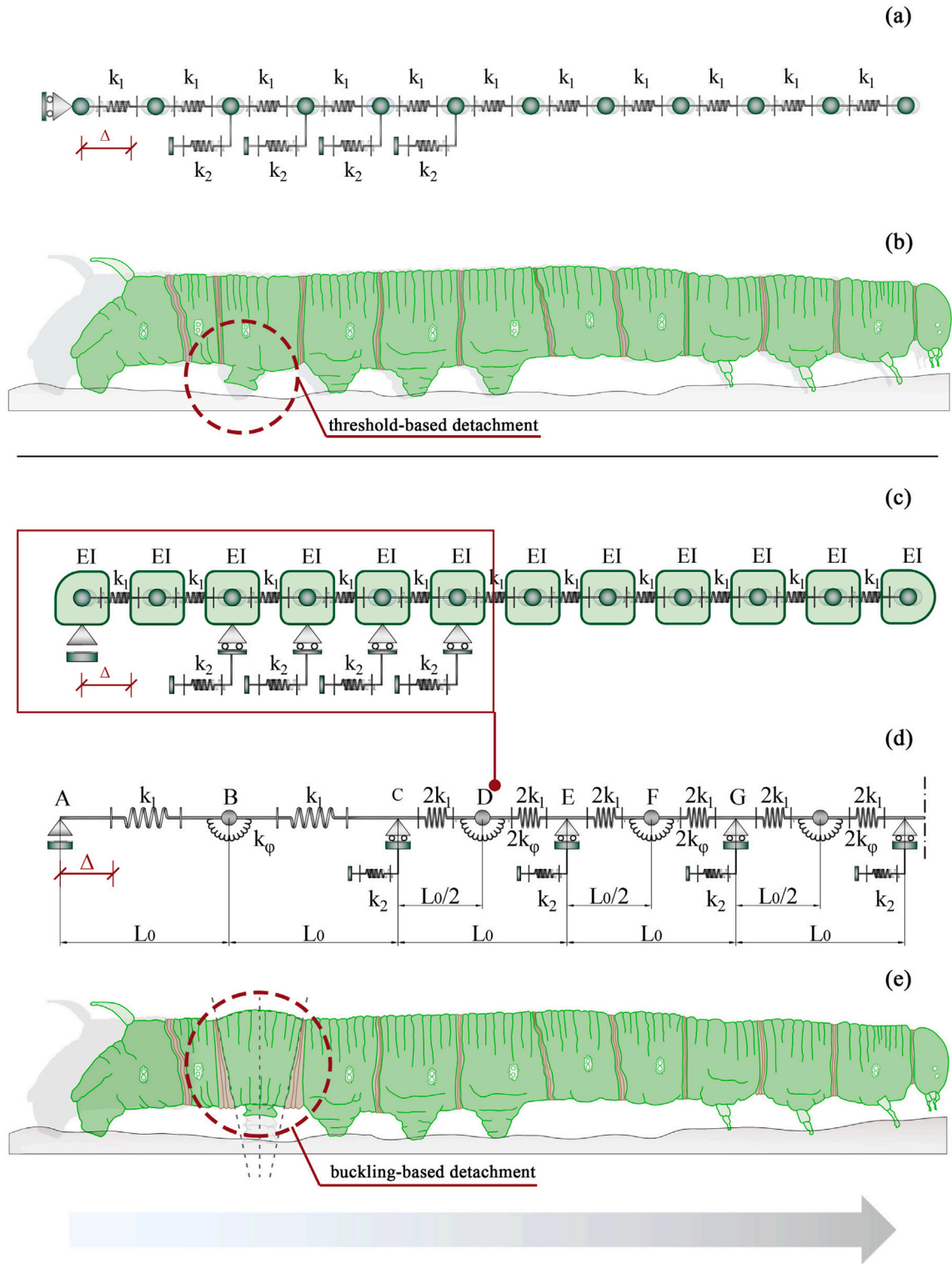


Fig. 2. Schematic representation of the mechanical modelling and detachment mechanisms of caterpillar locomotion. In the first part of the panel, respectively subfigures (a) and (b), the occurrence of threshold-based detachment has been depicted; the second part of the Figure, with subfigures (c), (d) and (e), refers to the second detachment contribution, which is based on the bending instability of the caterpillar segmental subunits. In real-life caterpillars, a superposition of these two locomotion triggers often occurs.

where λ_L and λ_T are respectively the longitudinal and the transverse stretch of the i th body segment, φ the relative rotation between the two subsequent elements, and k_0 the equivalent axial stiffness, by linearising the one related to the remaining part of the caterpillar structure. By assuming a neo-Hookean constitutive model (Argenziano et al., 2026c; Holzapfel et al., 2000) for caterpillar subunits, the integral of the strain density energy W_λ over the reference volume $V_0 = L^3$ can be made explicit as:

$$W_\lambda := \frac{1}{2} \mu (-3 + \lambda_L^2 + 2\lambda_T^2) + \frac{\mu(-1 + (\lambda_L \lambda_T^2)^{-2\beta})}{2\beta}, \quad (2)$$

being $\mu = \frac{E_Y}{2(1+\nu)}$ and $\beta = \frac{\nu}{1-\nu}$

where E_Y and ν represent respectively the Young's and Poisson's moduli of the body tissue.

By assuming null lateral stress on the caterpillar cuticle, we can make explicit the transverse stretch λ_T as a function of the longitudinal one, following the subsequent relationship:

$$\frac{\partial W_\lambda}{\partial \lambda_T} = 2\mu \lambda_T - 2\mu \lambda_L \lambda_T (\lambda_L \lambda_T^2)^{-1-2\beta} = 0$$

$$\Rightarrow \lambda_T = \lambda_L^{-\nu}. \quad (3)$$

By replacing λ_T into Eq. (2) and by integrating the strain energy density on the reference volume V_0 , the following expression of the total elastic potential energy Ψ_λ can be derived:

$$\Psi_\lambda = \frac{E_Y L^3}{4(1+\nu)} \left(-3 + \lambda_L^2 + 2\lambda_L^{-2\nu} + \frac{(1-2\nu)(-1 + \lambda_L^{-2\nu})}{\nu} \right). \quad (4)$$

Therefore, by assuming the Poisson modulus $\nu \rightarrow 0$, Ψ_λ particularises as follows:

$$\Psi_\lambda = \frac{1}{4} E_Y L^3 (-1 - 2 \log(\lambda_L) + \lambda_L^2), \quad (5)$$

whose derivative with respect to λ is plotted in Fig. 4, while, consequently, the axial stiffness depends on the sole longitudinal stretch, as here provided:

$$k_{NH}(\lambda_L) = \frac{1}{L^2} \frac{\partial^2 \Psi_\lambda}{\partial \lambda_L^2} = \frac{1}{2} E_Y L \left(\frac{1}{\lambda_L^2} + 1 \right) = \frac{1}{2} k_1 \left(\frac{1}{\lambda_L^2} + 1 \right), \quad (6)$$

where the tangent stiffness, denoted by k_1 , is equal to $E_Y L$ in the limit as $\lambda_L \rightarrow 1$.

Furthermore, the following constitutive law is employed for the rotational spring to penalise the rotation φ approaching $\pi/2$ (Palumbo et al., 2022), as graphically represented in Fig. 4 and here explicitly reported:

$$M_\varphi = k_\varphi \tan \frac{\Delta\varphi}{2}, \quad (7)$$

this relation intrinsically ensures geometric compatibility by preventing the longitudinal springs from overlapping. Due to the self-equilibrium conditions in the rotational hinge, the deformed configuration is symmetric, thus implying that $\Delta\varphi$ is 2φ . The equivalent rotational stiffness, labelled as $k_{\varphi NL}$ can be calculated as:

$$k_{\varphi NL}(\varphi) = \frac{\partial M_\varphi}{\partial \varphi} = \frac{\partial}{\partial \varphi} [k_\varphi \tan \varphi] = k_\varphi \frac{1}{\cos^2 \varphi} \quad (8)$$

where k_φ is the tangent rotational stiffness for φ approaching 0. Having defined that, the bending potential Ψ_φ of the rotational hinge can be obtained as:

$$\Psi_\varphi = -2 k_\varphi \log(\cos \varphi). \quad (9)$$

By specifying the expressions of Ψ_λ and Ψ_φ of Eqs. (5) and (9), the total elastic potential Π (Eq. (1)) definitely assumes the following form:

$$\begin{aligned} \Pi := \Pi(\lambda_L, \varphi) &= \frac{1}{2} E_Y L^3 (-1 - 2 \log(\lambda_L) + \lambda_L^2) + \\ &- 4 k_\varphi \log(\cos \varphi) + \frac{1}{2} k_0 (\Delta + 2L(\lambda_L \cos \varphi - 1))^2 \end{aligned} \quad (10)$$

It is worth highlighting that the Lagrangian coordinates of the mechanical system consist of the sole λ_L and φ . Under the specific loading hypotheses on the lateral surface assumed, λ_T is determined as a function of the longitudinal stretch. Meanwhile, the inelastic displacement Δ acts as the trigger for the buckling condition and is therefore excluded from the set of free parameters of the system.

Within this framework, by deriving the total potential elastic energy Π (see Eq. (10)) with respect to the two Lagrangian Coordinates λ_L and φ and equating them to 0, two equilibrium equations under the large deformations regime can be obtained:

$$\begin{aligned} \frac{1}{L} \frac{\partial \Pi}{\partial \lambda_L} &= E_Y L^3 (-1 + \lambda_L^2) (\lambda_L)^{-1} + \\ &+ 2 k_0 L \cos \varphi (-2L + \Delta + 2L \lambda_L \cos \varphi) = 0 \\ \frac{\partial \Pi}{\partial \varphi} &= -2 k_0 L \sin \varphi \lambda_L (-2L + \Delta + 2L \cos \varphi \lambda_L) + \\ &+ 2 k_\varphi \tan \varphi = 0. \end{aligned} \quad (11)$$

By solving the second equation in terms of λ_L , the two analytical solutions can be made explicit as follows:

$$\lambda_{L,1,2} = \frac{\sec \varphi \left(\pm \csc \varphi \sqrt{(\sin \varphi)^2 k_0 (8k_\varphi + k_0(\Delta - 2L)^2)} \right)}{4k_0 L} + \frac{\sec \varphi (k_0(-\Delta + 2L))}{4k_0 L} \quad (12)$$

It can be formally demonstrated that, within the feasible domain of the physical parameters (all mechanical and geometric constants are strictly positive and for geometric compatibility conditions $0 < \varphi < \pi/2$ and $\Delta < L$), the stretches always satisfy the subsequent inequalities $\lambda_{L,2} < 0$ and $\lambda_{L,1} > 0$. A comprehensive proof and a synoptic derivation of this consideration are provided in the [Appendix A](#).

After some algebra, by replacing $\lambda_{L,1}$ into Eq. 1 of (11), we obtain the following equation in the sole unknown φ , as provided here:

$$\begin{aligned} \frac{1}{L} \frac{\partial \Pi}{\partial \lambda_L} &= \frac{-8L \cos(\varphi) k_0 (E_Y L^3 - 2k_\varphi)}{D} + \\ &+ \frac{E_Y L \sec(\varphi) L((-2L + \Delta)^2 k_0 + 4k_\varphi)}{D} + \\ &+ \frac{E_Y L \sec(\varphi) (2L - \Delta) \sqrt{N}}{D} = 0, \end{aligned} \quad (13)$$

where $N = L^2 k_0 ((-2L + \Delta)^2 k_0 + 8k_\varphi)$
and $D = 2L(2L - \Delta)k_0 + 2\sqrt{N}$

By performing the first-order Taylor series expansion of the Eq. (13) in φ for $\varphi \rightarrow 0$, the linearised equation can be written as follows:

$$\begin{aligned} \frac{1}{L} \frac{\partial \Pi}{\partial \lambda_L} &\approx \frac{-8L k_0 (E_Y L^3 - 2k_\varphi)}{D} + \\ &+ \frac{E_Y L^2 ((-2L + \Delta)^2 k_0 + 4k_\varphi)}{D} + \\ &+ \frac{E_Y L (2L - \Delta) \sqrt{N}}{D}. \end{aligned} \quad (14)$$

By solving Eq. (14) in terms of Δ , two values of the critical inelastic displacement that potentially may trigger the bifurcation of the system, named $\Delta_{\text{crit},i}$, can be found. By assuming that all symbolic parameters should be positive and after some algebraic steps, a compact expression of Δ_{crit} is derived, reported below:

$$\Delta_{\text{crit},1,2} = 2L \pm \frac{2E_Y L^3 k_0 - k_\varphi (E_Y L + 4k_0)}{k_0 \sqrt{E_Y L (E_Y L^3 - 2k_\varphi)}} \quad (15)$$

By recalling that the product $E_Y L$ is the tangent axial stiffness k_1 (6), the closed-form solution of Δ_{crit} (15) can be re-arranged as follows:

$$\Delta_{\text{crit},1,2} = 2L \pm \frac{2k_1 L^2 k_0 - k_\varphi (k_1 + 4k_0)}{k_0 \sqrt{k_1 (k_1 L^2 - 2k_\varphi)}} \quad (16)$$

The critical inelastic displacement made here explicit determines the onset of the proleg detachment sequence for each mechanical configuration as a function of the tangent stiffness values and the geometric length L . These parameters should be calibrated depending on the mechanical configurations that the caterpillar can assume. Elements like the body shape and the global length, the number of legs, and how stiff or long the body is, all may change the animal's bending curvature. Interestingly, Eq. (16) automatically gives two inequality constraints on the parameters: the radicand $(k_1 L^2 - 2k_\varphi)$ should be always positive for ensuring the physical consistency of the equilibrium condition, i.e. $k_1 > 2k_\varphi (L^{-2})$, and the $\Delta_{\text{crit},1,2}$ (16) must be lower than $2L$, in order to respect geometric compatibility and avoid interpenetration. Assuming that all mechanical and geometric parameters are strictly positive and restricting the domain to the region where the radicand $(k_1 L^2 - 2k_\varphi)$ is positive, symbolic computations using Mathematica® (Wolfram Research, Inc., 2021) demonstrate that $\Delta_{\text{crit},1}$ is always greater than $\Delta_{\text{crit},2}$, with – more importantly – the former violates the geometric compatibility condition thus determining interpenetration. A graphical representation of this behaviour is presented in Section 3.

For the sake of clarity, the complete set of the mechanical parameters employed to obtain the critical inelastic contraction with their physical meaning and their relative source is synoptically reported in [Table 1](#).

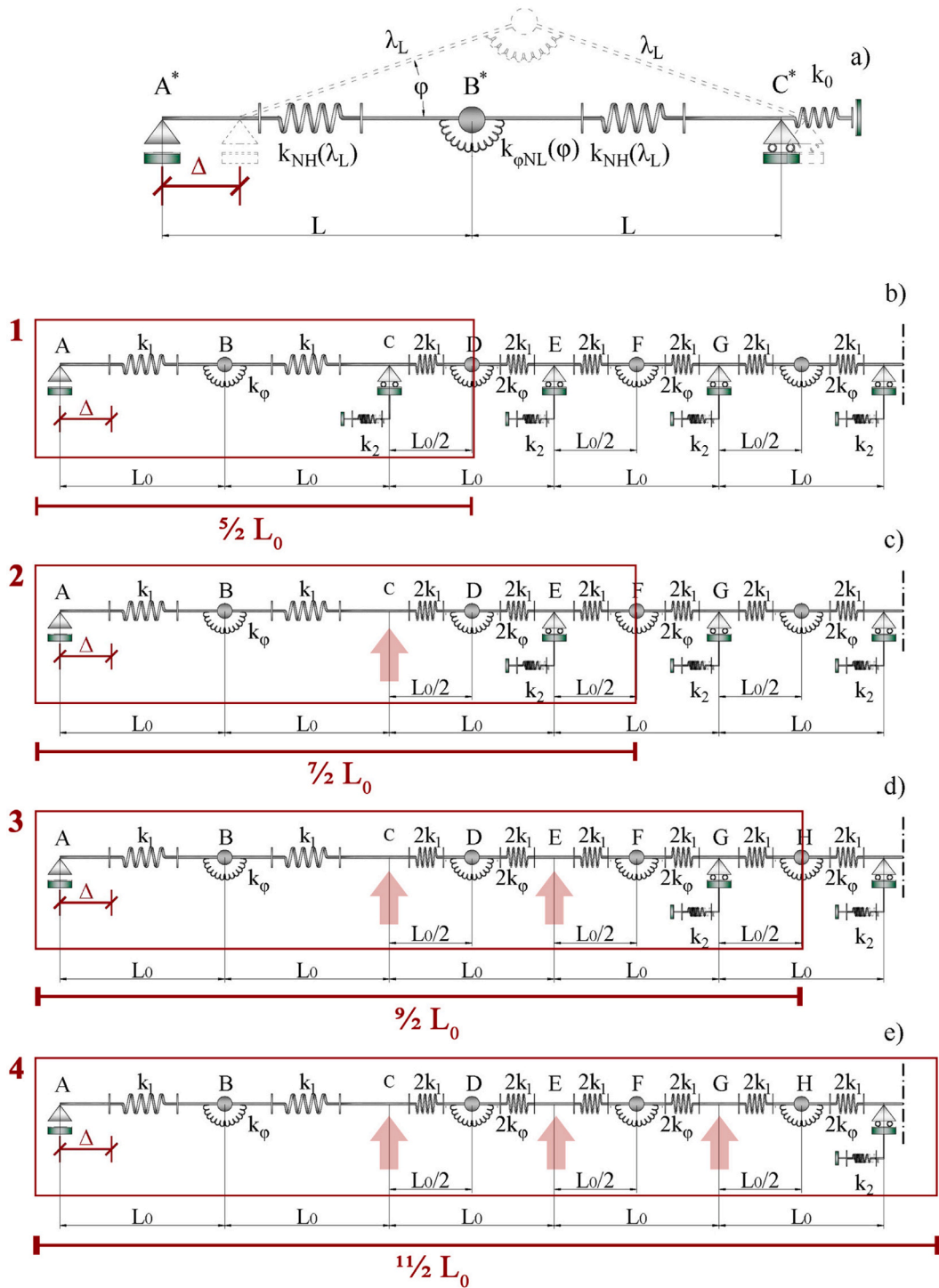


Fig. 3. Graphical sketch of the instability mechanism in the caterpillar locomotion system. Part (a) illustrates the paradigmatic model used to analyse the buckling mechanism, while parts (b) through (e) show the evolution of subsequent mechanical configurations. Notably, the proleg detachment at the onset of buckling for each stage is indicated by red arrows. In parts (b), (c), (d) and (e) of the Figure, by assuming the equivalent linear elastic configurations, we indicate as k_1 and k_ϕ the tangent values, respectively of the axial and rotational stiffness (see Eqs. (6) and (8)).

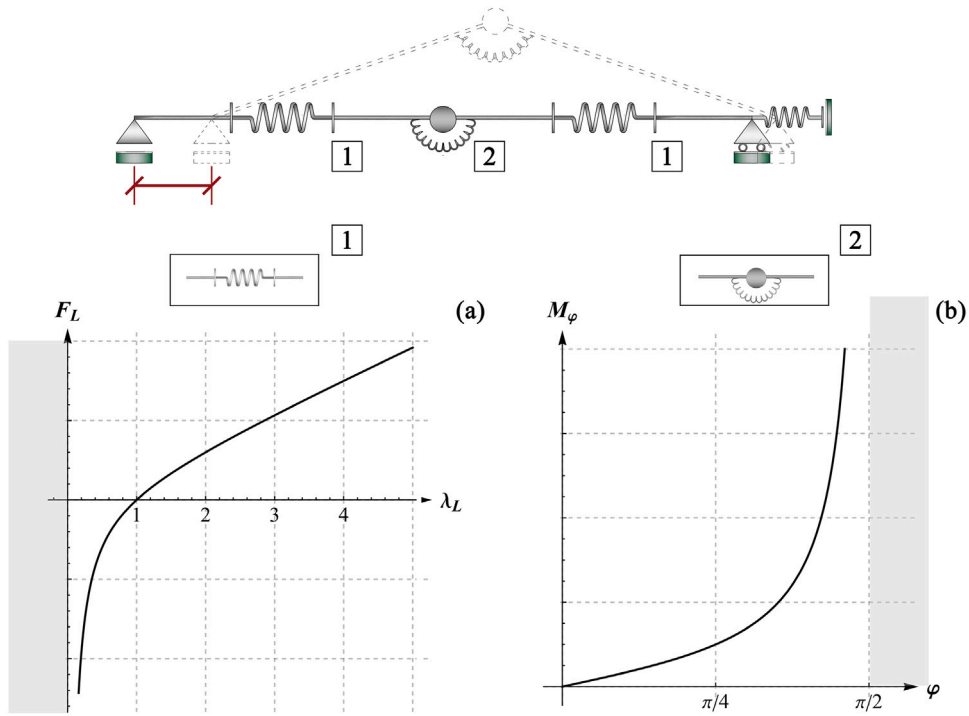


Fig. 4. Constitutive relations for the longitudinal and rotational springs of the mechanical model provided in the configuration (a) of Fig. 3. In detail, in plot (a), the graph shows the neo-Hookean relationship between the longitudinal force F_L and the stretch ratio λ_L . The curve passes through the origin at λ_L approaching 1, representing the stress-free state. The grey shaded region on the left side indicates the physical limit that cannot be exceeded for the stretch parameter. In plot (b), the graph depicts the elastic moment M_φ as a function of the rotational displacement φ . When $\varphi \rightarrow \pi/2$, the adopted law exhibits a significant stiffening, representing *de facto* the physical constraint prescribed for avoiding interpenetration.

Table 1

Physical meaning and origins of the parameters adopted in the mechanical model.

Model parameter	Physical meaning	Origin/Reference
L_0	Undeformed length of an individual body segment	Acquired via direct experimental measurement (Argenziano et al., 2026c, 2025)
L	Characteristic length of the reduced-order discrete mechanical model (see Fig. 3a)	Made explicit as a function of L_0 (see Section 2.3)
$A \sim L_0^2$	Resting cross-sectional area	Derived from the undeformed segment length
$I \sim L_0^4/12$	Inertia of the cross-section	Derived from the undeformed segment length
Δ	Prescribed localised muscle contraction	Evaluated through laboratory tracking (Argenziano et al., 2026c, 2025)
E_Y	Young modulus of the caterpillar tissue	Based on experimental data provided in the Dorfmann et al. (2007)
ν	Poisson modulus of the body tissue	Set to 0 according to the 1D assumption
$k_1 \propto E_Y A L_0^{-1}$	Linearised axial stiffness of the caterpillar body (when $\lambda_L \rightarrow 1$)	Computed analytically from mechanical and geometric properties (see Section 2.3)
$\alpha = k_2 k_1^{-1}$	Dimensionless stiffness parameter, being k_2 the constant stiffness of the Winkler-like constraints	Tuned to replicate the observed empirical kinematics (Argenziano et al., 2026c, 2025)
k_0	Equivalent linearised axial stiffness of the residual part of the caterpillar body that remains attached to the support at each mechanical configuration	Made explicit as a function of α and k_1 (see Section 2.3)
$k_\varphi \propto E_Y I L_0^{-1}$	Equivalent bending stiffness of caterpillar body units	Computed analytically from mechanical and geometric properties (see Section 2.3)

2.3. Towards a continuum beam model

As depicted in Fig. 3, the whole crawling cycle is discretised into four distinct mechanical configurations, each one characterised by a specific set of inelastic critical Δ that determines the buckling onset. The sequence of mechanical configurations is non-trivial, since the minimum critical Δ among all the configurations dictates their order. For instance, the sequence may skip one or more configurations (labelled 1–4 in Fig. 3) since it could be energetically more favourable to buckle directly into the i th configuration. Additionally, we assume that the caterpillar may modulate and increase its initial Δ from the minimum one up to the one required to detach all the abdominal prolegs. In our model, we hypothesise that the increment of the initial prescribed displacement can occur in quasi-static manner, thus neglecting all potential dissipative and inertial effects and remaining under the elasto-static regime. Therefore, the present analysis relies on a quasi-static assumption, which is highly appropriate for modelling the caterpillar crawling gait. As demonstrated in previous studies (Argenziano et al., 2026c, 2025), caterpillar locomotion operates in a strongly overdamped regime. The inertial components of these soft-bodied animals contribute negligibly to the overall dynamics, primarily due to their extremely small masses (on the order of $10^{-4} - 10^{-5}$ kg) relative to the dominant viscous and elastic forces. Explicit dynamic simulations incorporating linear viscosity and inertial terms confirm that the transient phases of locomotion are exceedingly brief, lasting on the order of 0.1 s. Following this short transient period, the system's displacements rapidly converge to the elasto-static solutions without exhibiting inertial oscillations. Consequently, the elasto-static approach is fully justified for describing the slow crawling typically exhibited by caterpillars, particularly under steady-state conditions, allowing dynamic effects to be safely neglected when capturing the essential aspects of locomotion. The primary limitation of this assumption pertains to the sole initial transient phase. As observed in Argenziano et al. (2026c), when hyperelastic models are adopted to accurately capture the large deformations of caterpillar tissue, dynamic effects can become more pronounced. Specifically, the rapid release of stored elastic energy during this phase can generate sharper initial velocity peaks, highlighting the localised relevance of transient dynamics during initial propulsion. Having said that, this limitation does not affect the essential mechanics of the buckling phenomenon proposed here to capture the empowerment effect during the lifting and detaching of the caterpillar's prolegs. For this reason, the quasi-static framework has been confidently retained in the present study.

To accurately capture the mechanics and the buckling onset of the crawling gait, the geometric length $L_{(i)}$ and the mechanical parameters $k_{\varphi}(i)$, $k_1(i)$ and $k_0(i)$ have to be calibrated for each mechanical configuration. As the organism progresses through its sequence of movements, the number of body segments detached and those anchored to the substrate varies, thereby altering the lengths, the bending and axial stiffnesses of the subunits, as well as the equivalent structural stiffness of the spring at the boundary. Consequently, in order to track the buckling-triggered caterpillar locomotion step-by-step and capture the deformation amplitude for each state, we shift from the discrete paradigmatic model to a calibrated continuous beam model, where the inelastic critical Δ to be applied is analytically calculated from the discrete scheme for each configuration, as made explicit in Section 2.2. Then, moving from the discrete paradigmatic scheme (see Fig. 5a) to an equivalent continuous model that better represents the continuous nature of the soft-invertebrate (see Fig. 5b), the boundary conditions are idealised as clamped to match the observable bending profile. Assuming the real organism maintains near-zero rotation where its body lifts from the ground, we model it as an equivalent continuous beam clamped at both ends. Additionally, an axial spring with stiffness $k_0(i)$ is applied to the right boundary. As above mentioned, $k_0(i)$ represents the equivalent linearised axial stiffness of the residual portion of the caterpillar body that remains anchored to the substrate during a specific i th mechanical configuration. As the caterpillar progresses through its crawling gait and sequentially lifts its abdominal prolegs, the number of body segments still firmly attached to the ground continuously changes, thus modulating the overall axial stiffness. Instead of modelling this complex, trailing posterior section for every step, its mechanical stiffness is condensed into a single equivalent spring. The calibration procedure for this parameter is carried out mechanically by isolating the one-dimensional axial response of the system. Sequentially, for each configuration, we analytically calculate the horizontal reaction force exerted by the substrate (represented by the Winkler-like spring) on the specific proleg that is on the verge of detaching. We then divide this restraining force by the corresponding axial displacement at that exact node. This ratio *de facto* yields $k_0(i)$, effectively lumping the structural stiffness of all the trailing, anchored body segments into one manageable parameter that seamlessly integrates into the reduced-order model. The step-by-step procedure for calculating the values of $k_0(i)$ for the i th configuration is reported in Appendix B and their analytical expressions are recalled in Table 2 as a function of α , that is $k_2 E_Y L_0^{-1}$.

For the reader's convenience, in Table 2, we report the four key parameters for each i th mechanical configuration. First, we provide the reference length $L_{(i)}$ (see Fig. 3b, 3c, 3d and 3e). Second, we make explicit the equivalent axial stiffness $k_1(i)$, that is, with respect to the continuum beam of resting cross-section area A , $E_Y A (L_{(i)})^{-1}$ and depends on the number of body segments highlighted by the red rectangles in Fig. 3. Finally, we recall the bending stiffness $k_{\varphi}(i)$, which is a function of $L_{(i)}$ and is evaluated using the left-clamped beam stiffness of inertia I , i.e. $4 E_Y I (2 L_{(i)})^{-1}$ and the values of $k_0(i)$ for each substep. Substituting the geometric and mechanical parameters from Table 2 into Eq. (16) yields the critical inelastic displacement expressions presented in Table 3. Notably, $\Delta_{\text{crit},2}$ for each configuration depends solely on the geometric parameters and the ratio between the tangent axial stiffness $E_Y L_0$ and the Winkler-like spring stiffness, i.e. α . By setting these parameters as input, we can calculate each pair of $\Delta_{\text{crit},2}$ and identify the minimum value between them (this is the actual inelastic displacement for the i th configuration). Indeed, it is important to emphasise that not all 4 mechanical configurations are strictly necessary to describe the step-by-step locomotion. Following the evaluation of the critical inelastic contraction, it may prove more energetically favourable for the caterpillar to bypass a specific configuration, resulting in the simultaneous detachment of two or more prolegs. For instance, the critical displacement Δ_{crit} of configuration 2 or superior could be lower than that of configuration 1, depending on the geometric parameters and the axial-to-bending stiffness ratios. Consequently, in such scenario, it becomes necessary to implement the model by proceeding directly to configuration 2 or higher. As a limit case, it may occur for some combinations of mechanical and geometric parameters that the lowest value of Δ may

Table 2

Parameters calibration for the corresponding (1)–(4) mechanical configurations depicted in Fig. 3.

Config.	$L_{(i)}$	$k_{\varphi}(i)$	$k_1(i)$	$k_0(i)$
1	$\frac{5}{4}L_0$	$\frac{4E_Y I}{2L_{(1)}}$	$\frac{E_Y A}{2L_{(1)}}$	$E_Y L_0 \frac{\alpha(2+\alpha)(2+\alpha(4+\alpha))}{1+\alpha(2+\alpha)(3+\alpha)}$
2	$\frac{7}{4}L_0$	$\frac{4E_Y I}{2L_{(2)}}$	$\frac{E_Y A}{2L_{(2)}}$	$E_Y L_0 \frac{\alpha(1+\alpha)(3+\alpha)}{1+\alpha(3+\alpha)}$
3	$\frac{9}{4}L_0$	$\frac{4E_Y I}{2L_{(3)}}$	$\frac{E_Y A}{2L_{(3)}}$	$E_Y L_0 \frac{\alpha(2+\alpha)}{1+\alpha}$
4	$\frac{11}{4}L_0$	$\frac{4E_Y I}{2L_{(4)}}$	$\frac{E_Y A}{2L_{(4)}}$	$E_Y L_0 \alpha$

Table 3Analytical critical displacements $\Delta_{\text{crit},1,2}$ for the corresponding (1)–(4) mechanical configurations represented in Fig. 3.

Config.	$\Delta_{\text{crit},1,2}(i)$
1	$\frac{5L_0}{2} \pm \frac{\left(125L_0^4 \alpha \alpha(2+\alpha)(2+\alpha(4+\alpha)) + 64I(A(1+\alpha(2+\alpha)(3+\alpha)) + 10L_0^2 \alpha(2+\alpha)(2+\alpha(4+\alpha)))\right)}{10L_0^2 \sqrt{A(25L_0^2 A - 128I)} \alpha(2+\alpha)(2+\alpha(4+\alpha))}$
2	$\frac{7L_0}{2} \pm \frac{343L_0^4 \alpha \alpha(1+\alpha)(3+\alpha) - 64I(A(1+\alpha(3+\alpha)) + 14L_0^2 \alpha(1+\alpha)(3+\alpha))}{14L_0^2 \sqrt{A(49L_0^2 A - 128I)} \alpha(1+\alpha)(3+\alpha)}$
3	$\frac{9L_0}{2} \pm \frac{729L_0^4 \alpha \alpha(2+\alpha) - 64I(A(1+\alpha) + 18L_0^2 \alpha(2+\alpha))}{18L_0^2 \sqrt{A(81L_0^2 A - 128I)} \alpha(2+\alpha)}$
4	$\frac{11L_0}{2} \pm \frac{1331L_0^4 \alpha \alpha - 64I(A + 22L_0^2 \alpha)}{22L_0^2 \sqrt{A(121L_0^2 A - 128I)} \alpha}$

be the one referred to the configuration (4): quite trivially, in this case, the soft-invertebrate prefers to detach all the first three prolegs simultaneously, converging immediately to the last mechanical step. The observations and plots reported in Section 3 can clarify this aspect.

2.4. Amplitude of the deformed shape

The amplitude of the bending deflection for each sub-step is determined using the Principle of Virtual Work. For a given mechanical configuration i , by prescribing the Δ_{crit} detailed in Table 3, the internal bending deformation energy $W_{\text{int-b}}(i)$ is evaluated as the difference between the external work $W_{\text{ext}}(i)$ done by the reaction forces (see Fig. 6) and the internal axial strain energy $W_{\text{int-ax}}(i)$ cumulated during locomotion by the n body segments, as follows:

$$\begin{aligned}
 W_{\text{int-b}}(i) &= W_{\text{ext}}(i) - W_{\text{int-ax}}(i) = \\
 &= \left(\int_0^{\Delta_{\text{crit}}(i)} R_1(i) d\Delta + W_W(i) \right) - \sum_{j=1}^{n-1} U_{\text{NH}}(u_{j+1}, u_j)(i) = \\
 &= U_{\text{NH}}(u_2, \Delta_{\text{crit}})(i) + W_W(i) - \sum_{j=2}^{n-1} U_{\text{NH}}(u_{j+1}, u_j)(i),
 \end{aligned} \tag{17}$$

where n is the number of animal subunits and, with reference to the i th configuration, $R_1(i)$ is the reaction of the support modelling the terminal proleg of the caterpillar, being instead $W_W(i)$ the work done by the elastic Winkler constraints reactions $R_{w,j}$ per the displacement solutions u_j (see Fig. 6), that can be calculated as:

$$W_W(i) = \frac{1}{2} \sum_{j=i+2}^6 R_{w,j} u_j(i), \tag{18}$$

and U_{NH} represents the neo-Hookean energy contribution of the j th subunit defined in (5). Still referring to the i th configuration and assuming a resting length L_0 for the body subunits, this term can be made explicit for j varying from 2 to n as a function of the horizontal nodal displacements u_j and u_{j+1} , as follows:

$$U_{\text{NH}}(u_{j+1}, u_j)(i) = \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(\frac{u_{j+1} - u_j}{L_0} \right) + \left(\frac{u_{j+1} - u_j}{L_0} \right)^2 \right)(i). \tag{19}$$

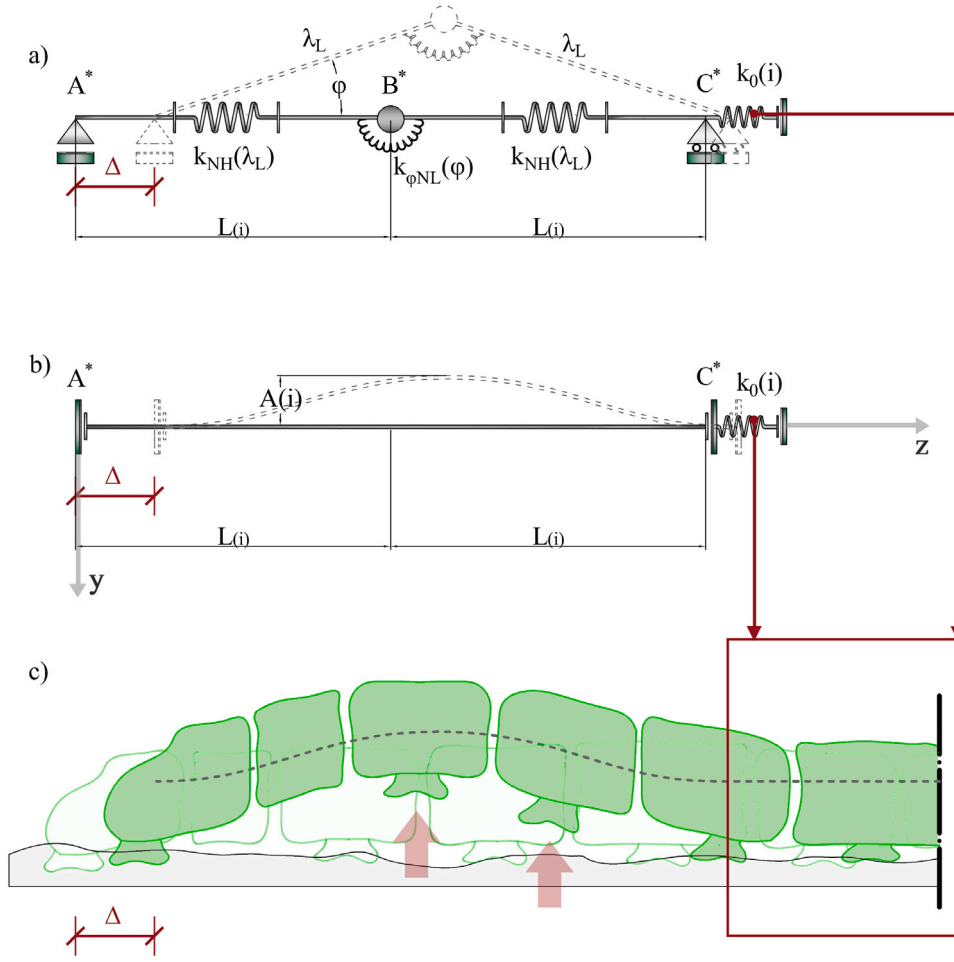


Fig. 5. Analogy between discrete and continuous models for tracing back the buckling onset that occurs during a crawling gait: the paradigmatic discrete structural scheme (a), the equivalent continuous clamped beam model undergoing buckling (b), and the corresponding bending curvature of the caterpillar experienced during locomotion, depicted in (c), where the red arrows indicate the prolegs detachment. In the last graphical sketch, the amplitude scale of the bending curvature has been intentionally enlarged to stress the effects of instability on the gait. Depending on the i th configuration, the equivalent stiffness $k_0(i)$, for both the discrete and the continuous model, represents the stiffness of the residual body segments that remain anchored to the substrate (highlighted by the red contours).

When j varies from 1 to 2, with respect to the first neo-Hookean spring, U_{NH} particularises as:

$$U_{NH}(u_2, \Delta_{crit})(i) = \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(\frac{u_2 - \Delta_{crit}}{L_0} \right) + \left(\frac{u_2 - \Delta_{crit}}{L_0} \right)^2 \right) (i). \quad (20)$$

The nodal horizontal displacements u_j have been computed in the non-linear 1D discrete model depicted in Fig. 2a, followed the methodology provided in Argenziano et al. (2026c). More explicit expressions of the internal bending deformation energy $W_{int-b}(i)$ have been reported in Appendix C. To correlate the energy state to the geometric configuration, with reference to the continuum model reported in Fig. 5b, a sinusoidal shape function $v(z)$, with z the longitudinal axis of the beam, is assumed for the buckled segment over the length $2L_0$:

$$v(z)(i) = A(i) \left[1 - \cos \left(\frac{2\pi z}{2L(i)} \right) \right] \quad (21)$$

By assuming a linear moment-rotation relationship for the continuum beam depicted in Fig. 5b, the amplitude $A(i)$ of the i th configuration is determined by equating – in the hypothesis of linearised curvature χ – the internal bending energy previously estimated to the following integral:

$$W_{int-b}(i) = \int_0^{2L(i)} \frac{1}{2} E_Y I \left(-\frac{\partial^2 v(z)}{\partial z^2} \right)^2 dz \quad (22)$$

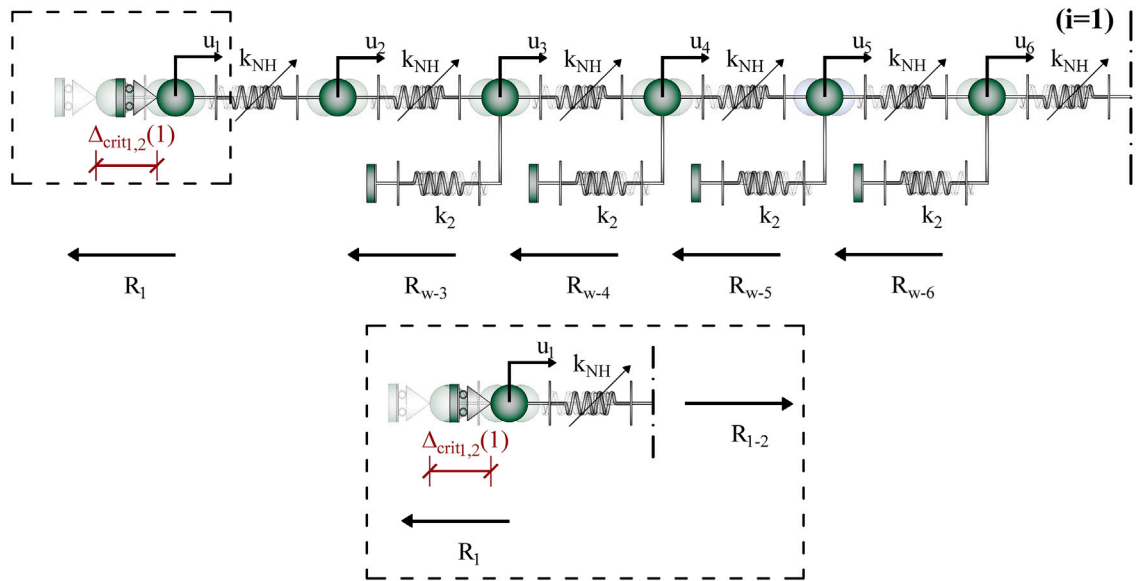


Fig. 6. Sketch representing the distribution of the reaction forces that define the external virtual work $W_{\text{ext}}(i)$ term as formulated in Eq. (17). Focusing on the sole axial regime, the model from Fig. 2a is recovered, graphically distinguishing the neo-Hookean spring, indicated by the inclined arrow, from the linear Winkler constraints. For the sake of example, the representation refers to the first mechanical configuration ($i = 1$) where all the Winkler springs are attached to the substrate.

Substituting the shape function (21) into Eq. (22) and by calculating $W_{\text{int-b}}(i)$ as (17), we can obtain the magnification factor $A(i)$, as follows:

$$W_{\text{int-b}}(i) = \int_0^{2L(i)} \frac{1}{2} E_Y I \left(-\frac{\partial^2 v(z)}{\partial z^2} \right)^2 dz = \int_0^{2L(i)} \frac{1}{2} E_Y I \pi^4 L(i)^{-4} A_{(i)}^2 \cos^2 \left(\frac{\pi z}{L(i)} \right) dz$$

$$\Rightarrow A(i) = \pm \left(\frac{2 W_{\text{int-b}}(i)}{E_Y I} \right)^{\frac{1}{2}} \frac{L(i)^{\frac{3}{2}}}{\pi^2} \quad (23)$$

The step-by-step procedure for determining the bending deflection amplitude for each i th configuration described in this section is summarised in Algorithm 1 at Appendix D. Quite trivially, the maximum bending displacement is $A_{\text{max}}(i) = 2 A(i)$.

3. Results

Starting from the mechanical model conceived, this section discusses the numerical experiments conducted to evaluate how geometric properties (i.e. the resting length, inertia and cross-sectional nominal area of the body unit) and stiffness parameters may affect the overall system kinematics. Specifically, the analysis first focuses on the sensitivity of the critical inelastic displacement, Δ_{crit} , which, as before demonstrated, plays a primary role in defining the bending curvature of the soft-invertebrate that arises during locomotion, depending on the selected crawl-step. Therefore, in the last subsection, numerical simulations reproducing an example of the deformed bending shape occurring during caterpillar locomotion are provided.

3.1. Numerical evaluation of geometric compatibility conditions for the critical displacement

In this subsection, we recover and numerically evaluate the geometric compatibility conditions for the initial critical Δ , by referring to the solutions made explicit in Section 2.2. To show this, in Fig. 7, for a selected set of geometric parameters, we compare in a graphic form both the two solutions of the critical inelastic displacements, $\Delta_{\text{crit1,2}}$ (see Table 2), as a function of the dimensionless stiffness ratio α . While one can easily recognise that Δ_{crit1} is always greater than Δ_{crit2} under the assumption of positive mechanical and geometric parameters, the agreement of the compatibility condition, that is the inequality $\Delta_{\text{crit1,2}} \leq 2L(i)$, is non-trivial and immediately noticeable. To graphically represent this, we report the evaluation of both the critical inelastic displacements, $\Delta_{\text{crit1,2}}$, as a function of the dimensionless stiffness ratio α (see Fig. 7). The analysis is performed across the four distinct potential mechanical configurations, labelled from (a) to (d), corresponding to the mechanical systems (1) to (4) in Fig. 3. The red line defines the upper limit of the inelastic Δ_{crit} , which separates the physically admissible solutions (the green curves) and the incompatible ones (the blue curves). As observed across all four configurations, the admissible critical displacement seems to converge to an asymptotic lower bound as the stiffness ratio increases, while different behaviours are registered for lower values of α . Interestingly, with reference to the first mechanical configuration, i.e. plot (a) in Fig. 7, the green curve exhibits a strongly nonlinear and monotonically decreasing trend when α approaches 0.

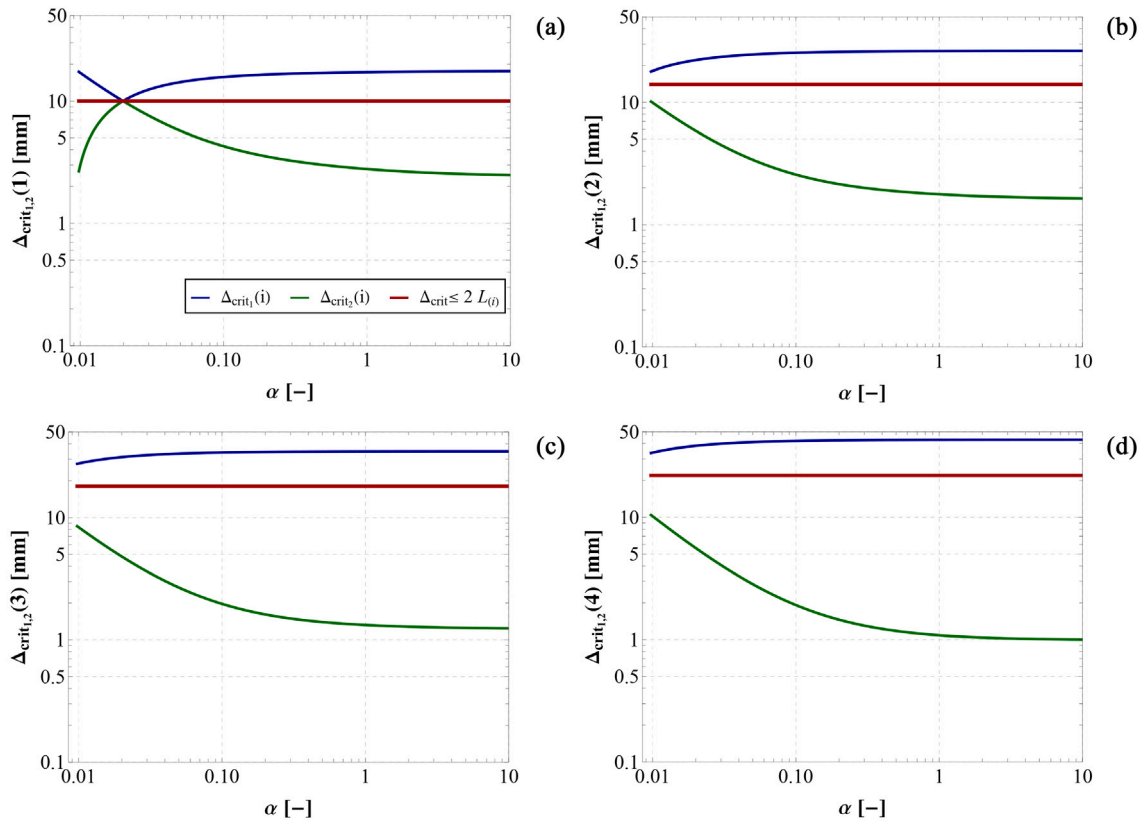


Fig. 7. Evaluation of the critical inelastic displacements $\Delta_{crit,i,2}$ (see Table 3) for the mechanical configurations from (1) to (4) (i.e. respectively, plots from a to d) as a function of the stiffness ratio $\alpha = k_2 (E_Y L_0)^{-1}$. In all plots, the red line indicates the upper limit of the critical inelastic displacement (i.e. $\Delta_{crit} = 2L_{(i)}$), thus separating the admissible curve (the green one) from the incompatible Δ_{crit} (the blue one). The set of parameters assumed for the panel is: $L_0 = 4 \times 10^{-3}$ m, $I \approx L_0^4/12 = 2.13 \times 10^{-11}$ m⁴ and $A \approx L_0^2 = 1.6 \times 10^{-5}$ m². The plots are reported in logarithmic scale on both the two axes.

3.2. Sensitivity analysis of the critical displacement by varying geometric parameters

Starting from the establishment of the admissible displacement boundaries, we implemented a sensitivity analysis, whose results are summarised in Fig. 8. In particular, we investigate the admissible inelastic critical displacement across the four mechanical configurations simultaneously, varying both the stiffness ratio α and the resting length L_0 . The sub-plots (a) through (d) correspond to increasing resting lengths $L_0 \in \{0.001, 0.002, 0.003, 0.004\}$, which consequently govern the corresponding cross-sectional resting area A and the moment of inertia I , as detailed in the relative caption of Fig. 8. The comparative analysis highlights several key aspects of the trend of the inelastic displacement Δ as a function of the α . First, a global scaling effect is registered: by comparing all sub-plots, we can notice that increasing the resting length of the individual body units, i.e. L_0 , linearly increments the magnitude of all the critical displacements. Second, when considering very low values of the stiffness ratio, i.e. $\alpha < 0.05$, the displacement curves display distinct, configuration-dependent behaviour. More in detail, configuration (1) exhibits a noticeable localised peak before transitioning to a decaying trajectory, suggesting a specific critical combination of flexibility and geometric arrangement. Although for the major part of the values of α , the $\Delta_{crit}(1)$ is greater than the ones provided for the other mechanical configurations, this tendency is suddenly reversed for low stiffness ratios, where the critical inelastic displacement is always the minimum one compared to the counterparts. Ultimately, for all plots, as the stiffness ratio α increases towards 10, the $\Delta_{crit}(4)$ is always lower than the other ones, thus demonstrating that, from an energetic point of view, for the caterpillar it is more convenient to detach the first three abdominal prolegs simultaneously, in order to immediately reach the fourth mechanical configuration, which is the most favourable. To further prove these considerations, we report two distinct examples in Fig. 9, where two limit cases of the possible sequence of mechanical configurations are displayed. More in detail, by considering the low stiffness ratio values shown in Fig. 9a and 9b, for the specific α value highlighted by the dashed red line, the system initiates at the Δ_{crit} corresponding to the first configuration. It then bypasses the second configuration, rearranging itself directly into the third and subsequently the fourth one. Notably, for this chosen α , $\Delta_{crit}(2)$ is lower than $\Delta_{crit}(4)$ but greater than $\Delta_{crit}(3)$, this implies that it is energetically more convenient for the system to buckle into the third configuration, completely bypassing the potential second one. Conversely, for large α values, such as the one selected as an example in Fig. 9c, the minimum critical inelastic displacement corresponds to

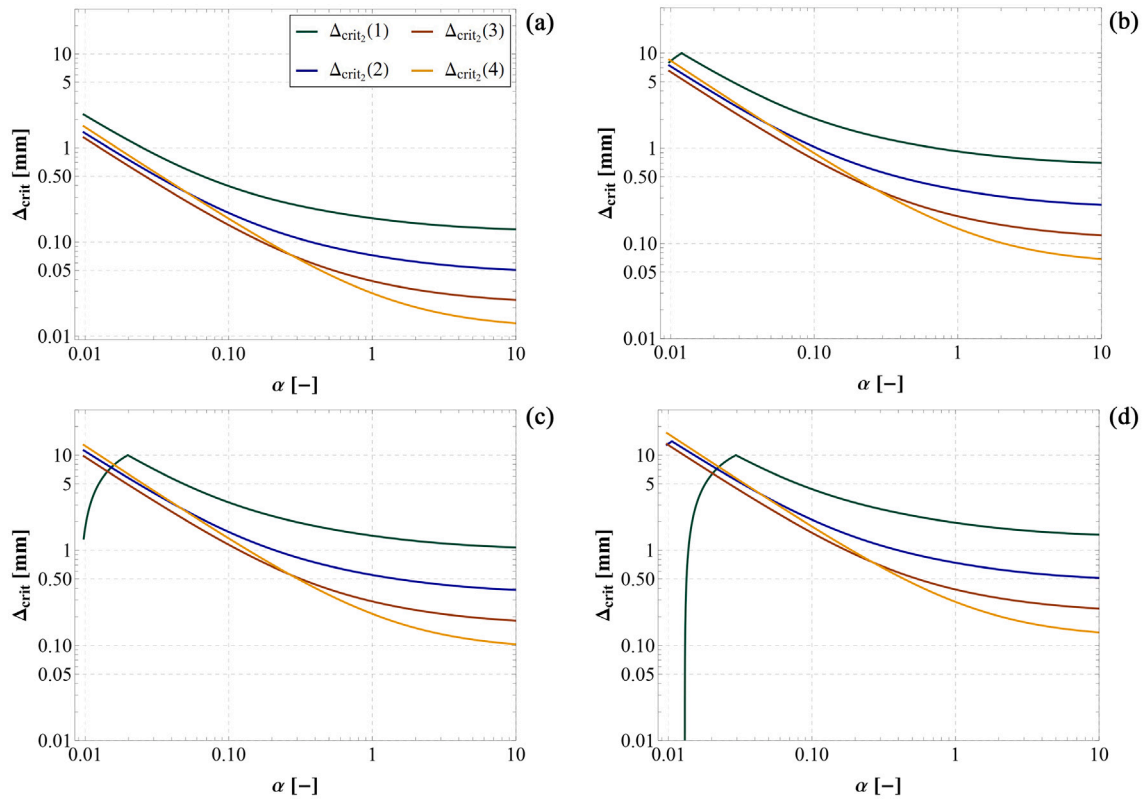


Fig. 8. Sensitivity analysis of the inelastic critical displacement Δ_{crit} (see Table 3) as a function of the stiffness ratio α , for varying resting lengths $L_0 \in \{0.001, 0.002, 0.003, 0.004\}$ m corresponding to sub-plots (a)–(d), respectively. Other parameters are fixed as $I \approx L_0^4/12$ and $A \approx L_0^2$, depending on which resting length is considered. The plots are reported in logarithmic scale on both axes.

the final configuration. Hence, the first three abdominal prolegs detach simultaneously, causing the system to immediately reach the fourth substep. Therefore, from the biological standpoint, the numerical results shown in this subsection seem to suggest that the geometric morphology and the relative position and number of the abdominal prolegs may be relevant for determining the locomotion modality and its efficiency.

3.3. Bending deformed shape of the caterpillar body during locomotion: computational simulations

Based on the implemented mechanical model, we selected a representative sample from the previous sensitivity analysis performed in Section 3.2. The graphical results of the corresponding numerical simulation are presented below and are displayed in Fig. 10. More in detail, starting from the set of parameters whose critical inelastic displacements have been reported in Fig. 9d, Fig. 10 illustrates a numerical simulation of the caterpillar locomotion with the analysis of the corresponding deformed shape at each mechanical step. The locomotion process is depicted across five consecutive stages (panels a–e), representing a complete crawling cycle plotted on a coordinate system of position versus vertical displacement amplitude. The cycle begins from an initial, undeformed state, here appointed as $A(0)$ and concludes with the net forward horizontal displacement – which is equal to $\Delta_{crit}(4)$ – at the final configuration $A(f)$. During the intermediate stages, i.e. parts b, c and d of Fig. 10, the motion is triggered through localised buckling, which induces a specific bending curvature to a portion of the caterpillar body and causes the sequential detachment of the abdominal prolegs. Importantly, in the selected example, we can immediately recognise that, due to the specific set of parameters assumed, the second mechanical configuration (see Fig. 3) is skipped and the system rearranges itself from the first directly to the third mechanical stage, thus detaching simultaneously two prolegs. This computational simulation demonstrates how the buckling-induced amplitude amplifies and shifts longitudinally, effectively translating the mechanical deformation into a successful forward horizontal crawling motion.

4. Discussions and conclusions

In this work, we developed a comprehensive theoretical framework, supported by numerical tests, in order to better investigate the effects of non-linear elasticity and buckling in caterpillar locomotion. By generalising previous 1D mechanical models into

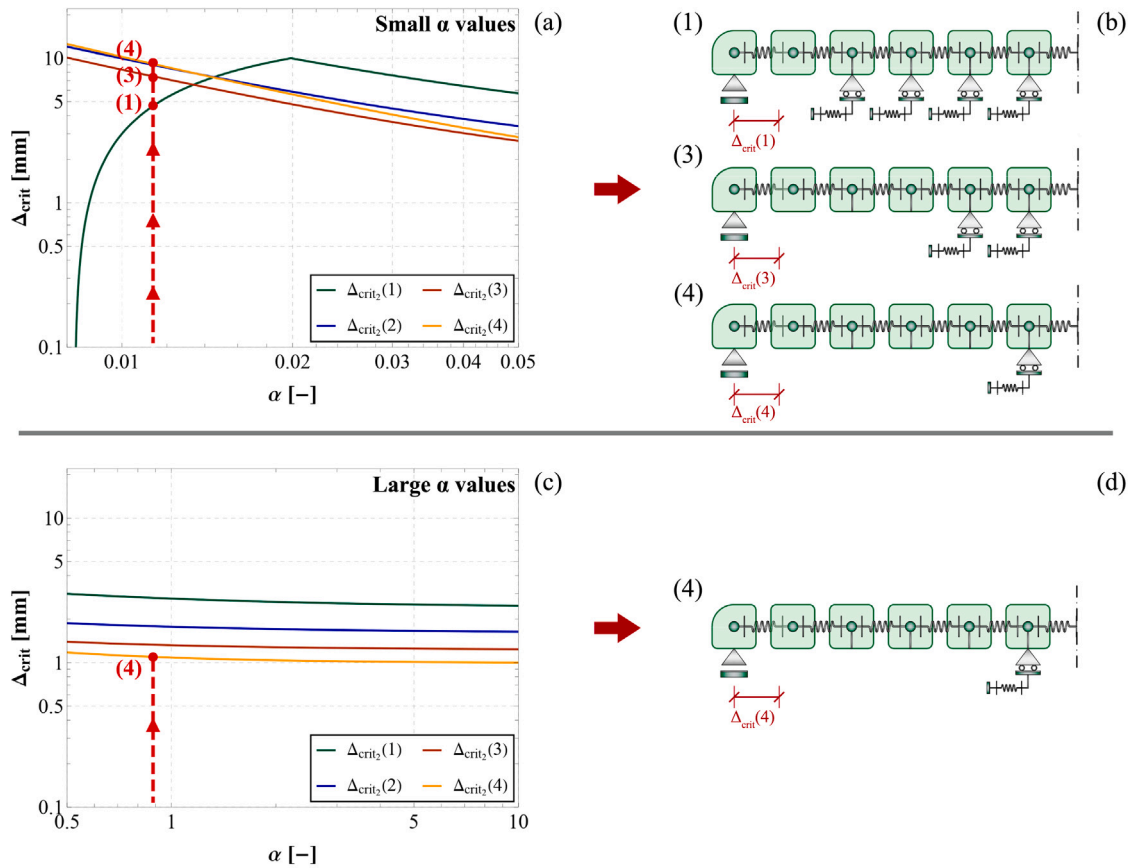


Fig. 9. Numerical examples showing the *consecutio* of mechanical configurations as a function of the selected stiffness ratio parameter α . Plot (a) illustrates a close-up zoom of plot (d) of Fig. 8 within the narrow stiffness ratio interval (0 – 0.05), with the corresponding sequence of the mechanical configurations experienced by the caterpillar reported in part (b). Similarly, plots (c) and (d) present an enlarged view of Fig. 8c for higher α values along with the final configuration into which the soft animal rearranges itself. The assumed set of parameters is: $L_0 = 0.004$ m, $I \approx L_0^4/12 = 6.75 \times 10^{-12}$ m⁴ and $A \approx L_0^2 = 9 \times 10^{-6}$ m². For mechanical configuration sequences depicted in plots (b) and (d), α is set respectively as 0.011 and 0.88.

a 2D discrete system, we successfully captured the bending curvature and the sequential detachment mechanisms of the soft invertebrate's body segments. The incorporation of a neo-Hookean hyperelastic formulation also allowed us to rigorously model the non-linear axial stiffness of body tissues undergoing large stretch deformations. Through the definition of a minimalist and deliberately essential paradigmatic scheme, we derived closed-form solutions for the critical inelastic displacements required to trigger structural buckling at each locomotion step. Hence, we demonstrated that the detaching of abdominal prolegs from the support is ruled by the adhesion–elasticity competition and also significantly powered by the buckling occurring at each subsequent mechanical configuration representing the crawl sub-cycle.

By shifting from the discrete scheme to an equivalent continuous clamped beam model, we then implemented a step-by-step procedure to reconstruct the deformed bending shape across all subsequent mechanical configurations. As an ancillary result, we also demonstrated that the progression through these successive configurations is non-trivial. More in detail, depending on the set of geometric and mechanical parameters, it may energetically more convenient for the system to bypass intermediate states. In such cases, the system can transition directly to a certain configuration to induce buckling at lower critical displacement, effectively skipping one or more steps by simultaneously detaching multiple abdominal prolegs. Additionally, it seems that the *consecutio* of mechanical configuration is also sensitive to the number and position of the prolegs with respect to the animal body, thus showing that morphological and biological aspects of the caterpillar can strongly influence the locomotion modalities and the lifting mechanism from the substrate. Within this framework, from a biological and evolutionary perspective, the ability to skip intermediate mechanical configurations highlights an effective strategy for energetic optimisation. Because bypassing specific steps allows the soft invertebrate to detach multiple prolegs simultaneously at a lower critical displacement threshold, the overall energetic cost of lifting from the substrate can be significantly minimised. This finding might suggest that the specific number, longitudinal spacing, and positioning of the abdominal prolegs across different caterpillar species are likely the result of an evolutionary adaptation process aimed at maximising crawling efficiency. By *ad hoc* tuning their morphological proportions — such as the resting

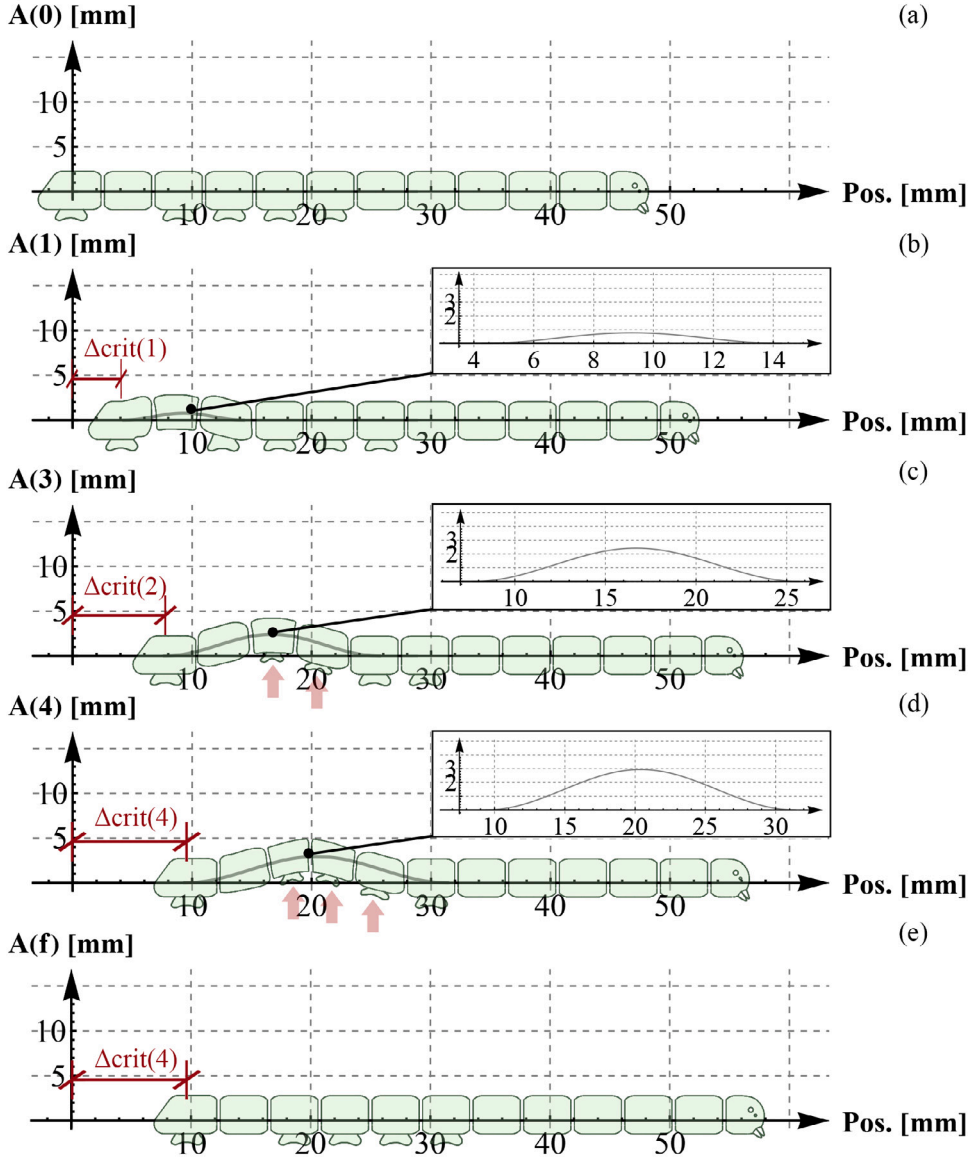


Fig. 10. Numerical simulation of caterpillar bending during locomotion triggered by buckling. The following set of parameters is considered: $L_0 = 0.003$ m, $\alpha = 0.011$ and $E_Y = 1$ kPa. Sub-panels (a) through (e) illustrate consecutive stages of locomotion for initiating and completing a whole crawling cycle plotted on a coordinate system of position [mm] versus deformation amplitude [mm], with the red arrows indicating the prolegs detaching. The sequence begins in part (a) with the soft-invertebrate in its initial state at $A(0)$ and terminates at step (e) with the final configuration $A(f)$. In subpanels (b), (c) and (d), the successive phases show how the motion is triggered and maintained, following the step-by-step series of mechanical configurations, by skipping the second one (see Fig. 9). Within these intermediate stages, critical displacement measurements are marked by $\Delta_{crit,i}$, thus resulting respectively 4.28×10^{-3} , 7.69×10^{-3} and 9.38×10^{-3} m. The corresponding maximum amplitudes $A_{max(i)}$ are respectively the following ones: 7.69×10^{-4} , 2.41×10^{-3} and 2.94×10^{-3} m.

length of individual body units — and tissue elasticity to their typical environmental substrates, caterpillars can passively select the most energetically advantageous locomotion sequence, exploiting their structural mechanics to simplify motion control and improve gait performance.

Ultimately, these findings reveal how caterpillars exploit the competition between adhesion and stiffness, leveraging non-linear elasticity and buckling as mechanical advantages to their locomotion pattern. We believe that the proposed mechanical models and the resulting numerical findings not only deepen our understanding of soft tissue mechanics in biological organisms but also can serve to define new design criteria and actuation strategies for novel bio-inspired soft robots.

CRediT authorship contribution statement

Mario Argenziano: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Massimiliano Zingales:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Massimiliano Fraldi:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of AI use

We have not used AI-assisted technologies in conceiving the topic and creating this article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Physical consistency of the critical stretches of the paradigmatic scheme

In order to evaluate the physical consistency of the two solutions of Eq. (10), we can easily recognise that λ_{L_1} remains positive under the constraint conditions on the parameters reported in the main text and here explicitly re-called, i.e.:

$$k_0 > 0, \quad k_\varphi > 0, \quad L > 0, \quad \Delta < L, \quad 0 \leq \varphi < \pi/2 \quad (\text{A.1})$$

However, some algebra is needed for demonstrating that the stretch λ_{L_2} remains strictly negative under the mentioned constraint conditions. Therefore, with reference to (12), we should verify if the following inequality is always respected under the previously declared assumptions (A.1):

$$\csc(\varphi) \sqrt{\sin^2(\varphi) k_0 L^2 (8k_\varphi + k_0 (\Delta - 2L)^2)} > k_0 L(2L - \Delta) \quad (\text{A.2})$$

Considering the domain of interest, we observe that the argument of the square root is non-negative for any set of non-negative parameters:

$$\sin^2(\varphi) k_0 L^2 (8k_\varphi + k_0 (\Delta - 2L)^2) \geq 0 \quad (\text{A.3})$$

By squaring both sides of the inequality (A.2) and by noting that for $\varphi \in (0, \pi/2)$, $\csc(\varphi) = 1/\sin(\varphi)$ and $\sin^2(\varphi)$ is an always positive quantity, the expression simplifies to:

$$k_0 L^2 (8k_\varphi + k_0 (2L - \Delta)^2) > (k_0 L(2L - \Delta))^2 \quad (\text{A.4})$$

Expanding the terms, we obtain:

$$k_0 L^2 (8k_\varphi + k_0 (2L - \Delta)^2) > k_0^2 L^2 (2L - \Delta)^2 \quad (\text{A.5})$$

By further simplifying the expression, we divide both members by the strictly positive term $k_0 L^2$, yielding to:

$$8k_\varphi + k_0 (2L - \Delta)^2 > k_0 (2L - \Delta)^2 \quad (\text{A.6})$$

Upon subtraction of the common positive term $k_0 (2L - \Delta)^2$ from both sides, the inequality definitely reduces to:

$$8k_\varphi > 0 \quad (\text{A.7})$$

Since rotational stiffness k_φ is assumed to be strictly positive based on the mechanical consistency of the system, the condition is always satisfied. This concludes the proof that the eigenvalue λ_{L_2} is consistently negative for any combination of positive geometric and mechanical parameters within the defined range $0 < \varphi < \frac{\pi}{2}$ and $\Delta < L$.

$$\Delta_{\text{crit},1} \leq 2L \iff k_1 > \frac{2k_\varphi}{L^2} \wedge \left(k_0 \neq \frac{k_1 k_\varphi}{-4k_\varphi + 2k_1 L^2} \right). \quad (\text{A.8})$$

Appendix B. Evaluation of k_0 for each mechanical configuration

To evaluate the equivalent stiffness k_0 for each i th subsequent configuration illustrated in Fig. 3 (steps 1 through 4), the analysis is simplified by considering the sole axial deformability of the system under a linear regime, as idealised in the mechanical model represented in Fig. 2a. Under this assumption, the rotational degrees of freedom and their associated stiffness contributions are neglected. Consequently, the parameter k_0 for each step is derived from the equivalent combination of the axial springs in series in that specific mechanical configuration, at the right-hand side of the proleg that has detached from the substrate.

Following the approach presented in Argenziano et al. (2026a, 2025), the one-dimensional mechanical model can be solved analytically by considering only axial deformability. Explicit expressions can be derived for both the displacements at each degree of freedom and the axial force within each spring across all mechanical configurations, accounting for the sequential detachment of the prolegs. Therefore, the equivalent k_0 at each configuration can be calculated as the ratio between the normal force of the i th Winkler-like spring that detaches and its corresponding displacement solution. By numbering the DoFs from the left to the right-hand side of the models depicted in Fig. 3b, 3c, 3d and 3e, the elasto-static solutions u_i for the (j) mechanical configurations can be provided in what follows:

$$\begin{aligned} u_{3(1)} &= \frac{(1 + \alpha(2 + \alpha)(3 + \alpha))\Delta}{1 + \alpha(1 + \alpha)(2 + \alpha)(7 + 2\alpha)} \\ u_{4(2)} &= \frac{(1 + \alpha(3 + \alpha))\Delta}{1 + \alpha(3 + \alpha)(4 + 3\alpha)} \\ u_{5(3)} &= \frac{(1 + \alpha)\Delta}{1 + \alpha(9 + 4\alpha)} \\ u_{6(4)} &= \frac{\Delta}{1 + 5\alpha} \end{aligned} \quad (\text{B.1})$$

where α is the stiffness ratio between the tangent stiffness for $\lambda \rightarrow 1$ with characteristic length the body unit one L_0 , and the stiffness of the Winkler-like springs k_2 . The normal forces of the i th Winkler spring at the (j) configuration can be made explicit as:

$$\begin{aligned} N_{W3(1)} &= \frac{E_Y L_0 \alpha(2 + \alpha)(2 + \alpha(4 + \alpha))\Delta}{1 + \alpha(1 + \alpha)(2 + \alpha)(7 + 2\alpha)} \\ N_{W4(2)} &= \frac{E_Y L_0 \alpha(1 + \alpha)(3 + \alpha)\Delta}{1 + \alpha(3 + \alpha)(4 + 3\alpha)} \\ N_{W5(3)} &= \frac{E_Y L_0 \alpha(2 + \alpha)\Delta}{1 + \alpha(9 + 4\alpha)} \\ N_{W6(4)} &= \frac{E_Y L_0 \alpha\Delta}{1 + 5\alpha} \end{aligned} \quad (\text{B.2})$$

By dividing point-by-point for each configuration the second set of expressions (B.2) by the first one (B.1), we obtain the equivalent k_0 parameter for each step:

$$\begin{aligned} k_{0(1)} &= \frac{E_Y L_0 \alpha(2 + \alpha)(2 + \alpha(4 + \alpha))}{1 + \alpha(2 + \alpha)(3 + \alpha)} \\ k_{0(2)} &= \frac{E_Y L_0 \alpha(1 + \alpha)(3 + \alpha)}{1 + \alpha(3 + \alpha)} \\ k_{0(3)} &= \frac{E_Y L_0 \alpha(2 + \alpha)}{1 + \alpha} \\ k_{0(4)} &= E_Y L_0 \alpha \end{aligned} \quad (\text{B.3})$$

Appendix C. Explicit calculations of the internal bending energy $W_{\text{int-b}}(i)$ for each mechanical configuration

In this subsection, detailed calculations to derive the internal bending energy $W_{\text{int-b}}(i)$ for each mechanical configuration (see Fig. 3 from part 1 to 4) are systematically reported. More in detail, it should be recalled that for each subsequent i th step, the displacement solutions (i.e. $u_j(i)$) of the 1D sole axial non-linear system (represented in part (a) of Fig. 2 and in Fig. 6 and explicitly evaluated following the approach by the paper Argenziano et al., 2026c) should be employed, by accounting for the progressive detachment of the abdominal prolegs. These solutions are obtained by minimising the total elastic potential energy, $U_{\text{NL}}(i)$, with respect to the unknowns $u_j(i)$. The calculation is here restricted to the sole 1D axial regime, where the prescribed displacement Δ

is set as the critical inelastic contraction for the given mechanical configuration (see Table 3), as detailed below:

$$\begin{aligned} \min_{u_j} U_{NL}(i) = & \min_{u_j} \left(\frac{E_Y L_0^3}{4} \left(-1 - 2 \log \left(\frac{u_2(i) - \Delta_{crit}(i)}{L_0} \right) + \left(\frac{u_2(i) - \Delta_{crit}(i)}{L_0} \right)^2 \right) + \right. \\ & + \frac{E_Y L_0^3}{4} \left(-1 - 2 \log \left(\frac{u_{j+1}(i) - u_j(i)}{L_0} \right) + \left(\frac{u_{j+1}(i) - u_j(i)}{L_0} \right)^2 \right) + \\ & \left. + \frac{1}{2} \sum_{j=2}^{n-1} k_2[j](i) (u_j(i))^2 \right), \quad n = 12, \end{aligned} \quad (B.4)$$

$$\text{where } k_2[j](i) = \begin{cases} \alpha E_Y L_0 & \text{if } j = \{3, 4, 5, 6\} \text{ and } i = 1 \\ \alpha E_Y L_0 & \text{if } j = \{4, 5, 6\} \text{ and } i = 2 \\ \alpha E_Y L_0 & \text{if } j = \{5, 6\} \text{ and } i = 3 \\ \alpha E_Y L_0 & \text{if } j = 6 \text{ and } i = 4 \\ 0 & \text{otherwise} \end{cases}.$$

Having evaluated the displacements u_j for each configuration, the formulations of the internal bending energy $W_{int-b}(i)$ are provided in what follows:

$$\begin{aligned} W_{int-b}(1) = & \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_2(1) - \Delta_{crit}(1)}{L_0} \right) + \left(1 + \frac{u_2(1) - \Delta_{crit}(1)}{L_0} \right)^2 \right) + \\ & + \frac{1}{2} \alpha E_Y L_0 (u_3(1))^2 + \frac{1}{2} \alpha E_Y L_0 (u_4(1))^2 + \frac{1}{2} \alpha E_Y L_0 (u_5(1))^2 + \frac{1}{2} \alpha E_Y L_0 (u_6(1))^2 + \\ & - \sum_{j=2}^{11} \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_{j+1}(1) - u_j(1)}{L_0} \right) + \left(1 + \frac{u_{j+1}(1) - u_j(1)}{L_0} \right)^2 \right), \\ W_{int-b}(2) = & \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_2(2) - \Delta_{crit}(2)}{L_0} \right) + \left(1 + \frac{u_2(2) - \Delta_{crit}(2)}{L_0} \right)^2 \right) + \\ & + \frac{1}{2} \alpha E_Y L_0 (u_4(2))^2 + \frac{1}{2} \alpha E_Y L_0 (u_5(2))^2 + \frac{1}{2} \alpha E_Y L_0 (u_6(2))^2 + \\ & - \sum_{j=2}^{11} \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_{j+1}(2) - u_j(2)}{L_0} \right) + \left(1 + \frac{u_{j+1}(2) - u_j(2)}{L_0} \right)^2 \right), \\ W_{int-b}(3) = & \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_2(3) - \Delta_{crit}(3)}{L_0} \right) + \left(1 + \frac{u_2(3) - \Delta_{crit}(3)}{L_0} \right)^2 \right) + \\ & + \frac{1}{2} \alpha E_Y L_0 (u_5(3))^2 + \frac{1}{2} \alpha E_Y L_0 (u_6(3))^2 + \\ & - \sum_{j=2}^{11} \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_{j+1}(3) - u_j(3)}{L_0} \right) + \left(1 + \frac{u_{j+1}(3) - u_j(3)}{L_0} \right)^2 \right), \\ W_{int-b}(4) = & \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_2(4) - \Delta_{crit}(4)}{L_0} \right) + \left(1 + \frac{u_2(4) - \Delta_{crit}(4)}{L_0} \right)^2 \right) + \\ & + \frac{1}{2} \alpha E_Y L_0 (u_6(4))^2 + \\ & - \sum_{j=2}^{11} \frac{1}{4} E_Y L_0^3 \left(-1 - 2 \log \left(1 + \frac{u_{j+1}(4) - u_j(4)}{L_0} \right) + \left(1 + \frac{u_{j+1}(4) - u_j(4)}{L_0} \right)^2 \right). \end{aligned} \quad (B.5)$$

Appendix D. Procedural summary: reconstructing caterpillar bending deflection

The step-by-step analysis carried out for determining each term of the caterpillar bending deflection is summarised in the following for the reader's convenience in the form of a procedural algorithm. It should be again highlighted that the set of subsequent mechanical configurations is not trivial and should be specified in the array appointed as (**Active_i**).

Data availability

No data was used for the research described in the article.

Algorithm 1 Step-by-step analysis for evaluating the axial displacements and the amplitude of the deformed bending shape for all the subsequent mechanical configurations.

Input: number of DoFs n , the resting length of individual body units L_0 , the stiffness ratio α , as well as the geometric and constitutive properties, namely Young's modulus E_Y , Poisson's ratio ν , the cross-sectional area A , and the moment of inertia I

Calibration of the mechanical model

- Calculate all the numerical values of $L_{(i)}$, $k_\varphi(i)$, $k_1(i)$, $k_0(i)$, as a function of the input parameters: see Table 2
- Evaluate $\Delta_{\text{crit}}(i)$ for the 4 potential subsequent configurations and evaluate which one/ones should be considered for the selected dataset: see Table 3
- Let **Active_i** = [...], i.e. the array representing the reduced/filtered subset of mechanical configurations involved
- Let $k = \text{length}(\text{Active_i})$, i.e. the total number of actual active configurations

Core: cycling steps for capturing axial and bending deflections

for $\zeta = 1$ to k **do**, where k is the total number of the progressive mechanical configurations

- $i = \text{Active_i}[\zeta]$ Map the current cycle step ζ to the corresponding configuration with index i
- Prescribe inelastic displacement $u_1(i) = \Delta_{\text{crit}}(i)$ at the support of the terminal subunit for the ζ -th cycle
- Evaluate the displacement solutions $u_j(i)$ for the i -th configuration by minimising the total elastic energy $U_{\text{NL}}(i)$ (see Eq. (B.4))
- By uploading the solutions $u_j(i)$ for the ζ -th step, make explicit the expression of the $W_{\text{int-b}}(i)$ (see expressions Eq. (B.5))
- Calculate the amplitude magnitude $A(i)$ of the bending deformed shape according to the Eq. (23)

Output of cycle (ζ): axial displacement values $u_j(i)$ and amplitude magnitude $A(i)$ at the ζ -th crawl substep
end for

Final Output: axial displacement solutions and amplitude magnitude of the bending curvature for each progressive mechanical configuration.

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