Manipulate the coiling and uncoiling movements of Lepidoptera proboscis by its conformation optimizing

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Many kinds of adult Lepidoptera insects possess a long proboscis which is used to suck liquids and has the coiling and uncoiling movements. Although experiments revealed qualitatively that the coiling movement is governed by the hydraulic mechanism and the uncoiling movement is due to the musculature and the elasticity, it needs a quantitative investigation to reveal how insects achieve these behaviors accurately. Here a quasi-one-dimensional (Q1D) curvature elastica model is proposed to reveal the mechanism of these behaviors. We find that the functions of internal stipes muscle and basal galeal muscle which locate at the bottom of proboscis are to adjust the initial states in the coiling and uncoiling processes, respectively. The function of internal galeal muscle which exists along proboscis is to adjust the line tension. The knee bend shape is due to the local maximal spontaneous curvature and is an advantage for nectar-feeding butterfly. When there is no knee bend, the proboscis of fruit-piercing butterfly is easy to achieve the piercing movement which induced by the increase of internal hydraulic pressure. All of the results are in good agreement with experiential observation. Our study provides a revelatory method to investigate the mechanical behaviors of other 1D biologic structures, such as proboscis of marine snail and elephant. Our method and results are also significant in designing the bionic devices.

keywords: Curvature, Proboscis, Equilibrium shape

I. INTRODUCTION

After millions of years of evolution, many lives possess particular biological functions to adapt the environment. These adaptive capacities usually present as predominance to capture food, defend enemy and disease, obtain isomerism, and so on. For instances, the lotus leaves\textsuperscript{1,2} have the self-cleaning ability due to plentiful micro- and nano-protrusions on the surface and similar structure also be found on the feet of geckoes\textsuperscript{3}. The hummingbird uses the liquid-trapping method that changes configuration and shape of the tongue dramatically to pick up liquids because it is highly efficient\textsuperscript{4}. The above phenomena indicate that the morphogenesis of structures in biological system govern biological functions. So research on the conformations of biological organs can give a deep insight to understand the relationships between their geometric shapes and biological functions, and it also can give us inspiration in designing the bionic devices.

The Lepidoptera (butterflies and moths) are one of the most diverse taxa of animals with about 160,000 described species contained in 47 superfamilies\textsuperscript{5}. The adult Lepidoptera often have a long proboscis that is used to suck floral nectar and other liquid substances\textsuperscript{6}. The proboscis usually is coiled like a clockwork spring. When it needs to suck, the coiled proboscis can uncoil and extend to a considerable length, and after that it uncoils to the initial condition\textsuperscript{7}. The coiling and uncoiling movements of proboscis attract many researchers’ attention\textsuperscript{8–11}. Experiments observed that, although the proboscises of different species have different length and muscle distribution, they have the same mechanism movements: hydraulic pressure and muscle tensile force drive the coiling and uncoiling movements\textsuperscript{10, 11}. However, proboscises of different species also have difference. See Fig. 1 the extended proboscis of nectar-feeding butterfly (Pieris canidia) has the knee bend and has two particular movements: the up-and-down movement of whole proboscis and the front-and-back movement of the distal region.
terflies to manipulate their proboscis are significant and challenging to understand the mechanism of proboscis movement quantitatively.

In this paper, we construct a quasi-one-dimensional (Q1D) curvature elastic model to study the movements of proboscis theoretically. Making use of the energy-minimizing principle, we derive an equilibrium shape equation of the proboscis. Four typical movements in one circulation of the coiling and uncoiling movements of proboscis are achieved, which are in good agreement with experimental observations. Our results reveal that the knee bend which is achieved by a local maximal spontaneous curvature is a disadvantage if the proboscis is needed to pierce into a target. Our findings not only provide an insight into the mechanics behaviors of proboscis, but also can give us elicitation to study other biological behaviors, such as the movement of proboscis of marine snail and elephant, and the growth of twigs of plants and hairs.

II. MODEL

The long proboscis often has a much bigger length to width ratio and although its cross section area is variational along its central line \( \mathbb{L} \), there is no evident difference of microstructure on different cross section \( \mathbb{L} \), which make it can be taken as isotropic 1D material. However, the volume and corresponding volumetric energy of proboscis can not be ignored due to there is hydraulic pressure in it. So, we look it as a Q1D elastic structure. An uncoiling process needs about 1 second and a coiling process needs about 2.5 seconds \( \hat{\mathbb{L}} \). We suppose one circulation is a long time so that each state in whole process can be taken as an equilibrium configuration.

Considering most of movements of proboscis are in a plane, we simplify its motion in the planar case. Taking the central line of proboscis as a 1D elastic structure in the \( x-y \) plane, letting \( Y \) be the Young’s modulus and \( I_z \) be the moments of inertia of the cross section around the \( z \) axis, we model the elastic energy density for proboscis

\[
\mathcal{F} = \frac{1}{2} \kappa (K - C)^2 + f - \Delta P \sigma_a,
\]

where \( \kappa = Y I_z \) is the bending rigidity, \( C \) is the spontaneous curvature and \( f \) is the inner line tension which depends on the contraction of muscles along proboscis, \( \Delta P = P_{in} - P_{out} \) is the pressure difference between the inner and outer of proboscis and \( \sigma_a \) is the empty area of the cross section of proboscis. On the right hand side of the Eq. 1, the first and second terms compose the typical 1D model \( \mathbb{L} \), but the last term which derives from \( \Delta P \) makes it should be taken as Q1D model. Traditionally, \( \kappa \), \( C \), \( f \) and \( \sigma_a \) are taken as invariable constants. But if the cross section area of a Q1D structure is variational along the arc length of its central line: \( s \), such as proboscis has a decrescent cross section area departing from its bottom to tip \( \mathbb{L} \), we should choose \( \kappa = \kappa(s) \). Here we choose a more general case that \( \kappa = \kappa(s) \), \( C = C(s) \), \( f = f(s) \) and \( \sigma_a = \sigma_a(s) \) depend on \( s \).

The general equilibrium shape equations for the model in Eq. 1 have been studied by many researchers \( \mathbb{L} \) and similar models were used to investigate DNA, filaments and climbing plants \( \mathbb{L} \). Letting \( \psi = \psi(s) \) be the angle between the \( x \) axis and the tangent to the central line of proboscis, we have \( K = d\psi/ds = \psi \) and the equilibrium shape equation for the model in Eq. 1 becomes

\[
2\kappa (\psi - C) + 4\kappa (\psi - C) + 2\kappa (\psi - C) + \kappa (\psi - C) + \kappa (\psi^2 - C^2) - 2(f + \Delta P \sigma_a) \psi = 0, (2)
\]

The expression of \( \kappa = \kappa(s) \), \( C = C(s) \), \( f = f(s) \) and \( \sigma_a = \sigma_a(s) \) depend on the structure of proboscis.

In ref. \( \mathbb{L} \), the author measured 24 proboscises came from the same kind of butterfly, and obtained that the average total length is about 13 mm and also provided the cross section area at different length proportions. We simulated the results and obtained the cross section area \( \sigma = \sigma(s) \) shown in Fig. 2(a). Here we should note the empty area \( \sigma_a \) should be smaller than \( \sigma \) at the same \( s \). Choosing \( \sigma_a = \epsilon \sigma \) where the constant \( 0 < \epsilon < 1 \) and considering there is always the multiplier \( \Delta P \) before \( \sigma_a \) in Eq. 2, the constant \( \epsilon \) can be absorbed in \( \Delta P \) and we can simply choose \( \sigma_a = \sigma \).

For simplicity, we choose \( Y = 1 \) and have \( \kappa = I_z \). The inertia moment \( I_z \) which depends on the irregular cross section of proboscis \( \mathbb{L} \). Considering a 1D structure which has a rectangle cross section with the high \( h \) and width \( b \), when bending it around its central line which parallels to the width, the inertia moment is \( I = \frac{1}{12} bh^3 \). If the cross section is a ring with the radius \( R \), we have \( I = \frac{1}{4} R^4 = \frac{1}{4} \pi R^2 \). Comparing the above two results, if the cross section is irregular, it is reasonable that the inertia moment can be written as \( I = \lambda bh^3 \), where \( h \) is high, \( b \) is width and \( \lambda \) is a shape factor which is determined by the shape of cross section. Experimental results indicate that the cross section of proboscis at different length proportions are similar \( \mathbb{L} \), so we can think the shape factor \( \lambda \) is a constant and have \( I_z = \lambda bh^3 \). Making use of the experimental data in ref. \( \mathbb{L} \), we obtained the relationship between \( bh^3 \) and \( s \) shown in Fig. 2(b). In our calculation we choose \( \lambda = 1 \) and \( I_z = bh^3 \). Clearly, \( Y = 1 \) and \( \lambda = 1 \) are corresponding to the parameters change: \( F \rightarrow \frac{F}{\lambda}, \kappa \rightarrow \frac{F}{\lambda \kappa}, f \rightarrow \frac{F}{\lambda f} \) and \( \Delta P \rightarrow \Delta P\lambda \). In the following text we will use these changed parameters.

It is found that the butterfly proboscis has a loosely coiled state which only depends on the elasticity of the proboscis \( \mathbb{L} \). For the nectar-feeding butterfly, there are an evident knee bend when proboscis uncoils \( \mathbb{L} \). Experiment results indicate there isn’t evident deference at the knee bend region \( \mathbb{L} \). In our model we think these phenomena are due to the spontaneous curvature \( C \). However, to precisely obtain it by
state. In our calculation we choose \( s_0 \) and third terms on the left hand side will make sure the bend shape when the proboscis uncoiling. The second has distribution feature and it has a local maximum at \( s = 0 \). At the two end points we choose \( \sigma = 0 \) and \( bh^3 = 0 \).

\[ C = C_2 \exp[-(s - s_0)^2/\tau_1] + C_1 \exp[s/\tau_2] + C_0. \]  

where \( C_0, C_1, C_2, \tau_1, \tau_2 \) and \( s_0 \) are constants which are determined by the microcosmic structure of proboscis. In the above equation, the first term on the right hand side has distribution feature and it has a local maximum at \( s = s_0 \). We will see that this term will induce the knee bend shape when the proboscis uncoiling. The second and third terms on the left hand side will make sure the proboscis is coiled with few turns in the loosely coiled state. In our calculation we choose \( C_0 = 0.55 \text{ mm}^{-1} \), \( C_1 = 0.05 \text{ mm}^{-1} \), \( C_2 = 0.3 \text{ mm}^{-1} \), \( \tau_1 = 1 \text{ mm}^2 \), \( \tau_2 = 4 \text{ mm} \) and \( s_0 = 4.44 \text{ mm} \) which is 35% of the proboscis length [10].

Along proboscis it distributes many internal galeal muscles and their function is to coil proboscis from the loosely coiled state with few turns to the tightly coiled resting position with more turns [10]. Considering the internal galeal muscle has degressive cross section area, we choose the following gradually decreasing line tension which can be own to the constriction of internal galeal muscles

\[ f = f_1 \exp[-s/\tau_3], \]  

where \( f_1 \) is a constant which can be adjusted by the internal galeal muscle. \( \tau_3 \) reflects the decreasing rate of the cross section of internal galeal muscles along proboscis. Here we choose \( \tau_3 = 50 \text{ mm} \).

Moreover, the initial conditions \( \psi_0 = \psi(0), \dot{\psi}_0 = \dot{\psi}(0) \) and \( \ddot{\psi}_0 = \ddot{\psi}(0) \) in Eq. 2 should be given. We note that the internal stipes muscle and the basal galeal muscle [11] (or the proximal basal muscle and the distal basal muscle [10]) locate at the bottom of the proboscis. It is reasonable to think that they can adjust the initial conditions \( \psi_0, \dot{\psi}_0 \) and \( \ddot{\psi}_0 \) between the proboscis uncoiling and coiling processes.

### III. Results

Now, we will explain how a butterfly manipulates its proboscis. According to the experimental observations, the coiling and uncoiling processes can be divided into four different movements and we will begin with the loosely coiled state coiled about 1~2 loops [10].

First movement: coiling from the loosely coiled state to the resting position. This movement is only driven by muscles and is not related to the pressure \( \Delta P \) [10]. Two kinds of muscle are involved in this movement: the internal galeal muscle and the internal stipes muscle [11]. In our study, the former one adjusts the line tension \( f \) and the later one controls the initial conditions. In the loosely coiled state, there are \( \Delta P = 0, f_1 = 0 \) and the shape is determined by spontaneous curvature \( C \). From Fig. 3(a) to Fig. 3(d), we give a list of shapes obtained from Eq. 2 with the increase of the tension \( f \). In Fig. 3(a) it is the loosely coiled state with \( \Delta P = 0, f_1 = 0 \) and coiled about 2 turns, which is in good agreement with the experimental data [10]. We find that the initial conditions should be adjusted simultaneously with the increase of \( f_1 \), otherwise the shape will coil irregularly and self-intersected badly. So it needs the two kinds of muscles involved in this movement to coordinate with each other. This mutual coordination can be achieved due to there are several sensilla on proboscis [22]. From Fig. 3(d) to Fig. 3(f), it is only the initial condition \( \psi_0 \) is changed, which makes the tightly coiled shape is bend to the resting position. After that proboscis touches on the labium and is fixed by microtrichia after a slight countermovement which is due to the muscles have been loosened [7, 11]. The final shape in Fig. 3(f) coiled 3~4 turns is in accordance with experimental result [10]. Actually, the above two separate processes can be coupled together.

Second movement: uncoiling from the resting position to the loosely coiled state. When it needs to use proboscis, butterfly unlocks its proboscis at the tightly coiled resting position and consequently proboscis uncoils to the loosely coiled state only due to its elasticity [5, 11].
FIG. 3: Coiling process from loosely coiled state (a) to resting position (f), the unit of coordinates axes for each figure is mm. From (a) to (d) is the coiling process own to the contraction of the intrinsic galeal muscle and the internal stipes muscle. The former one increases the tension \( f \) and the later increases the initial conditions \( \psi_0 \) and \( \psi_0 \). From (d) to (f), the proboscis is flexed to the resting position due to the contraction of the internal stipes muscle which induces the increase of the initial condition \( \psi_0 \). This two processes can be coupled together.

FIG. 4: From (a) to (e) is the uncoiling process from loosely coiled state to extended state, which owns to the increase of \( \Delta P \) and the dierezes of initial condition \( \psi_0 \) and \( \psi_0 \). From (e) to (f), the proboscis turns back to the resting position due to the elasticity. The unit of coordinates axes for each figure is mm.

The process can be taken as the inverse process from Fig. 3(a) to Fig. 3(f).

Third movement: uncoiling from the loosely coiled state to extended state with a knee bend. This movement is driven by the pressure \( \Delta P \) and the basal galeal muscle \[10, 11\]. Choosing loosely coiled state in Fig. 3(a) as the initial shape, gradually increasing \( \Delta P \) and \( \psi_0 \) we obtain the shapes from Fig. 3(a) to Fig. 3(d). Where we need the initial condition \( \psi_0 \) controlled by the contraction of basal galeal muscle and the pressure \( \Delta P \) are increased compatibly. We can see coiled proboscis is opened gradually in this process. In Fig. 3(c) and Fig. 3(d) there is an evident local bend for each shape at the position \( s = s_0 \), which just is the knee bend and is due to the local maximal spontaneous curvature. In Fig. 3(c) the shape is composed by two almost strait parts, and between them is the knee bend. In this case, if butterfly adjusts \( \Delta P \), the tip region is ease to bend backward like Fig. 3(b) or forward like Fig. 3(d). This is in accordance the experimental phenomenon \[21\] that the tip region is agile. But if butterfly continually increase \( \Delta P \), Fig. 3(d) will have more local bends like a wave and it is very difficult to become to be a totally straight shape with no local bends. Which implies that the nectar-feeding butterfly with knee bend on proboscis is difficult to achieve piercing movement because it needs the proboscis to extend to almost a straight line \[4, 11\]. In the later text we will see that if there is no knee bend, proboscis can easy be unwound totally. The above whole process is consistent with experimental results in Fig. 3 of ref. \[7\].

Fourth movement: coiling from the extended state to loosely coiled state. This process ordinarily is only due to the elasticity of proboscis. But the \( \Delta P \) and initial conditions turn back to the corresponding values in Fig. 3(a) that needs a short time \[7\]. From Fig. 3(d) to Fig. 3(f), we show this coiling process through decreasing \( \Delta P \) and \( \psi_0 \). After Fig. 3(f), the shape turns back to loosely coiled state in Fig. 3(a). Experiment results indicate that the tip region will form a small ring at first and consequently the distal region begin to coil \[7\]. We can see that Fig. 3(e) and Fig. 3(f) are in good agreement with this phenomenon. It should be noted that this coiling process cannot be simply taken as the inverse process from Fig. 3(a) to Fig. 3(d). The shapes Fig. 3(b) and Fig. 3(e) have the same \( \Delta P \), but the different initial condition \( \psi_0 \) leads they have different morphology. Similar results also be shown in Fig. 3(a) and Fig. 3(f). This small difference is due to the delicate relationship between \( \Delta P \) and \( \psi_0 \).

Besides the above four movements there are two other movements which cannot be ignored. It is found that the extended proboscis has two particular movements: up-and-down movement of the total proboscis and front-and-back movement of the distal region \[6, 11\]. Calculation indicates the former movement is due to that the initial condition \( \psi_0 \) is adjusted by the muscles at the bottom of proboscis. The later movement is driven by the change of \( \Delta P \). Fig. 5 shows this two movements which can explain the experimental phenomenon well. In Fig. 5(a), the change of \( \psi_0 \) induces total proboscis moves up and down. In Fig. 5(b), the change of \( \Delta P \) leads to the distal region turning around the knee bend, which can be taken as the front-and-back movement. The above two movements make the tip of proboscis can reach a much bigger area region so that butterfly has the possibility to suck more nectar. However, only changing the line tension also can induce the similar front-and-back movement in Fig. 5(b). (It needs \( f_1 \) to be negative in Eq. 4 in this case.). Actually, experimental investigation indicates the front-and-back movement is caused either by pressure or galeal muscle \[7\]. It also finds that there are slight difference between the two kinds of galeal muscles in the knee bend region \[7\]. These phenomena imply the line tension in Eq. 4 which is induced by the galeal muscles locating along proboscis is possible to have complicated distribution feature like the spontaneous curvature in Eq. 3. We also can presume the butterfly can adjust the local line...
tension by controlling the extension and constriction of local galeal muscles along proboscis to achieve a more complicate movement. In the Movie S1, we give a full circle of the coiling and uncoiling processes containing the front-and-back and up-and-down movements.

There are other kinds of butterflies that their proboscis have no evident knee bend but they have a particular ability: piercing. We note that the piercing action occurs if and only if proboscis extends to an almost straight line \[8\]. Considering our former result that proboscis which has knee bend cannot be completely extended, we can believe that knee bend is disadvantageous to the piercing action. Thus, the proboscis of fruit-piercing butterfly has no evident knee bend. In order to demonstrate how the piercing action occurs, we choose the following spontaneous curvature which has no local maximum to induce the knee bend

\[
C = 0.1 \exp[-s/50] + 0.4. \tag{5}
\]

There isn’t any configuration parameters of proboscis of fruit-piercing butterfly, we simply choose the results in Fig. 2. Calculation shows piercing action can be archived easily in this case. Fig. 6 shows the piercing action induced by the increase of internal pressure. We can see an evident straight movement of the tip along the direction of the proboscis, which helps proboscis to pierce into fruit and other softer targets. The final state with \(\Delta P = 1\) in Fig. 6 is nearly a straight line. Actually choosing the spontaneous curvature in Eq. 3 also can achieve the straight shape. But we find it needs a much higher pressure: \(\Delta P > 10\). Compared with the straight shape in Fig. 6 only needs \(\Delta P = 1\), so higher pressure is not convenient (or impossible) for butterfly. So, knee bend is no need for a fruit-piercing butterfly.

**Discussion**

Through our analysis, we find the achievement of whole coiling and uncoiling movement subtly depends on these parameters: \(\kappa, C, \sigma\) and \(f\). In Fig. 2 we used the quintic functions of \(s\) to fit \(\sigma\) and \(\kappa = bh^3\). We also tried other fitting functions with lower orders, but we found quintic functions can make sure the coiled proboscis is more regular than others. The \(\sigma\) and \(\kappa = bh^3\) in Fig. 4 seem to reach their local mutation points at the same length \(s \approx 4\) mm which is close to the knee bend location \(s = 4.44\) mm. But our calculation indicates the local mutation of \(\sigma\) and \(\kappa = bh^3\) can not induce knee bend if there isn’t local maximum of \(C\). Even if choosing invariable \(\sigma\) and \(\kappa\), we also can not attain knee bend if there isn’t local maximum of \(C\). So we make sure it is the local maximum of spontaneous curvature that leads the knee bend. Further, our study reveals that \(\Delta P\) and the initial conditions should be changed compatibly, which needs the different kinds of muscles involved in each movement to coordinate with each other. Besides the plentiful sensilla on proboscis which can help butterfly to achieve this mutual coordination, there are other particular movements that make for this cooperation. Experimental details indicate that the uncoiling movement is a step-by-step process resulting from the step-by-step increase of the hemolymph pressure [7]. So the change of \(\Delta P\) is discontinues, which implies there is a short stagnant time after each change of \(\Delta P\). In this short buffer time, the initial conditions can be adjusted by galeal muscles to the optimal values to cooperate with the pressure and consequently whole shape can reach the equilibrium state.

It is believable that the construction and behavior of proboscis are due to the evolution. So, the proboscis of nectar-feeding butterfly has knee bend that is in order to adapt the environment. Fig. 4 has indicated that knee bend will induce proboscis has two particular movements: up-and-down movement and front-and-back movement, and the couple of them can ensure the tip of proboscis to reach a much bigger area than a strait proboscis without knee bend can. Apparently, the more reachable area the more possibilities to get nectar. However, this advantage will be a disadvantage when proboscis is used to pierce into a target, because it needs a much higher pressure when compared with a no knee bend proboscis. In order to avoid this disadvantage, fruit-piercing butterflies choose the proboscis without knee bend to obtain the piercing ability. But why the knee bend locates at the
35% length from the bottom of proboscis is an interesting problem. May be this structure can well adapt the shape of flowers or it is the result of whole body structure optimization. For instance, in Fig.\[1\] the knee bend locates at 30% length from the bottom of proboscis, which deviates the value 35% in Ref. [10]. So we think this proportion is variational for different kinds of butterfly.

There are other animals that have long proboscises [24], such as the marine snail [24, 26] and elephant [27]. The proboscis of marine snail is used to catch fish and the details of its movements still are unknown. As to the elephant, proboscis is the most important and versatile appendage and has higher flexibility to achieve complex movements relying on it has more than 15000 muscle fascicles. In our study, we choose a simpler line tension in Eq. [3] to reflect that the muscles along proboscis can adjust the shape of proboscis. But we believe the line tension can be adjusted locally in some cases by butterfly and other animals to achieve complex movements. The more muscles it has, the more complex movements it can achieve. So, to ascertain the line tension $f$ is an important step to investigate the complex behaviors of the proboscis with plentiful muscles. But this is very difficult, because the feedback control loop composed by the brain, nerves and abundant sensilla on proboscis which manipulates the line tension is unquantifiable at present time. Whereas, our study provide a revelatory method to investigate the mechanical behaviors of proboscis and other QID biologic structures, such as the growth of twigs of plants and hairs. Twigs of plants often have variable cross section, so they probably have nonlinear $\kappa$, $\sigma$ and C. Although they have no muscles, the increase of internal hydraulic pressure can induce the curved twigs to straight and upwardly grow up.

In summary, we revealed that, in the coiling and uncoiling process of butterfly proboscis, the function of muscles located the bottom of proboscis is to adjust their initial states that govern the corresponding movement of the coiling and uncoiling processes respectively, the function of muscles existed along proboscis is to control the line tension, and the knee bend determined by the local maximal spontaneous curvature is a disadvantage for piercing action. The knee bend induces that the tip of proboscis has two particular movements: the up-and-down movement and the front-and-back movement, and the combine of them leads to the tip can reach a bigger area region when compared with the no knee bend state. Our study indicates that the nonlinear construction parameters: $\kappa$, $\sigma$ and $C$ of proboscis make it is very difficult to accurately control whole coiling and uncoiling process. But we believe these parameters have been optimized by long time of evolution to insure animals can obtain the maximal advantage. Two typical advantages present that proboscis has higher retractility and particular movements, which can help butterfly to get more food. Beside Lepidoptera, our model gives a general method to study the mechanical behaviors of long proboscis of other animals as well as twigs of plants. Moreover, our method and results can be used to design bionic devices.

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