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How caterpillar crawling gait takes advantage of non-linear elasticity

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ABSTRACT

The vast majority of existing models of caterpillar locomotion successfully uses linear elasticity to describe how these *Lepidoptera*, at the larval stage, activate and coordinate the movement of the body segments during their crawling gait. Although linear mechanics is extremely effective for capturing the key features of the locomotion of these insects and for providing some helpful analytical results, large deformations actually experienced by the moving caterpillar structures suggest that nonlinear elasticity could play an important role in faithfully and quantitatively predicting their behaviour. To incorporate these experimental evidences, the present study, by employing a discrete lumped-mass model, introduces a neo-Hookean constitutive law for the segmented caterpillar body. Apart from consistency with observations, the proposed hyperelastic approach energetically penalised high compressive stresses and contractions with respect to tensile stresses and stretches, as actually occurs during realistic locomotion, also intrinsically preventing interpenetration between adjacent body tracts at any step of the numerical simulations, so inherently enforcing compatibility conditions that, in linear elastic formulations, would have required the introduction of additional constraints for avoiding unphysical results. In particular, we propose that locomotion is triggered by a localised inelastic muscle contraction of the terminal caterpillar body segment, which interacts with the abdominal prolegs responsible for substrate attachment and detachment, leading to a competition between gripping forces and internal body deformations. The consequence is that detachment and forward progression occur only when the adhesive energy threshold of the abdominal prolegs – modelled as Winkler foundation of elastic springs that disengage upon reaching a critical tensile load – is exceeded. Finally, by uploading inertial and dissipative effects for reproducing dynamic conditions, we demonstrate that caterpillar crawling gait is essentially a steady-state process, however highlighting how nonlinear elastic energy stored during muscle contraction is redistributed and partly converted into kinetic energy during locomotion for activating initial propulsion. It is felt that the results of the present work may contribute to shed new light on the fundamental mechanisms ruling crawling in living organisms, which could also guide the design of next-generation bio-inspired soft robots, capable of exploiting cumulated elastic energy for propulsion and efficient motion while adhering on substrates.

1. Introduction

Nowadays, the study of locomotion mechanisms observed in living organisms has gained increasing prominence, owing to their outstanding adaptability and efficiency across a wide variety of complex environmental scenarios (Iida and Laschi, 2011; Kortman et al., 2025). These biological features have progressively established themselves as a key inspiration for the design of innovative bioinspired systems aimed at addressing several challenges in various engineering realms (Trimmer, 2008; Hochner, 2011; Rus and Tolley, 2015; Cianchetti et al., 2014, 2015; Laschi et al., 2016; Umedachi et al., 2016; Calisti et al., 2017; Cornejo et al., 2024).

Among the broad spectrum of biological locomotion paradigms and examples (Lissmann, 1945; Dethier, 1989; Quillin, 1999; Gray, 1968;

Tanaka et al., 2012; Zimmermann et al., 2009; Gazzola et al., 2014; Rens and Merks, 2020; Palumbo et al., 2021; Carotenuto et al., 2020; Ishimoto et al., 2025), caterpillars represent a particularly remarkable case study due to their segmented and highly deformable body morphology, which may make them ideal candidates for the advancement of soft robotics research (Wu et al., 2023; Guo et al., 2022; Kim and Cha, 2023). Their characteristic crawling gait ensures a highly stable and effective motion modality (Gray, 1968; Trimmer and Issberner, 2007; Saunders et al., 2011; Van Griethuijsen and Trimmer, 2014; Trimmer and Lin, 2014; Vaughan et al., 2018). Various morphological and biological aspects are crucial to the way these organisms adapt their locomotion to the substrate (Hayashi and Sugiura, 2021). The

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caterpillar's body, enveloped by a compliant cuticle, is generally divided into 12–14 segments, several of which are equipped with prolegs or legs (Trimmer et al., 2006; Trimmer and Issberner, 2007; Trimmer, 2008; Trimmer and Lin, 2014; Van Griethuijsen and Trimmer, 2014; Kondakath et al., 2025). In particular, the abdominal prolegs, functioning analogously to suction cups, are primarily employed for surface attachment and detachment, while the thoracic legs mainly serve exploratory and sensory purposes (Van Griethuijsen and Trimmer, 2014; Lin et al., 2009; Lin and Trimmer, 2010; Lin, 2011; Lin and Trimmer, 2011; Argenziano et al., 2025b). Furthermore, the body includes highly extensible longitudinal muscles capable of contracting to less than half of their resting length and elongating to nearly twice that value (Dorfmann et al., 2007; Lin et al., 2009; Simon et al., 2010). Experimental observations reported in the literature (Simon et al., 2010; Van Griethuijsen and Trimmer, 2014) demonstrate that locomotion is initiated through a contraction of the musculature portion localised at the terminal segment. This posterior section acts as an anchor or pivot point on the substrate, initiating and propelling the wave of contraction forward. This energy is then elastically redistributed to sequentially detach each proleg from the substrate in a posterior-to-anterior order. Once the anterior region has fully detached, the reattachment sequence begins from the rear, thereby establishing a periodic and efficient crawling cycle.

In our past research (Argenziano et al., 2025b, 2026b), we highlighted the fundamental interplay between body elasticity and adhesion in driving and stabilising caterpillar locomotion by combining experimental findings with a deliberately simplified one-dimensional mechanical (1D) model accurately reproducing the observed gait. Experimental evidence supports that, as the muscle contraction triggers the locomotion, the suction-cup-like prolegs progressively overcome their adhesive threshold, lifting the posterior region and enabling forward progression in a smooth and coordinated way. From a mechanical standpoint, several modelling frameworks for crawling systems inspired by such locomotion have been proposed, encompassing both continuous and discrete formulations (Challamel and Zingales, 2025a,b; Schuldt et al., 2015; Zhou and Wang, 2024). In this regard, our model presented in Argenziano et al. (2025b) consists of a discrete, lumped-mass, 1D mechanical system intentionally designed to capture the essential contributions of adhesive interactions and elastic energy flow during motion. Specifically, as biologically grounded, the onset of locomotion is described as a localised inelastic contraction prescribed to the terminal segment, mimicking the pivot-like role of the rear end, which generates an anterograde deformation that propagates along the soft body and induces forward displacement (Woods, Jr. et al., 2008; Johnston and Levine, 1996; Saunders et al., 2011). The interplay with the substrate is modelled through horizontal 1D Winkler-type elastic foundations (Hetényi, 1946; Gerolymos and Gazetas, 2006; Paola and Zingales, 2012), whose stiffness competes with the internal elasticity of the body, thereby governing the overall locomotion mechanism.

Although linear elasticity adopted in prior research (Zimmermann et al., 2009; Schuldt et al., 2015; Argenziano et al., 2025b, 2026b; Qin et al., 2024) can be useful for capturing the fundamental aspects of locomotion modes, the high deformation values experienced by caterpillar body units, together with the different stiffness values approaching compression with respect to tensile regime, forces us to refine the already proposed mechanical model and to introduce hyperelastic non-linear stress–strain constitutive relations (Holzapfel et al., 2000; Cowin and Doty, 2007; Bigoni, 2012; Palumbo et al., 2018, 2021). In particular, the introduction of non-linear elasticity is motivated on the basis of two main considerations: (i) empirical and experimental tests carried out in the inherent scientific literature (Dorfmann et al., 2008; Lin et al., 2009) support the efficacy of hyperelastic neo-Hookean stress–strain laws for faithfully replicating the biomechanical behaviour of caterpillar soft tissues, and (ii) non-linear constitutive relations with penalisation in the compression phase intrinsically avoid interpenetration between adjacent body segments,

by imposing a greater energetic cost (that asymptotically tends to infinity when stretch is vanishing) on contractions with respect to extensional ones, thereby ensuring the satisfaction of compatibility conditions without necessitating auxiliary constraints typically added in linear elastic models.

The effect of the constitutive non-linearity incorporated into the system demonstrates that, given the same Young modulus and resting lengths for body units and Winkler-like springs, the neo-Hookean model allows for exploration of high deformations that are significantly closer to those experimentally observed. Moreover, when subjected to the same inelastic trigger input, the non-linear model enables a more pronounced locomotion of the caterpillar in terms of displacements. The results presented in the paper are discussed, and the adoption of the non-linear model – which generalises the one used in the previous study – reveals additional effects, particularly in terms of cumulated compressive energy that can be released for aiding motion and making the gait trajectory more stable.

In a first stage, inertial and dissipative effects are disregarded and an elasto-static approach is initially implemented. Subsequently, the model is extended to dynamic conditions to investigate the effects of non-linear elasticity during the transient phase, highlighting its role in the initial propulsion of the motion.

The paper is structured as follows. Section 2, after motivating through experimental observations the need of non-linear elasticity for faithfully capturing the locomotion mechanism, introduces the neo-Hookean constitutive law for inter-masses springs under quasi-static conditions. The theoretical framework for modelling caterpillar locomotion has been extensively developed, and some notes on closed-form expressions have also been reported in the Appendix section. Then, in Section 3, by implementing inertial and dissipative terms, comparisons between linear and non-linear dynamic analyses are provided. Finally, in Section 4, Discussions and conclusions, the core aspects of the study are revisited and the principal outcomes are systematically summarised, also putting emphasis on their implications for future developments in the field.

The findings of this research are expected to deepen the current understanding of caterpillar locomotion while simultaneously offering valuable guidelines and design principles for the realisation of soft robotic platforms capable of autonomously traversing complex and confined environments. Such systems would be able to adapt to obstacles and surface irregularities, thus extending their applicability across a wide range of engineering domains.

2. Non-linear elasticity for accounting actual large deformations in caterpillar locomotion

In previous modelling approaches (Schuldt et al., 2015; Argenziano et al., 2026b, 2025b), the mechanical response of the caterpillar body has been frequently represented through a linear elastic setting, which assumes small deformations and proportional stress–strain behaviour. This simplified formulation may allow for a straightforward analytical treatment and offers valuable qualitative insights into the fundamental mechanisms governing locomotion. However, by definition, such linear models neglect constitutive non-linearities that become relevant when the body undergoes substantial stretches during crawling.

Consequently, although linear elasticity is extremely useful in the first initial stage for capturing the essential aspects of caterpillar locomotion and for easily managing the system's equations in a fully analytical way, experimental tests in the inherent literature (Dorfmann et al., 2007) demonstrate that non-linear stress–strain relations are observed for the larvas' body, as well as large deformation values are experienced during the crawl-cycles, as also one can notice in panel (a) of Fig. 1 and the in-zoom views of the terminal part of the body in Fig. 2. More in detail, in our laboratory observations, we register significant cycling stretching and compression in the posterior body segments, with measured lengths of the corresponding mechanical

configuration ranging from 5.6 mm to 8.7 mm over successive time steps, corresponding to engineering strains greater than 30% (see subplots (b) and (c) of Fig. 1). These deformations are relatively large compared to the dimensions of the body units and cannot be accurately described using linear elastic assumptions. Although the deformation of the entire caterpillar body can be effectively modelled as a linear elastic system, as experimentally demonstrated in Argenziano et al. (2026b, 2025b), this approximation does not hold at the scale of individual body segments, as further proved by the data obtained from the experimental setup and reported in Table 1. More specifically, we can recognise that during the contraction phases of the terminal body portion, the stretch λ (i.e. the ratio between the final length and the resting one) is approximately equal to 0.70–0.75 with values no lower than 0.67. Although the locomotion pattern is almost the same, a quite large variance is registered on the net forward displacement for each cycle. By looking at the panel (a) of Fig. 1 and at the registered total lengths of the soft animal during locomotion in Table 1, the contraction is strongly localised on the terminal portion and on the abdominal segments, the whole body being less affected by the deformation pattern. It is therefore confirmed that such large deformations for the individual body units require the adoption of a hyperelastic non-linear constitutive model to faithfully describe the mechanical behaviour, thus enabling more realistic simulations of its soft-bodied biomechanics. Additionally, in Fig. 2 and in Table 2, we focus on a single crawl cycle, whose duration is approximately 1.0–1.2 s, by comparing the locomotion on two distinct supports: the wooden one (reproducing the caterpillar's natural environment) and the plastic surface (Acrylonitrile Styrene Acrylate, i.e. ASA thermoplastic). From the analysis, we can quantitatively derive the stretch values along a single crawl substep corresponding to the detachment of a single proleg once at a time (see Fig. 2). As the data demonstrate in Table 2, the analysis reveals approximately the same order of magnitude of λ of the posterior segments, with a slight difference: on the wooden support, the λ grows uniformly up to the unitary value corresponding to the last motion step, reaching lower peaks with respect to what happens on the plastic substrate, where the contraction appears flatter during the step-by-step locomotion. However, despite this aspect, the locomotion pattern is qualitatively the same for both supports. By comparing the two substrates, another difference emerges in the initial propulsion at the two time instants 0.1 and 0.3 s (see Fig. 2). Specifically, the intrinsic anisotropy of the wood facilitates the movement, as well as increases the grip on the support, thus guaranteeing the optimal balance between body elasticity and adhesion. This substrate characteristic has significant implications for the locomotion modes. On rough surfaces, the optimal balance between elasticity and adhesion maximises forward propulsive grip and avoids backward slipping. Conversely, on slippery or smooth surfaces, like plastic supports, the reduced effective adhesive friction disrupts the elastic-adhesive balance, potentially causing the posterior segments to not have sufficient grip during contraction and thereby to cumulate less elastic energy to give the optimal propulsion and determining an inefficient and decreased forward net displacement. Importantly, from Fig. 2, one can immediately notice two aspects: the overall inelastic contraction is reduced in the case of plastic support with respect to the wooden substrate and, in addition, by considering the same time steps, the soft invertebrate needs to calibrate twice the initial displacement of the terminal body segments for triggering locomotion (compare, for instance, the snapshots of the two substrates at 0.1 and 0.3 s of the Fig. 2). Further details on the locomotion behaviour of caterpillars on several substrates with different surface roughness are provided in Argenziano et al. (2026a).

Therefore, to capture the fundamental mechanical principles underlying caterpillar locomotion, a 1D discrete lumped-mass model, previously introduced in Argenziano et al. (2026b, 2025b) and schematically depicted in Fig. 3, is here recovered. In this formulation, the caterpillar body is idealised as a chain of discrete lumped masses connected in series by springs representing its axial elasticity. The interaction with

Table 1

Measured data – at a fixed 1 s time step – resulting from the laboratory tests whose findings have been represented in Fig. 1 and have been here analytically reported in terms of the posterior segment stretch (λ), the total length of the caterpillar during locomotion (L), and the net forward displacement (d), that is, the forward displacement evaluated with respect to the previous step.

t [s]	λ [–] posterior segment	L [mm] total length	d [mm] net forward displacement
0	1	38.00	0
1	0.68	34.74	3.48
2	1.06	35.32	1.26
3	0.82	35.42	2.94
4	1.06	36.46	0.85
5	0.79	35.78	3.45
6	0.95	35.45	1.04
7	0.94	35.54	0.26
8	0.94	37.74	0.01
9	0.94	38.22	0.04
10	0.93	38.33	0.05
11	0.71	36.75	2.09
12	1.04	36.38	1.23
13	0.93	35.94	3.66
14	0.67	36.10	2.90
15	0.90	36.88	1.53
16	0.95	36.65	3.00
17	0.95	35.90	0.35
18	0.95	36.13	0.23
19	0.93	36.90	0.14
20	0.91	36.96	3.07
21	0.88	36.45	2.00
22	0.70	36.97	1.23
23	0.94	37.55	1.27
24	0.94	36.57	1.28
25	0.99	34.22	1.53

Table 2

Time evolution of the stretch λ measured on wood and plastic substrates during a single crawl-cycle that has a time duration approximately of 1-1.2 s.

t [s]	λ [–] on wood	λ [–] on plastic
0	1	1
~ 0.1	0.76	0.90
~ 0.3	0.83	0.80
~ 0.6	0.95	0.90
~ 0.9	1.00	1.00
~ 1.2	0.99	1.00

the substrate is still described through Winkler-type elastic constraints that mimic the adhesive behaviour of the abdominal prolegs, which are assumed to be mainly engaged during the locomotion process, being the contribution of thoracic legs neglected. The attachment-detachment cycles of the prolegs are governed by a linear elastic law incorporating a critical tensile displacement u_y , corresponding to the adhesion threshold required for proleg release. The locomotion trigger is idealised as an inelastic muscle contraction, whose amplitude is Δ and it is prescribed to the terminal segment.

However, with respect to our previous research (Argenziano et al., 2025b), a non-linear hyperelastic constitutive model is here employed for the inter-masses springs, in order to not only enable a more accurate reproduction of large deformations registered by laboratory observations, but also to ensure physical consistency by also capturing the characteristic increase in stiffness under compression compared to tension, while inherently preventing interpenetration between adjacent body segments. To gain insights into the effects of such structural behaviour on the gait, incompressible neo-Hookean elastic law ($\nu \rightarrow \frac{1}{2}$, with ν Poisson modulus) has been adopted for body springs (see Fig. 3). For the single inter-mass link connecting the i and $i+1$ subunit, the

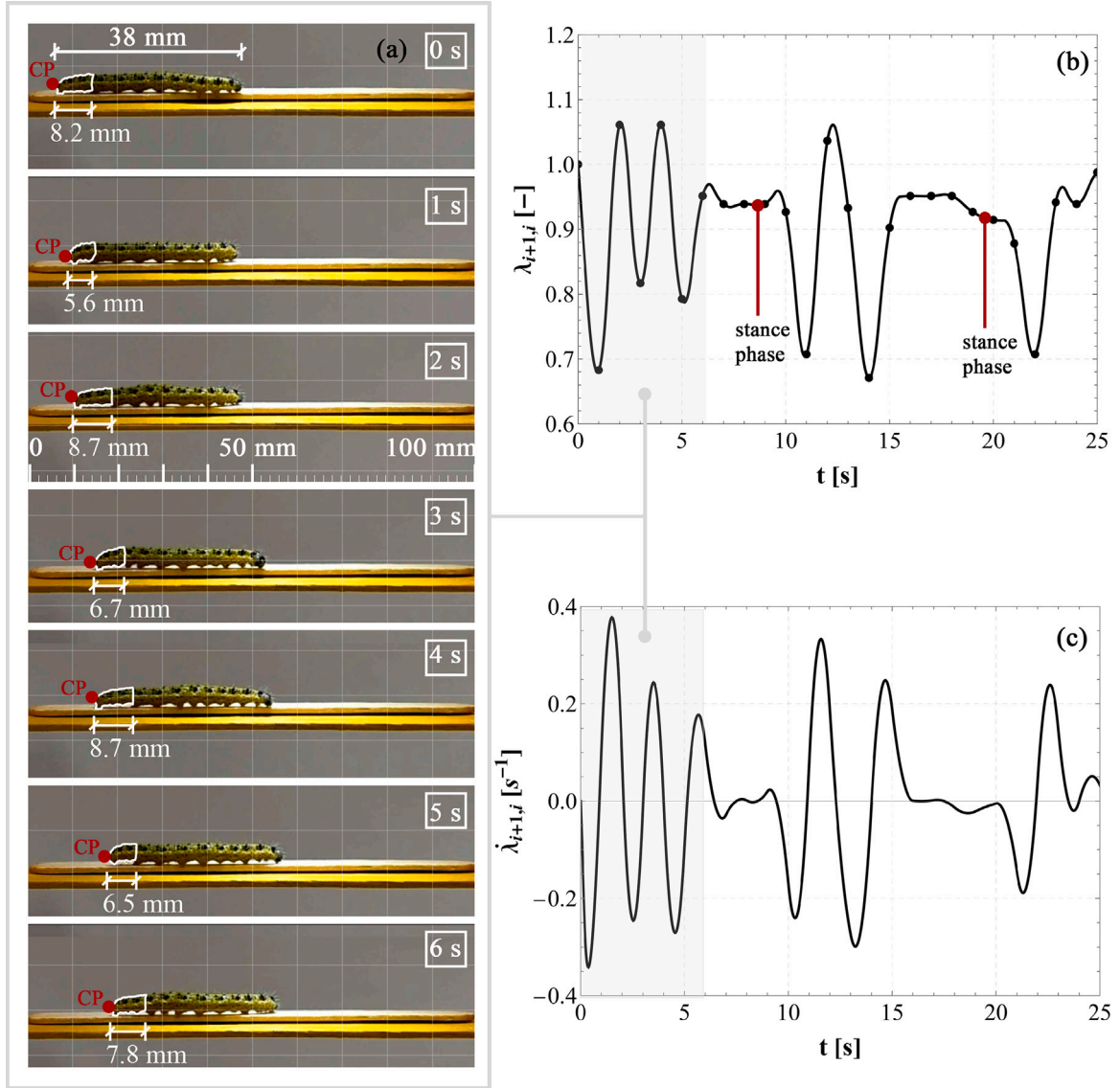


Fig. 1. Experimental observations of large tissue deformations of caterpillar body belonging to the *Pieris brassicae* species. More in detail, part (a) reports sequential frames of a caterpillar during crawling on a horizontal wooden substrate, measuring body deformation of the terminal part and forward progression over time (0–6 s). The body length and local segmental stretch vary during locomotion as adhesion and contraction alternate. Subplot (b) provides the time evolution of the longitudinal stretch $\lambda_{i+1,i}$ (identified by the ratio between the final and the resting length) for a representative body segment, highlighting stance and dynamic phases over time (0–25 s). The stretch history is reconstructed by fitting a second-order polynomial to the discrete data points extracted from video analysis through capture–playback software, shown as black circles. The resting length of the highlighted body segment is 8.2 mm. Finally, part (c) refers to the numerical time derivative of the stretch $\dot{\lambda}_{i+1,i}$, indicating contraction–extension sequence associated with the crawling gait (interval 0–25 s). The displacement measures are conducted with reference to the control point (CP) highlighted by the red circle at the terminal part of the animal. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

elastic potential energy can be made explicit as:

$$U_{NH} = \frac{k_1 l_0^2}{6} (\lambda_{i+1,i}^2 + 2\lambda_{i+1,i}^{-1} - 3), \quad (1)$$

where $\lambda_{i+1,i}$ is the longitudinal stretch of each body unit along the locomotion axis and k_1 is the tangent stiffness, i.e. the ratio between the Young modulus E times the underformed cross-section area A_0 over the resting body subunit length l_0 . Additionally, while in the linear model, further constraint conditions should be added to the set of the system's equations to ensure compatibility, as above-mentioned, the neo-Hookean constitutive relation automatically avoids interpenetration, by penalising the compression phase with respect to the tensile regime from an energy point of view. In this light, non-linear elasticity naturally allows to overcome this additional constraint condition, achieving higher α values compared to the linear system, by also

preserving the fact that stretches of links connecting adjacent masses should be always greater than 0. Although the caterpillar body is naturally anisotropic (Dorfmann et al., 2007), we have modelled it using an isotropic neo-Hookean law. While an anisotropic model would quantitatively alter local stress distributions, the global kinematics of locomotion are driven primarily by the interplay between essentially 1D large deformations and directional adhesion to the substrate. This simplification allows us to keep the mathematical model tractable and avoid an excessive number of material parameters to experimentally calibrate.

By assuming as Lagrangian parameters the horizontal displacements of each lumped mass m_i , that are $u_i(t)$, the longitudinal stretch $\lambda_{i+1,i}$ is evaluated as:

$$\lambda_{i+1,i} = \frac{u_{i+1}(t) - u_i(t)}{l_0} + 1, \quad (2)$$

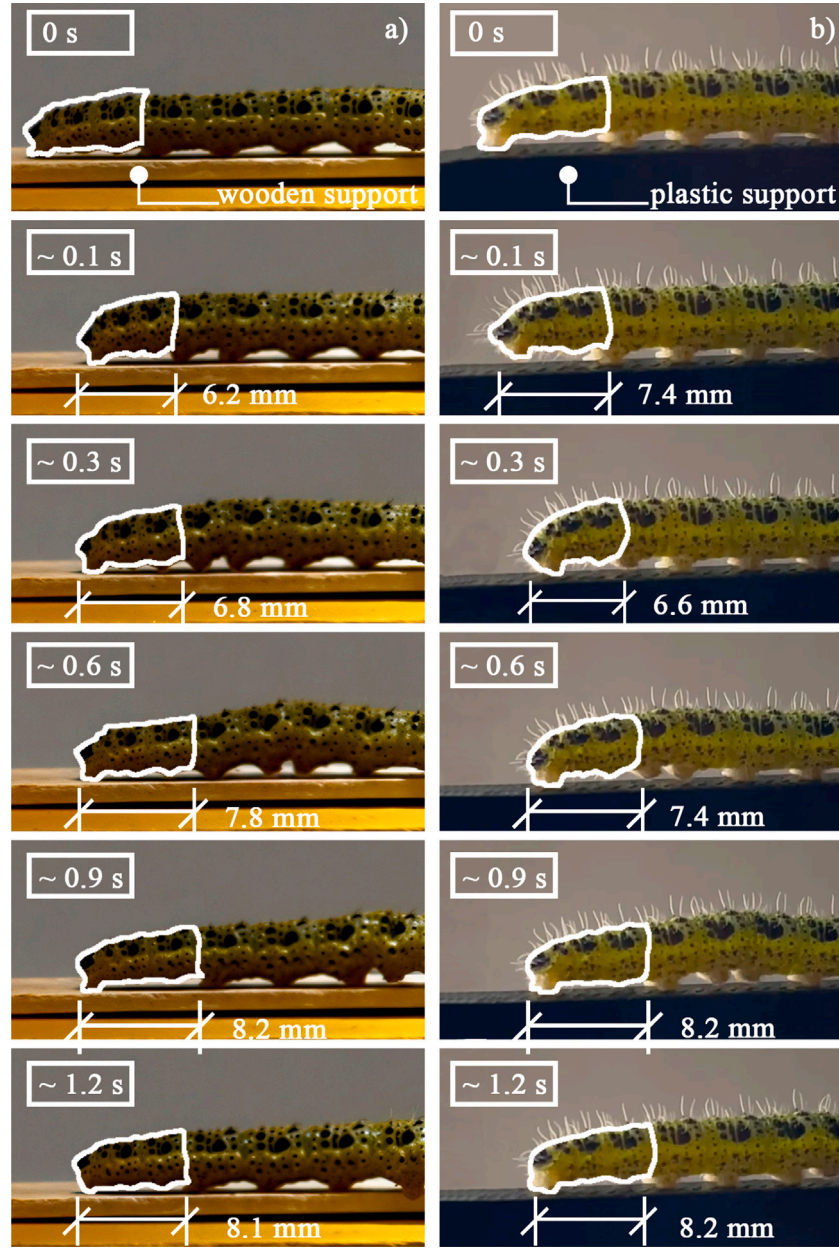


Fig. 2. Time-step sequence of the terminal body segment elongation-contraction during locomotion on (a) a wooden support and (b) a thermoplastic ASA substrate. More in detail, the column (a) reports the images extracted from 0 to 1.2 s of the same movie whose snapshots have been reported in Fig. 1 with a larger time-step. White Annotations highlight the measurement of longitudinal stretch (in mm) at specific time intervals (from 0 to 1.2 s, that is, the duration of a crawling cycle), displaying the large experimental deformations registered. As above-mentioned, it should be underlined that the resting length of the posterior segment is 8.2 mm at the configurations at 0 s. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and by deriving two times, Eq. (1) in the longitudinal stretch variable $\lambda_{i+1,i}$, the stiffness can be formulated as a stretch-dependent function given by:

$$k_{NH} = \frac{k_1}{6} (2 + 4 \lambda_{i+1,i}^{-3}). \quad (3)$$

It is worth recalling that when $\lambda_{i+1,i}$ approaches 1 (i.e. the link restores its resting length and u_{i+1} tends to u_i), the tangent stiffness of the equivalent linearised model is recovered ($k_{NH} \rightarrow k_1$). Consequently, by uploading the non-linear neo-Hookean constitutive law to the inter-mass springs, the total potential energy of the system, say U_{NL} , can be

specified as:

$$U_{NL} = \frac{k_1 l_0^2}{6} \left(\left(\frac{u_2(t) - \Delta}{l_0} + 1 \right)^2 + 2 \left(\frac{u_2(t) - \Delta}{l_0} + 1 \right)^{-1} - 3 \right) + \frac{k_1 l_0^2}{6} \sum_{i=2}^{n-1} \left(\left(\frac{u_{i+1}(t) - u_i(t)}{l_0} + 1 \right)^2 + 2 \left(\frac{u_{i+1}(t) - u_i(t)}{l_0} + 1 \right)^{-1} - 3 \right) + \frac{1}{2} \sum_{i=2}^{n-1} k_2[i] (u_i(t))^2, \quad n = 12, \quad (4)$$

where $k_2[i] = \begin{cases} \alpha k_1 & \text{if } i = \{3, 4, 5, 6\} \text{ and } u_i \leq u_y, \text{ with } \Delta \leq l_0, \\ 0 & \text{otherwise} \end{cases}$

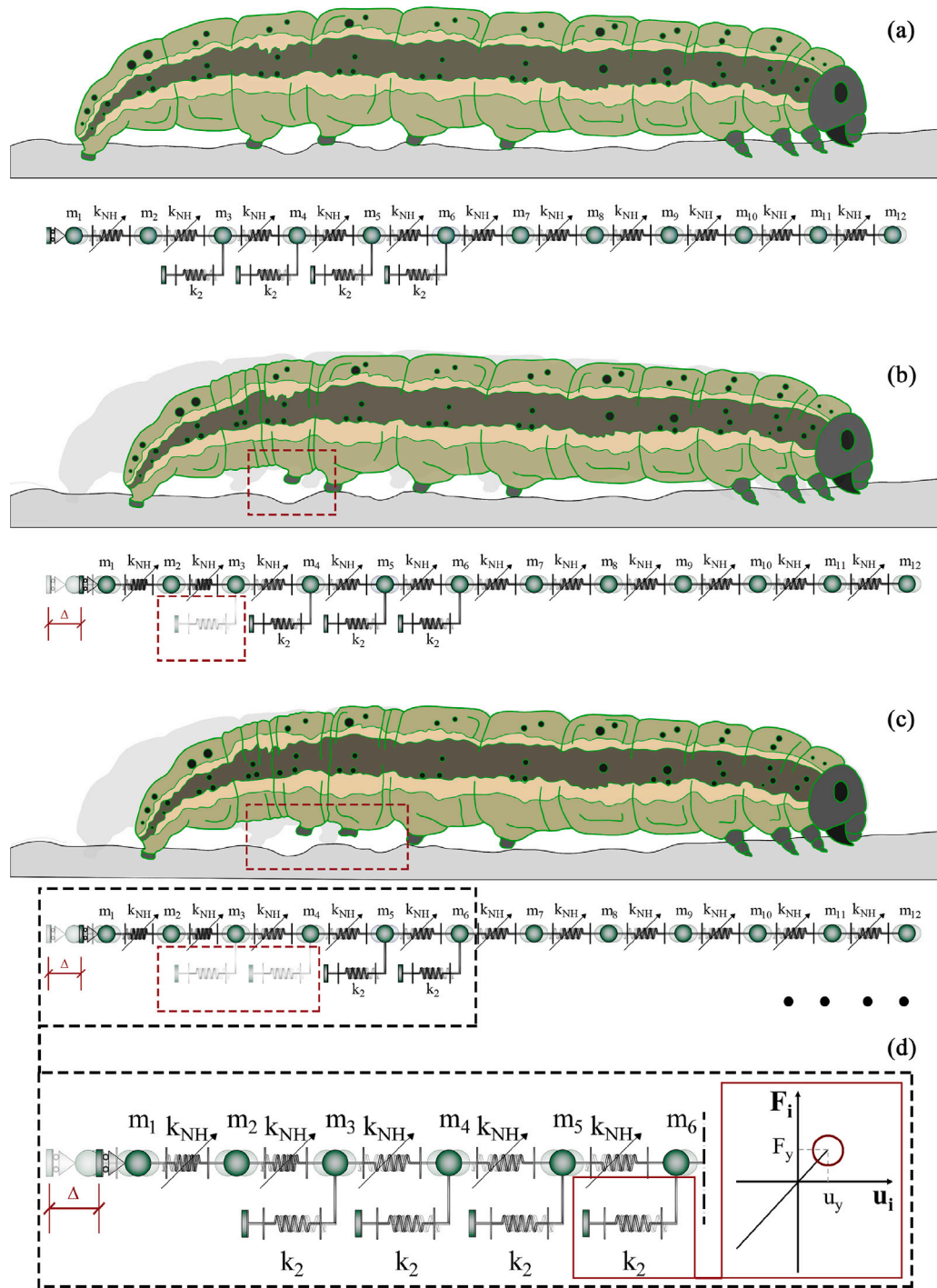


Fig. 3. Schematic illustration showing the sequential phases of caterpillar crawling and the corresponding mechanical model: (a) a lumped-mass representation of the body segments during the stance phase; (b) an inelastic muscle contraction of amplitude Δ initiates movement and causes the first abdominal proleg to detach from the support; (c) schematic view of the second sub-step, where the second abdominal proleg detaches. The crawling cycle continues until all four abdominal prolegs have lifted and subsequently reattach after the caterpillar's body has shifted by a total distance of Δ , completing its crawling cycle. In the zoomed-in view of part (d), a detail of the 1D mechanical model is provided. The non-linear springs are indicated by inclined arrows, while the horizontal linear Winkler-type springs refer to the body-support interplay. The constitutive relation of the latter is provided on the right hand: when the internal force of the spring attains the adhesion threshold, the constraint is turned off, thus simulating the detachment of the corresponding proleg.

being α the ratio between k_2 , the Winkler-like springs stiffness and the tangent stiffness k_1 , that is $EA_0 l_0^{-1}$ and recalling that u_y is the adhesion threshold of the abdominal prolegs, as schematically represented on the right side of Fig. 3, panel (d).

Quite trivially, when $\lambda_{i+1,i}$ tends to 1, i.e. when small displacements are assumed, and the number of DoFs n remains 12, the linear elastic case is recovered and the total potential energy falls into the linearised one already made explicit in Argenziano et al. (2026b, 2025b), as follows:

$$\lim_{\lambda_{i+1,i} \rightarrow 1} U_{NL} = \frac{1}{2} \sum_{i=2}^{n-1} k_2 [i] (u_i(t))^2 + \frac{1}{2} k_1 \sum_{i=2}^{n-1} (u_{i+1}(t) - u_i(t))^2 + \frac{1}{2} k_1 (u_2(t) - \Delta)^2. \quad (5)$$

Initially, a quasi-static approach has been initially adopted and the time-dependence of the displacements has been neglected. By minimising U_{NL} with respect to the unknowns u_i , the i th equation referred to the i th DoF of the lumped mass system (Fig. 3) assumes the following form:

$$\frac{1}{3} k_1 l_0 \left(\left(1 + \frac{u_i - u_{i-1}}{l_0} \right) - \left(1 + \frac{u_i - u_{i-1}}{l_0} \right)^{-2} \right) + k_2 [i] u_i + \frac{1}{3} k_1 l_0 \left(\left(1 + \frac{u_{i+1} - u_i}{l_0} \right) - \left(1 + \frac{u_{i+1} - u_i}{l_0} \right)^{-2} \right) = 0. \quad (6)$$

More detailed mathematical steps of the i th equation and the solution of the i th DoF have been explicitly reported in Appendix. Starting from Eq. (1), one can calculate the Cauchy stress P_i referring to the current updated mechanical configuration of each caterpillar body unit in each subsequent step. More in particular, P_i can be expressed as follows:

$$P_i = \frac{F_{i+1,i}}{a} = \frac{\partial U_{NH}}{\partial \Delta u_{i+1,i}} \frac{1}{a}, \quad (7)$$

where a is the current cross-sectional area of the hyperelastic neo-Hookean link modelling body units' elasticity and $\delta \Delta u_{i+1,i}$ (see Eq. (2)) can be made explicit as:

$$\begin{aligned} \delta \Delta u_{i+1,i} &= \frac{\partial \Delta u_{i+1,i}}{\partial \lambda_{i+1,i}} \delta \lambda_{i+1,i} = \frac{\partial (u_{i+1} - u_i)}{\partial \lambda_{i+1,i}} \delta \lambda_{i+1,i} \\ &= \frac{\partial ((\lambda_{i+1,i} - 1) l_0)}{\partial \lambda_{i+1,i}} \delta \lambda_{i+1,i} = l_0 \delta \lambda_{i+1,i} \end{aligned} \quad (8)$$

Therefore, the Cauchy stress P_i can be re-written in the following form:

$$P_i = \frac{F_{i+1,i}}{a} = \frac{\partial U_{NH}}{\partial \Delta \lambda_{i+1,i} l_0} \frac{1}{a}. \quad (9)$$

However, following the Nanson's formula in the framework of the non-linear mechanics (Holzapfel et al., 2000), the current area of the cross-section a can be evaluated with reference to the undeformed transversal section A_0 with dimensions $l_0 \times l_0$ as:

$$a = \lambda_{T,i}^2 A_0 = \lambda_{T,i}^2 l_0^2, \quad (10)$$

being $\lambda_{T,i}$ the transversal stretch of the body segment. By assuming uniaxial stress distribution that requires the lateral surface of the subunit is unloaded, it can be easily demonstrated that $\lambda_{T,i} = \lambda_{i+1,i}^{-\nu}$ (Fraldi et al., 2021). Therefore, by adopting the Poisson modulus $\nu \rightarrow \frac{1}{2}$, the longitudinal Cauchy stress P_i has definitely the following form:

$$P_i = \frac{\partial U_{NH}}{\partial \Delta \lambda_{i+1,i}} \frac{\lambda_{i+1,i}}{l_0^3} = \frac{k_1}{3 l_0} \left(\lambda_{i+1,i}^2 - \frac{2}{\lambda_{i+1,i}} \right) \quad (11)$$

By numerically solving Eqs. (6), the displacements u_i of each body segment which replicate the caterpillar locomotion, can be accurately determined. The algorithm previously proposed in our earlier works (Argenziano et al., 2026b, 2025b) – which reconstructs motion at each substep throughout an entire crawl cycle – has been revisited and adapted to the non-linear framework here provided, as summarised in

the Algorithm 1 implemented in the symbolic and numerical environment of Mathematica® (Wolfram Research, 2021). This step-by-step procedure enables the evaluation of the longitudinal stretch and the corresponding stress in the current mechanical configuration at each crawling substep, as defined in Eqs. (2) and (11), respectively.

Algorithm 1 Sequential analysis of caterpillar locomotion by assuming quasi-static conditions

Input: number of DoFs n , resting length and tangent stiffness (when $\lambda \rightarrow 1$) of inter-masses springs, respectively l_0 and k_1 , stiffness ratio α and detachment threshold for the Winkler-like constraints u_y
Boundary Condition: apply inelastic displacement $u_1 = \Delta$ at the support of the terminal subunit
for $j = 1$ **to** k **do** $\triangleright k$ is the total number of crawl cycles
 for $i = 1$ **to** h **do** $\triangleright h$ is the number of abdominal prolegs
 if $i = 1$ **then**
 Solve the system by minimizing the total elastic energy U_{NL} (4)
 Identify the spring whose elongation reaches the threshold u_y
 Update the system by removing the identified (detached) spring
 else
 Solve the system updated at substep $(i - 1)$
 Identify the next spring reaching the threshold u_y
 Update the system by removing the newly detached spring
 end if
 end for
 Output of cycle j : displacement values u_i for each DoF during the j -th crawl substep
end for
Final Output: displacement values u_i for each DoF across all k crawl cycles.

The parameters used in the following calculations have been specifically calibrated to reproduce the experimental observations presented in Figs. 1 and 2, as well as Tables 1 and 2. To ensure the numerical simulations align with the experimental results (reported in Fig. 4), the stiffness ratio parameter α has been carefully tuned, based on the geometric and mechanical parameters which have been measured or derived from literature. More in detail, the caterpillar's geometric features have been experimentally measured (i.e. the resting length and the inelastic contraction Δ), the Young's modulus of its tissue is estimated in the kPa range, as provided in Dorfmann et al. (2007), and an adhesion force for *Pieris brassicae* larvae of the order of magnitude of 0.05 N per proleg on wood is derived from our previous findings (Argenziano et al., 2025b). Furthermore, to account for the significantly lower adhesion on the plastic substrate, the numerical values for both u_y and Δ have been roughly reduced by half. This reduction maintains a constant ratio between Δ and u_y , in agreement with experimental observations. For the reader's convenience, Table 3 summarises all the mechanical parameters involved and the source of the numerical values adopted in simulations.

In Fig. 4, the distribution of the longitudinal stretch λ along the DoFs of the caterpillar body during the crawling cycle highlights the presence of significant local deformations with higher values recovered for the locomotion on the wooden substrate with respect to the plastic one. For instance, during the first substep, values of λ decrease to approximately 0.74, indicating substantial compression in certain segments. These compressive stretches are progressively reduced in the subsequent substeps as the body recovers towards its undeformed configuration. The magnitude of these deformations strongly motivates the adoption of a non-linear neo-Hookean constitutive model, as linear elasticity would fail to accurately capture the observed behaviour. In particular, when using a linear elastic model with the same set of parameters employed

Table 3
Mechanical meaning and source of the parameters adopted in the elasto-static model.

Model parameter	Physical meaning	Source
l_0	body unit resting length	experimentally measured
$k_2 u_y = \alpha k_1 u_y$	adhesion force	derived from literature (Argenziano et al., 2025b)
Δ	inelastic contraction	experimentally measured
E	Young modulus of the body tissue	derived from literature (Dorfmann et al., 2007)
$A_0 \sim l_0^2$	resting cross-section area	obtained from the resting length
$k_1 = E A_0 l_0^{-1}$	tangent stiffness	obtained from the other parameters
$\alpha = k_2 k_1^{-1}$	stiffness ratio	calibrated in order to best-fit the experimental results

to describe the experimentally observed locomotion of the *Pieris brassicae* caterpillar on wood, the predicted displacement field leads to inconsistencies. Specifically, by evaluating the displacement Δ needed for initiating and maintaining the motion, according to the kinematic compatibility condition derived from the linear model formulation (reported in Argenziano et al. (2025b)), one obtains a value of $\Delta = 0.0098$ m. This result is incompatible with the physical system, as it exceeds the resting length of the inter-mass springs, which is set to 0.00317 m. This discrepancy reveals a fundamental limitation of the linear model in simulating large compressive strains, which are often intrinsic to the crawling caterpillar mechanics. Conversely, this issue is inherently resolved by adopting the hyperelastic neo-Hookean constitutive law, which naturally penalises compression more than tension and automatically prevents interpenetration between adjacent subunits. Additionally, based on the simulations, Fig. 4 confirms the experimental findings, that is, the caterpillar exhibits a much more efficient crawling gait on the wooden substrate compared to the plastic one. Specifically, the caterpillar experiences significantly greater segment deformation on the wooden surface, with its longitudinal stretch dropping to 0.74, compared to a minimum of 0.86 on the plastic substrate. Consequently, these larger deformations generate higher compressive Cauchy stresses, reaching approximately -3.3 MPa on wood versus -1.7 MPa on plastic. This enhanced propulsion during the locomotion phase ultimately yields greater average forward displacements on the wood compared to the plastic support.

In continuation of the numerical investigations previously presented – where theoretical results were compared to the experimental case to validate the model’s predictive capabilities – additional more general sensitivity analyses are conducted in order to elucidate the role of key mechanical parameters in the system’s behaviour. Specifically, the analysis depicted in Fig. 5 examines how variations in the stiffness ratio affect the mechanical response of the caterpillar locomotion mechanism. This parameter α is relevant to determine how stresses and deformations are distributed along the body unit during the crawl cycle. Importantly, the considered range of α values is a biologically informed estimate specifically addressed in our previous paper (Argenziano et al., 2025b). In fact, even under the limitations of the linear model, we demonstrated that the natural variation in geometric parameters and body/proleg elasticity across different species (e.g., *Pieris brassicae*, *Uresiphita gilvata*, *Amphipyra pyramidea*, and *Papilio machaon*) heavily influences both the gait-triggering action and also the quality of the locomotion. For instance, when α is very small, as in the case of $\alpha = 0.01$, the displacement distributions across the entire body are quite uniform. As α increases to 0.1 and then 0.5, the response becomes more localised in relation to the inelastic contraction. When $\alpha = 1$, the deformation is highly lumped near the terminal segments, and a significant jump occurs from the first substeps to the last one in terms of displacement magnitude in order to complete the crawl cycle. This tendency has also been explicitly addressed in subplot (e) of Fig. 5, where one can observe snapshots capturing the caterpillar progresses during a crawling cycle.

The stiffer the body with respect to the Winkler-like springs (i.e., the lower the α), the lower are the scatters among the displacements of the substeps with respect to the end of the crawl cycle.

Therefore, tuning α qualitatively changes the nature of the locomotion: lower values promote smoother and diffuse motion, while higher values increase the gradient among the displacements of the rear and the front body subunits.

In order to compare the linear model and the neo-Hookean constitutive relation, a further numerical analysis is presented in Fig. 6, by adopting the same geometric and mechanical parameters, also preserving the same tangent stiffness when the stretch λ tends to 1. The comparison is structured in two columns: the left column (a–c) refers to linear elasticity, while the right column (d–f) corresponds to the non-linear (neo-Hookean) one. As highlighted by subplots (a) and (d) of Fig. 6, for both the linear elastic and neo-Hookean constitutive law, the total potential energy of the system increases monotonically with α , with the non-linear case exhibiting a more pronounced curvature, achieving higher values with respect to the linear counterpart, by fixing – for both cases – the inelastic contraction as a function of the stiffness ratio α , as detailed in Argenziano et al. (2025b), where the compatibility relations between Δ and α are provided. Therefore, thanks to the neo-Hookean relation, by triggering the locomotion with the same inelastic muscle contraction $\tilde{\Delta}$, the cumulated elastic energy dramatically grows in the non-linear case in comparison with the linear one for all the subsequent crawl-substeps. With reference to the stretch and stress distribution subplots in Fig. 6, it is evident that in the non-linear framework, lower values of stretch and stress are observed at each substep compared to the linear elastic case. This behaviour is primarily attributed to the asymmetry of the constitutive relation, which becomes more pronounced in the compressive regime. As a consequence, the non-linear model exhibits enhanced locomotion stability, as the variations in stretch and stress magnitudes across the DoFs are less significant than in the counterpart linear case.

3. Effects of inertial and dissipative terms on the caterpillar locomotion in the non-linear elasticity framework

To assess the effects of elasto-static hypotheses before assumed, the dynamic behaviour of the system has been analysed by incorporating both inertial and dissipative terms, following standard dynamic modelling strategies adopted for discrete systems (Meirovitch, 2010; Argenziano et al., 2023, 2025a). Linear viscous damping has been introduced in parallel with the elastic inter-mass connections, effectively creating a series of Kelvin–Voigt (KV) elements, as depicted in Fig. 7.

To characterise the system’s dynamics, the kinetic energy, denoted by T , and the dissipation function, indicated by D under the assumption of linear damping proportional to absolute velocities of each subunit,

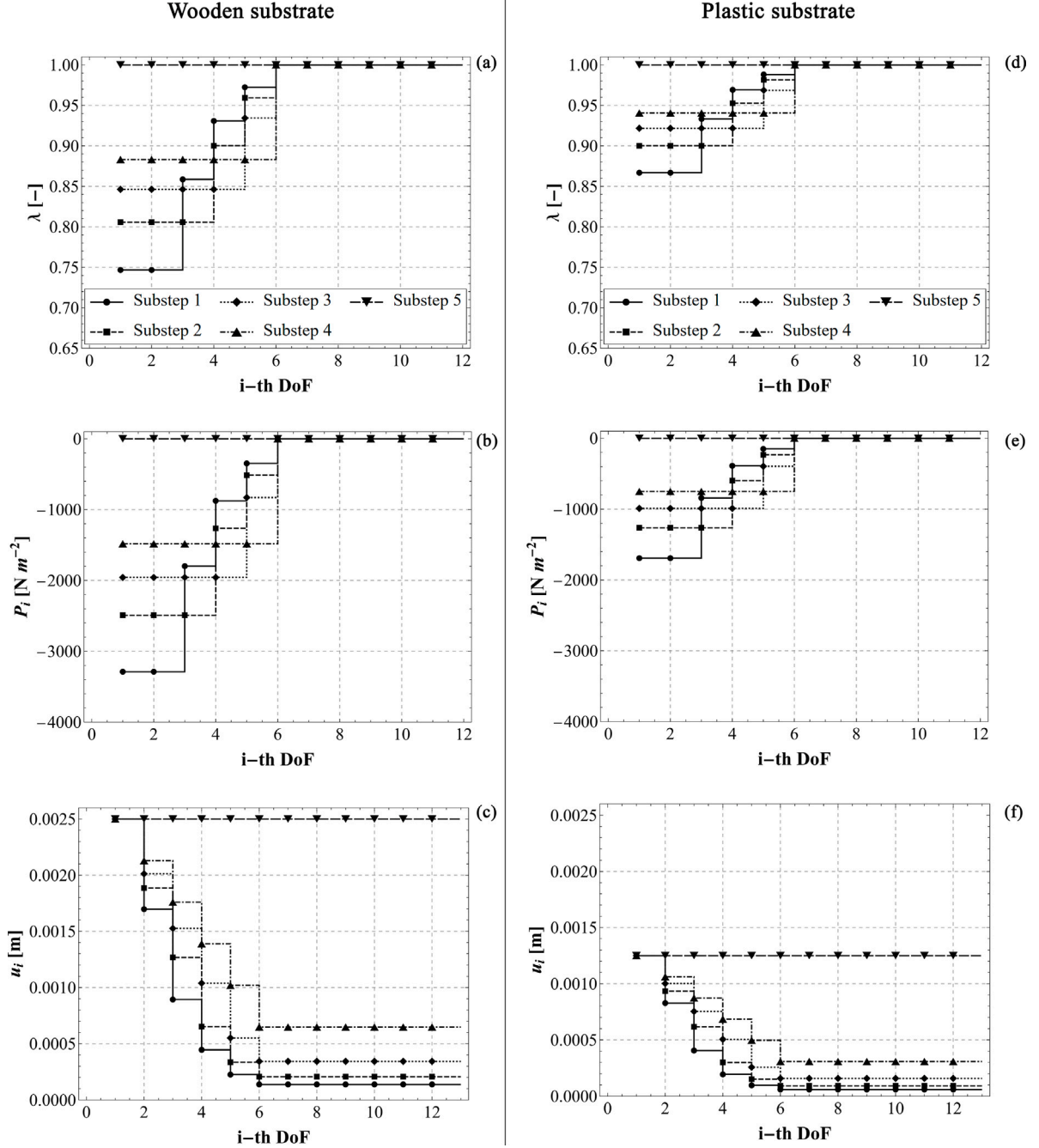


Fig. 4. Numerical simulations of caterpillar locomotion on wood and plastic substrates, corresponding to the experimental data in Fig. 2 and Table 2. For both substrates, the panels display: (a, d) longitudinal stretch λ ; (b, e) axial stress P_i at the degrees of freedom along the body during five sequential crawling substeps; and (c, f) segment displacements. The model parameters are $l_0 = 3.17 \times 10^{-3}$ m, $k_1 = 40$ N m $^{-1}$, and $\alpha = 0.65$. For the wooden substrate, the adhesion threshold is $u_y = 2 \times 10^{-3}$ m and the inelastic displacement is $\Delta = 2.5 \times 10^{-3}$ m; both values are halved for the plastic substrate. The plots illustrate the propagation of deformation and internal forces during motion. Comparing the two substrates reveals higher stretches, stresses, and displacements on wood, confirming that an optimal balance of adhesion and elasticity enables a more efficient gait.

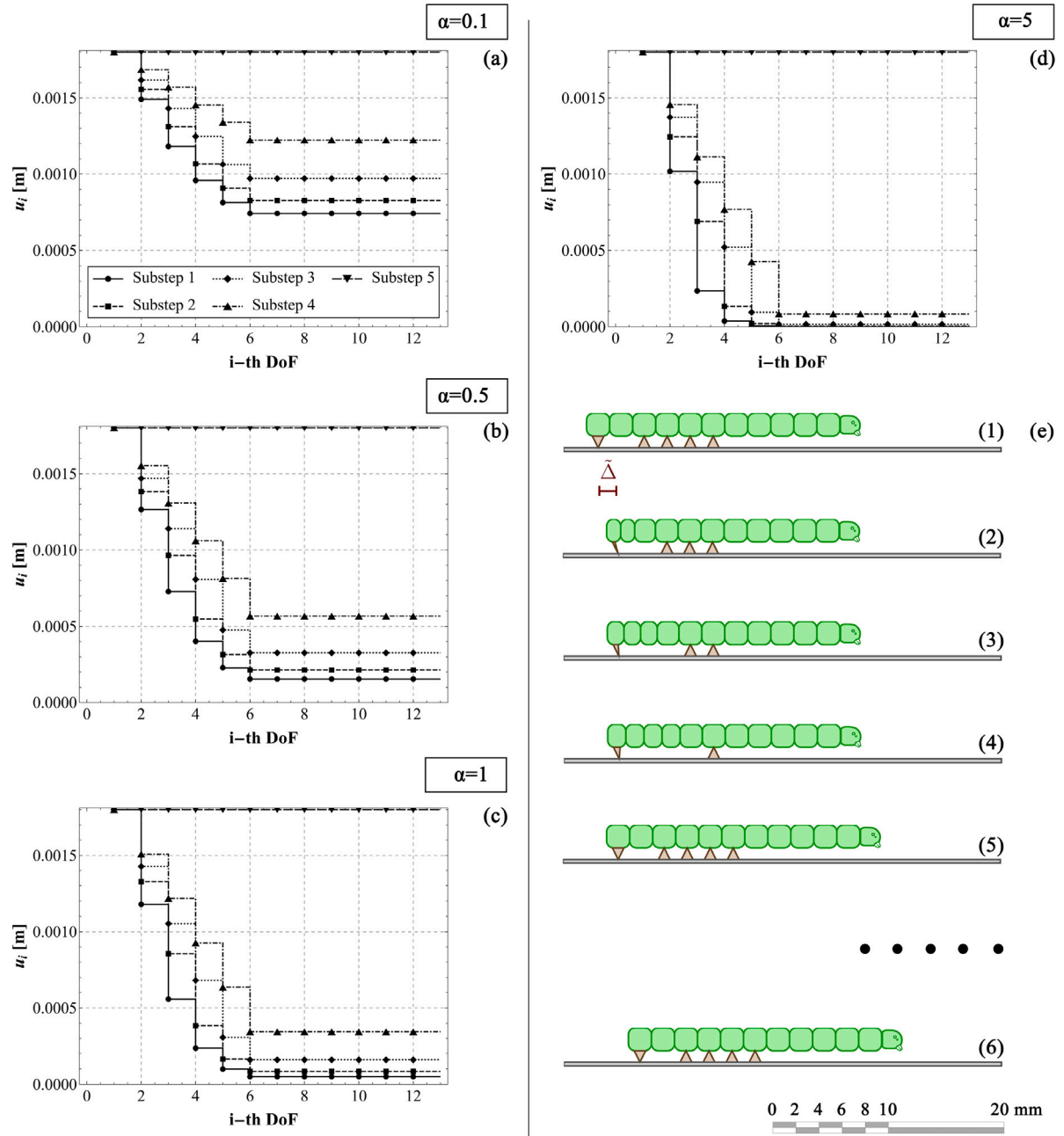


Fig. 5. Sensitivity elasto-static analysis of the caterpillar locomotion (a-d) in terms of the stiffness ratio $\alpha = \{0.1, 0.5, 1, 5\}$, by uploading neo-Hookean elasticity for inter-masses springs and by setting the following parameters: $l_0 = 2 \times 10^{-3}$ m, $u_y = 2.5 \times 10^{-4}$ m, $k_1 = 5$ N m $^{-1}$, and $\Delta = 1.8 \times 10^{-3}$ m. In subplot (e), all the substeps of the whole crawl cycle ($\alpha = 0.5$) whose numerical results are depicted in part (d), are represented in graphic form to highlight the subsequent detachment of the prolegs (the brown triangles) and the progression of the larva; the inset (6) is instead referred to the last frame of the second crawl-cycle.

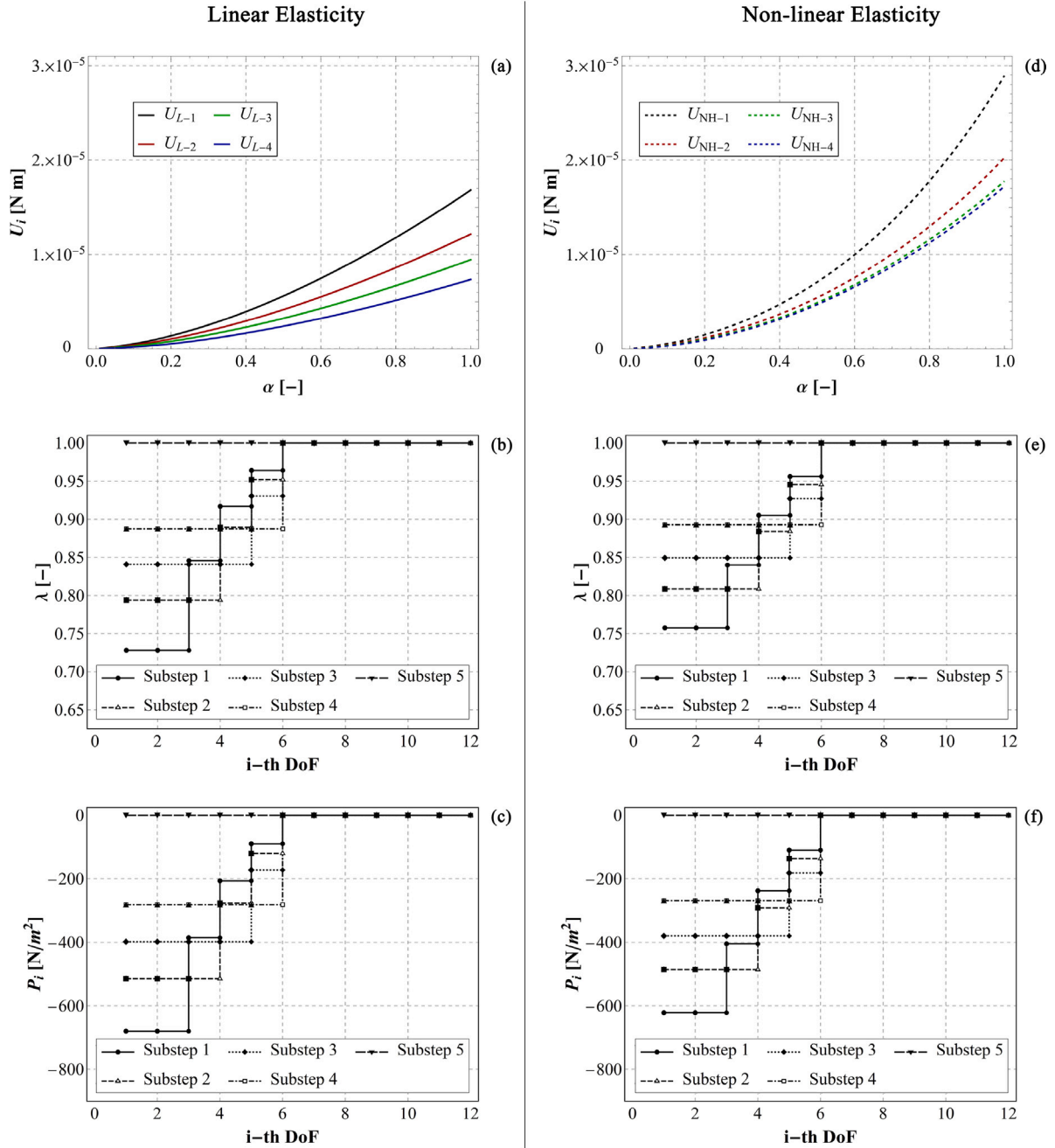


Fig. 6. Comparison between linear and non-linear model of caterpillar locomotion in terms of total potential energy ((a) and (d)), stretch ((b) and (e)) and Cauchy stress ((c) and (f)) for each mechanical configuration reproducing the subsequent substeps. Numerical simulations were performed using the following set of parameters: $l_0 = 2 \times 10^{-3}$ m, $u_y = 6 \times 10^{-4}$ m, $k_1 = 5$ N m $^{-1}$ for all subplots. Specifically in parts (a) and (d), in accordance with the compatibility equations provided in Argenziano et al. (2025b), Δ is computed as a function of α , which ranges from 0 to 1, being instead both parameters respectively set to 0.3 and 1.873×10^{-3} m. In subplots (a) and (d), the total potential energy of the system for both linear and non-linear case has been reported for the substeps from 1 to 4, being instead the other subplots referred to substeps from 1 to 5, where the last one corresponds to resting phase, after the whole crawl-cycle is completed.

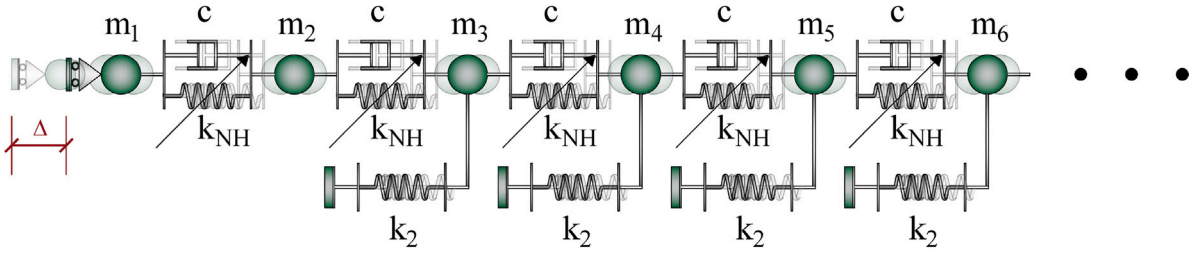


Fig. 7. Schematic representation of the discrete dynamic model used to simulate caterpillar locomotion dynamics, where each body segment is idealised as a lumped mass. Viscous effects of the cuticle and muscle tissue are captured via linear dashpots—characterised by a damping coefficient c , arranged in parallel with elastic springs between masses, effectively forming a chain of Kelvin–Voigt (K–V) elements. As in the elasto-static phase, substrate interaction is modelled using Winkler-type springs with a certain level of threshold displacement u_y to account for ground contact interplay.

are explicitly expressed as follows:

$$T = \sum_{i=1}^n \frac{1}{2} m(\dot{u}_i(t))^2, \quad (12)$$

$$D = \sum_{i=1}^n \frac{1}{2} c(\dot{u}_{i+1}(t) - \dot{u}_i(t))^2,$$

where c denotes the damping coefficient and the over-dot indicates the time derivative of the i th displacement $u_i(t)$.

During the dynamic analysis, as in the elasto-static model, two distinct scenarios were examined: the first one assumes linear elastic behaviour, while the second one incorporates neo-Hookean elasticity.

Conventional methods from analytical mechanics provide a systematic framework for deriving the equations governing the system's dynamics. In particular, as well-established, the Lagrangian functional, denoted as $\mathcal{L}(\mathbf{u}(t), \dot{\mathbf{u}}(t), t)$, is defined as the difference between the total kinetic energy T and the non-linear elastic potential energy U_{NL} , as described in Eq. (13), as provided in what follows:

$$\mathcal{L}(\mathbf{u}(t), \dot{\mathbf{u}}(t), t) = T - U_{NL}. \quad (13)$$

The corresponding Euler–Lagrange equations for the generalised coordinates $\mathbf{u}(t)$ can be formulated as:

$$\frac{\partial \mathcal{L}}{\partial u_i}(\mathbf{u}(t), \dot{\mathbf{u}}(t), t) - \frac{d}{dt} \frac{\partial \mathcal{L}}{\partial \dot{u}_i}(\mathbf{u}(t), \dot{\mathbf{u}}(t), t) = \frac{\partial D}{\partial u_i}(\mathbf{u}(t), \dot{\mathbf{u}}(t), t) \quad \forall i \in \{1, \dots, n\}, \quad (14)$$

While the linear case has been explicitly reported in Argenziano et al. (2025b, 2026b), the i th time-varying non-linear elastic i th differential equation has the following form:

$$\begin{aligned} & \frac{1}{3} k_1 l_0 \left(\left(1 + \frac{u_i(t) - u_{i-1}(t)}{l_0} \right) - \left(1 + \frac{u_i(t) - u_{i-1}(t)}{l_0} \right)^{-2} \right) + k_2 [i] u_i(t) + \\ & + \frac{1}{3} k_1 l_0 \left(\left(1 + \frac{u_{i+1}(t) - u_i(t)}{l_0} \right) - \left(1 + \frac{u_{i+1}(t) - u_i(t)}{l_0} \right)^{-2} \right) + m \ddot{u}_i(t) = \\ & = -2\xi \sqrt{k_1 m} (\dot{u}_i(t) - \dot{u}_{i-1}(t)) + 2\xi \sqrt{k_1 m} (\dot{u}_{i+1}(t) - \dot{u}_i(t)), \end{aligned} \quad (15)$$

being the damping coefficient c has been made explicit as $2\xi \sqrt{k_1 m}$ and ξ the nondimensional damping ratio. It is important to emphasise that, within the dynamic framework as well, the term $k_2 [i] u_i$ becomes inactive once the displacement u_i exceeds the threshold value u_y , as occurs for the elasto-static phase.

The system of $n-1$ coupled differential equations, corresponding to the $n-1$ unknown displacements u_i , is initialised with homogeneous initial conditions. The motion is driven by an imposed inelastic displacement $\tilde{\Delta}$ applied at the terminal proleg. By numerically solving the governing equations for the $n-1$ DoFs – from $u_2(t)$ through $u_{12}(t)$ – it is possible to reconstruct the time evolution of both displacements and velocities throughout the system.

As an illustrative case, Fig. 8 presents the time evolution of the displacements u_2 and u_{12} , corresponding to the two limits of the system, being instead u_6 referring to the middle part, during the first crawl substep, prior to the detachment of the first Winkler-type spring. The results are shown for both linear and non-linear elastic models governing the inter-mass spring behaviour. According to existing studies (Schuldt et al., 2015), overdamped systems characterised by damping ratios in the range $1 < \xi \leq 5$ are generally effective in replicating the mechanical response of caterpillars. Based on this evidence, a damping ratio of ξ equal to 5 has been selected. According to our laboratory measurements, the mass of each body segment is on the order of 10^{-5} – 10^{-4} kg, depending on the larval stage. The remaining physically realistic parameters have been set in accordance with the framework adopted for the elasto-static model in the previous section (see Table 3). The additional parameters specific to the dynamic model are summarised in Table 4. Under these conditions, it is observed that for both the linear and non-linear configurations, the transient dynamics of the system are very brief—lasting less than 0.2 s. In both cases, the displacement trajectories rapidly stabilise to the asymptotic trend and closely align with the corresponding static solutions, as depicted in Fig. 8. This outcome supports the understanding that inertial and dissipative contributions have a minimal influence on the fundamental features governing locomotion, a conclusion also corroborated by prior findings in Argenziano et al. (2025b, 2026b). Importantly, by comparing the displacement and velocity histories of the linear case (a and b) with the ones resulting from the non-linear elastic constitutive law (c and d), by fixing the same set of mechanical parameters, one can notice that in the non-linear elasticity case, the initial velocity peaks are significantly higher for both considered DoFs. This amplified velocity response can be attributed to the larger amount of elastic potential energy accumulated during the deformation phase. The neo-Hookean constitutive law leads to a stiffer behaviour at increasing compression strains, resulting in greater energy storage prior to the relaxation phase. Once the inelastic displacement Δ is imposed and the system begins to evolve dynamically, this extra stored energy is rapidly released, giving rise to sharper transient peaks in the velocity curves. Despite this initial burst, the system quickly dissipates energy due to the high damping ratio ($\xi = 5$), and displacement and velocity histories converge rapidly towards their static values, typically within 0.05–0.1 s.

It should be highlighted that, since the system's dynamics is inherently overdamped (Schuldt et al., 2015) and the numerical values of the masses measured in our laboratory are extremely small (10^{-4} – 10^{-5} kg), the inertial component of the soft-bodied animal has a negligible contribution to the overall dynamics when compared to the dominant viscous and elastic forces. Because caterpillar locomotion operates in this strongly overdamped regime – where the dimensionless damping ratio is much greater than 1 – a large-deformation viscous formulation has not been employed. Instead, as reported above, an equivalent linear dashpot has been deliberately adopted. From an engineering standpoint, an equivalent linear dashpot is physically adequate to capture the macroscopic energy dissipation and the global dynamic

Table 4

Mechanical meaning and source of the inertial and dissipative parameters adopted in the dynamic model.

Model parameter	Physical meaning	Source
m	body unit mass	experimentally measured
ξ	dimensionless damping ratio	derived from literature (Schuldt et al., 2015)

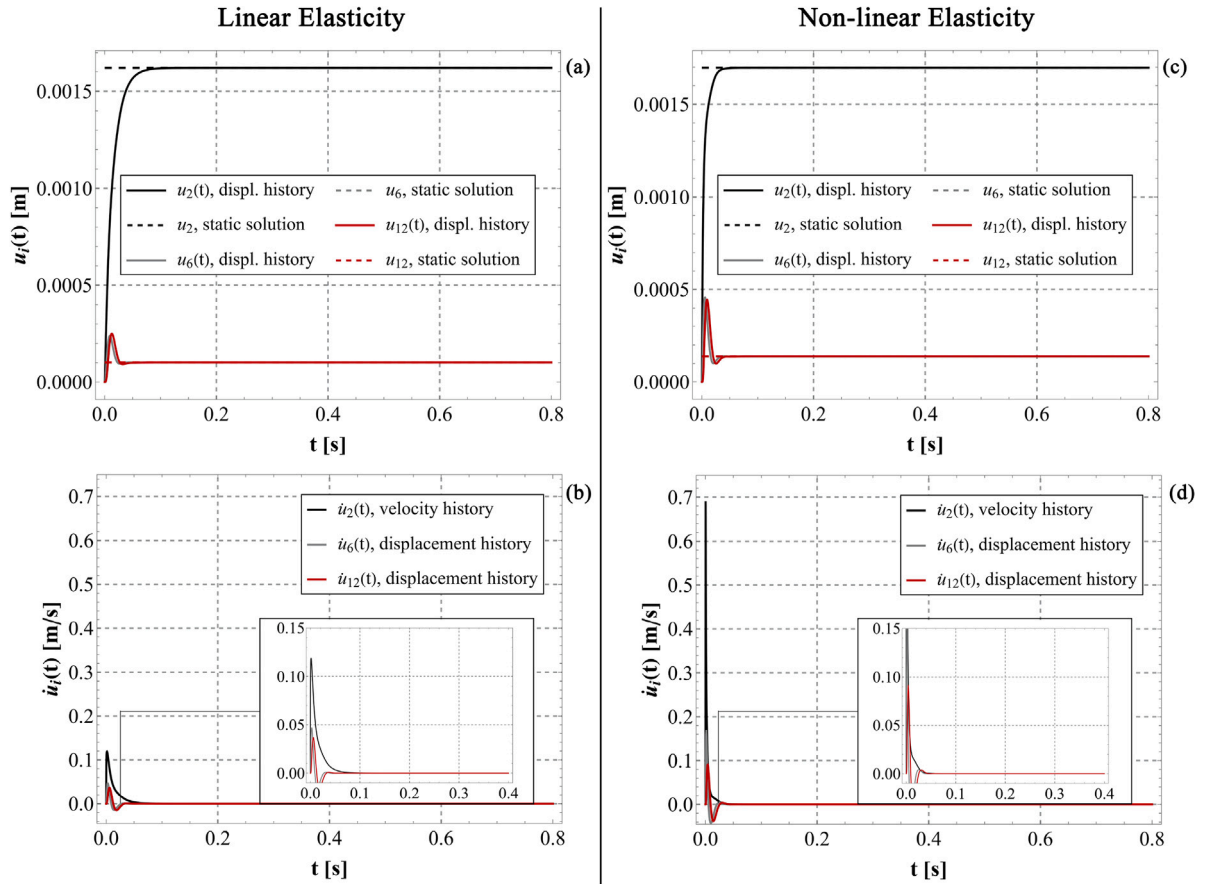


Fig. 8. Comparison between linear and non-linear elasticity in terms of the dynamic response of the system, by fixing the same set of mechanical parameters for the elasto-static simulations. The numerical results in terms of displacement and velocity histories are provided respectively in plots (a) and (b), for the 2nd and the 12th DoFs, by uploading the following set of parameters: $k_1 = 40 \text{ N m}^{-1}$, $\Delta = 2.5 \times 10^{-3} \text{ m}$, $u_y = 2 \times 10^{-3} \text{ m}$, $l_0 = 3.17 \times 10^{-3} \text{ m}$, $m_i = 1 \times 10^{-4} \text{ kg}$, $\xi = 5$ and $\alpha = 0.65$.

response under these specific conditions. Introducing a non-linear, rate-dependent formulation for the viscosity would have significantly increased the computational complexity and the number of parameters without providing substantial gains in accuracy for this specific overdamped system.

Within these physically realistic parameter ranges, and by assuming that the imposed contraction amplitude Δ is on the order of magnitude of the non-linear springs' resting lengths, the transient dynamics always rapidly converge to the steady elasto-static solution without exhibiting inertial oscillations. Importantly, while a linear approach is sufficient for the damping, the animal's tissue mechanics heavily influences the initial stage of locomotion. Unlike the linear model, the neo-Hookean elastic model accounts for the tissue's asymmetric mechanical response to compression versus tension. This asymmetry produces a significantly more energetic initial transient phase, which is particularly evident in the velocity domain (see Fig. 8). This energy amplification scales primarily with the caterpillar's elastic properties and the magnitude of the inelastic contraction Δ that triggers locomotion, remaining largely independent of inertial and viscous parameters.

4. Discussions and conclusions

Building upon previous research where we employed a linear elastic model to describe the key aspects of caterpillar crawling, this study extends and generalise that framework by introducing non-linear elastic constitutive relations, which are necessary to account for the large deformations experimentally obtained in caterpillar tissues. The enhanced model offers a more comprehensive insight into how non-linear elasticity, together with the animal's adhesion to the substrate, influences its mechanical behaviour throughout the crawl-cycle. To emphasise this, we first recovered our 1D lumped mass model and then adopted a hyperelastic neo-Hookean constitutive law for inter-masses springs with the aim of tracing back the large deformation values typically observed during the performed laboratory tests. Similarly to our previous research (Argenziano et al., 2025b, 2026b), locomotion is triggered through prescribed inelastic contraction localised at the terminal segment, thus leading to selective proleg detachment once local adhesion thresholds are exceeded. More in particular, the neo-Hookean constitutive law serves a dual function: on the one side, it faithfully

captures the real mechanical behaviour of the caterpillar tissue, on the other side, the employed hyperelastic relation automatically ensures the geometric compatibility, thus avoiding interpenetration between adjacent body segments and further, reproduces the non-symmetric behaviour of the compressive regime with respect to the tensile one.

After presenting the elasto-static framework, which replicates – through an *ad hoc* conceived algorithm – the step-by-step crawling cycle, inertial and dissipative terms are then incorporated to account for dynamic conditions. Dynamic analyses, also corroborated by the new experimental tests carried out, confirm the robustness of the modelling strategy adopted in our earlier linear analyses, while also demonstrating that including non-linear elasticity introduces sharper transient dynamics and more accurate energy storage representation, effectively reproducing the great propulsion registered in the first initial stage of caterpillar locomotion.

Therefore, this study improves our previous 1D model and provides a practical refined tool for designing next-generation soft robots. It is felt that it would help create micro- or nano-devices that can easily adapt to rough and uneven surfaces, also defining how these nature-inspired systems can store and release energy to obtain higher propulsive effects, and maintain smooth and periodic movement.

Regarding future developments, several key observations are noteworthy. While the current 1D model accurately represents the locomotion of most caterpillars, it fails to capture the arching effects seen in specific species that, due to their distinct morphologies, exhibit two-dimensional (2D) behaviour. To address this limitation and enhance our modelling approach, future research might develop a 2D mechanical model capable of capturing bending curvature. Additionally, implementing an anisotropic constitutive model to faithfully replicate body tissue behaviour and refining the adhesion model of proleg microstructures interacting with substrates may probably give further insights to realistically map body stress distributions and establish supplementary design criteria for bio-inspired devices.

CRedit authorship contribution statement

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

Declaration of AI use

We have not used AI-assisted technologies in 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

With reference to the i th DoF (see Fig. 9), Eq. (6) can be re-written by collecting the i th $u_i(t)$ unknown, thus resulting in a third-order complete polynomial equation, as reported in what follows:

$$\begin{aligned} u_i(t)^3 & \left(\frac{3k_1\alpha[i]}{l_0^2} \right) + u_i(t)^2 \left(\frac{6k_1\alpha[i]}{l_0} - \frac{6k_1u_{i-1}(t)\alpha[i]}{l_0^2} - \frac{k_1u_{i-1}(t)}{l_0^2} + \right. \\ & \left. + \frac{k_1u_{i+1}(t)}{l_0^2} + \frac{2k_1}{l_0} \right) + \\ & + u_i(t) \left(3k_1\alpha[i] + \frac{3k_1u_{i-1}(t)^2\alpha[i]}{l_0^2} - \frac{6k_1u_{i-1}(t)\alpha[i]}{l_0} + \frac{2k_1u_{i-1}(t)^2}{l_0^2} + \right. \\ & \left. - \frac{2k_1u_{i-1}(t)u_{i+1}(t)}{l_0^2} - \frac{6k_1u_{i-1}(t)}{l_0} + \frac{2k_1u_{i+1}(t)}{l_0} + 4k_1 \right) + \\ & - \frac{k_1u_{i-1}(t)^3}{l_0^2} + \frac{k_1u_{i-1}(t)^2u_{i+1}(t)}{l_0^2} + \frac{4k_1u_{i-1}(t)^2}{l_0} - \frac{2k_1u_{i-1}(t)u_{i+1}(t)}{l_0} + \\ & - 5k_1u_{i-1}(t) + k_1u_{i+1}(t) = 0, \end{aligned} \quad (16)$$

$$\text{where } \alpha[i] = \begin{cases} \alpha & \text{if } i = \{3, 4, 5, 6\} \\ 0 & \text{otherwise} \end{cases} \quad \text{being } u_i \leq u_y,$$

whose closed-form $u_i(t)$ solutions as a function of the adjacent DoFs (i.e. $u_{i-1}(t)$ and $u_{i+1}(t)$), by denoting ι as the imaginary unit, can be made explicit in what follows:

$$\begin{aligned} u_{i,1}(t) &= \frac{1}{9\alpha[i]} \left(u_{i-1}(t) - u_{i+1}(t) + (9\sqrt{3}A + B)^{1/3} + \right. \\ & \quad - 2l_0 + 6u_{i-1}(t)\alpha[i] - 6l_0\alpha[i] + \\ & \quad \left. + \frac{(-u_{i-1}(t) + u_{i+1}(t) + l_0(2 - 3\alpha[i]) + 3u_{i-1}(t)\alpha[i])^2}{(9\sqrt{3}A + B)^{1/3}} \right), \\ u_{i,2-3}(t) &= \frac{1}{36\alpha[i]} \left(-2(1 \mp \iota\sqrt{3})(9\sqrt{3}A + B)^{1/3} + \right. \\ & \quad - \frac{2(1 \pm \iota\sqrt{3})(-u_{i-1}(t) + u_{i+1}(t) + l_0(2 - 3\alpha[i]) + 3u_{i-1}(t)\alpha[i])^2}{(9\sqrt{3}A + B)^{1/3}} + \\ & \quad \left. - 4(-u_{i-1}(t) + u_{i+1}(t) - 6u_{i-1}(t)\alpha[i] + l_0(2 + 6\alpha[i])) \right), \end{aligned} \quad (17)$$

where

$$\begin{aligned} A &= (l_0^3\alpha[i]^2(l_0^3(3\alpha[i] + 4)^2(6\alpha[i] - 1) + \\ & - 6l_0^2(2 - 3\alpha[i])^2(3u_{i-1}(t)\alpha[i] - u_{i-1}(t) + u_{i+1}(t)) + \\ & + 6l_0(3\alpha[i] - 2)(3u_{i-1}(t)\alpha[i] - u_{i-1}(t) + u_{i+1}(t))^2 + \\ & - 2(3u_{i-1}(t)\alpha[i] - u_{i-1}(t) + u_{i+1}(t))^3)^{1/2} \end{aligned}$$

and

$$\begin{aligned} B &= l_0^3(3\alpha[i] + 1)(9\alpha[i]^2 + 60\alpha[i] - 8) + \\ & - 3l_0^2(2 - 3\alpha[i])^2(3u_{i-1}(t)\alpha[i] - u_{i-1}(t) + u_{i+1}(t)) + \\ & + 3l_0(3\alpha[i] - 2)(3u_{i-1}(t)\alpha[i] - u_{i-1}(t) + u_{i+1}(t))^2 + \\ & - (3u_{i-1}(t)\alpha[i] - u_{i-1}(t) + u_{i+1}(t))^3, \end{aligned}$$

being ι the imaginary unit. These expressions make up a highly coupled non-linear system of equations including all the DoFs for which only numerical solutions are available for the n unknowns, as provided in the main text of the paper. However, the above-reported relations can serve as a benchmark for validating the numerical solutions, since, quite trivially, the results in (17) should hold for each triad of DoFs.

Data availability

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

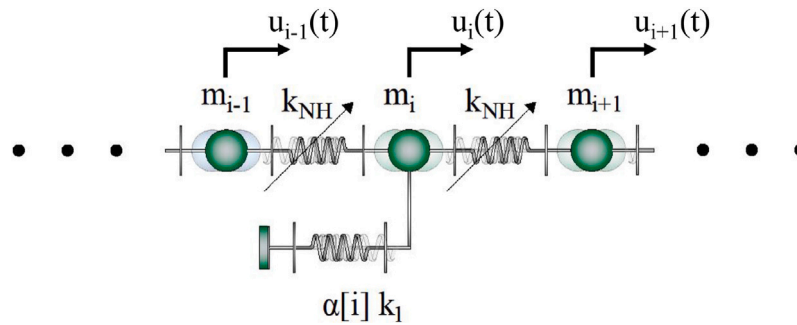


Fig. 9. Sketch representing the general i th DoF exerted from the lumped mass chain modelling the caterpillar locomotion.

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