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ON THE ROLE OF THE PRINCIPLE OF OPTIMAL COST IN THE LEAF TWIST OF THE BIRCH LEAF ROLLER (*DEPORAUS BETULAE*)

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The biological literature has a widespread view that the mathematical aspect of the leaf cone construction of the birch leaf roller is that the S-shaped, serpentine incisions cut by the beetle on the leaf blade are the ideal geometric shape to minimize the work needed to roll the leaf halves. The generally accepted view, that the leaf cone construction of *Deporaus betulae* is determined by the principle of optimal cost, is refuted in this work. A new biomathematical description and a biomechanical explanation are presented for the shape of the incisions, on the basis of which their asymmetry can be explained, too.

Keywords: biomathematics, bionics, ethology, principle of optimal cost.

Introduction

The ethology of the birch leaf roller

The Rhynchitinae provide peculiarly for their descendant, they twist leaf cigars as cradles for offspring to protect and feed the grubs. The most interesting and most studied species of the Rhynchitinae is the birch leaf roller *(Deporaus betulae)*.

The birch leaf roller rolls a regular, conical, well-closed, slender lear cigar. This beetle gnaws partly through the midrib of the leaf to wilt the lower leaf part, and cuts two special S-shaped incisions into the leaf blade to make the twist easier. Among the Rhynchitinae, *Deporaus betulae* cuts the most complicated patterns and it rolls the most regular, closed leaf cones from the leaves. In spring the 3-5 mm long female beetle deposits its eggs into these leaf cigars.

Deporaus betulae rolls its leaf cone from birch leaves (Betula) and, rarely, from other leaves (Alnus, Corylus, Carpinus). It can be observed that the beetle always cuts the same shaped patterns into the leaf lamina for different leaf kinds and leaf sizes. Only the starting point and the size of the incisions are varied. The beetle walks round and maps the leaf before it begins to cut the incisions. After this walk it chooses the starting point and size of the patterns according to the shape and size of the leaf [1].The beetle starts to cut the first incision on the leaf border far from the petiole on the larger leaves and near the petiole on the smaller leaves, so that the rolled leaf mass nearing an optimum value is within the leaf cone. This optimal twisted leaf mass is suitable for the nutrition of the grubs and for the muscular power of the beetle.

This paper won first prize in the competition for young biophysicists conducted by Jenő Ernst Foundation. It was written on the basis of the lecture given by the author at the 15th conference of the Hungarian Biophysical Society (Szeged, July 3–5, 1989).

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The birch leaf roller twists its cigar in the following way [1]: on the upper part of the leaf, near the peduncle, the beetle cuts into the border of the leaf sheet, and makes the first S-shaped incision towards the midrib. It then chews the midrib, and climbs over to the other leaf half. Then it cuts the second S-shaped incision from the midrib to the leaf edge but this is flatter than the first one. Soon the leaf begins to droop, then the female starts to roll it. It climbs over to the back side of the leaf and rolls the first leaf half with its feet into a slender cone. Then it twists the second leaf half in a similar way around the rolled first leaf half. Thus arises a massive leaf cone from the leaf.

The beetle climbs into this cone and cuts into the skin tissue of the leaf at some points. It deposits its eggs in these cuts then crawls out of the leaf funnel, rolls the under edge of the cone to a small cornet, and so closes its eggs into this green package. The task takes about 30–60 minutes. When a female has finished a leaf funnel, it starts another one.

In a few months the wind or the rain tears the browned leaf funnels from the branches. The grubs gnaw through the walls of the leaf cigars and dig into the earth, where they become chrysalises. In Fig. 1 we can see the main stages of the *Deporaus betulae*'s leaf twist [1]. Only the female beetle is able to roll leaf cigars, and if it is interrupted in its activity, the work does not suffer, it can continue the twist where it stopped.

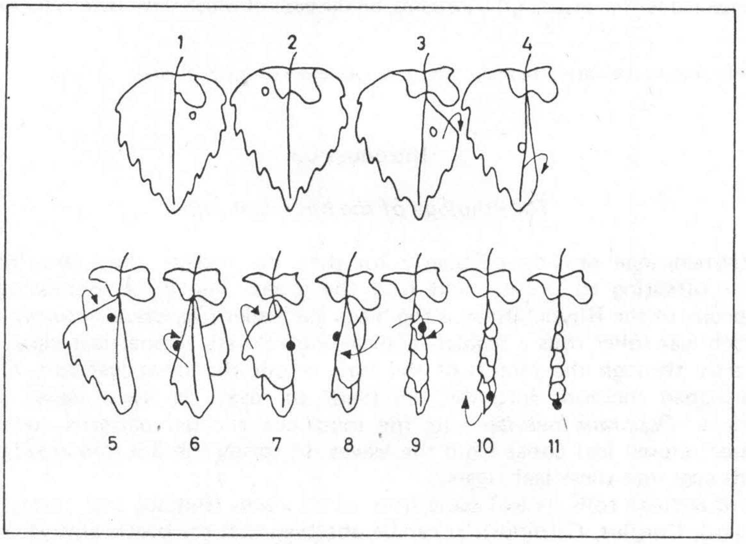

Fig. 1. *Deporaus betulae*'s leaf twist. (The front of the birch leaf.) In stages 1, 2 the beetle cuts the incisions, in 3, 4 it rolls the leaf cone from the first leaf half. In stages 1–4 the beetle works on the back side of the leaf, in 5–9 it twists the second leaf half around the leaf cone, it then works on the front of the leaf. In stages 10, 11 the beetle closes the leaf funnel below. Symbol ● shows the position of the beetle during the twist on the front side and symbol ○ shows its position on the back [1]

In Fig. 2 the incisions of the birch leaf roller can be seen for different leaf sizes and for two kinds of leaf (birch and alder) [1]. For leaves of different sizes the patterns are represented on the largest leaf after proportional enlargement of the smaller leaves. The incisions near the petiole and distant from it are characteristic of the smaller and larger leaves, respectively. The shape of the birch leaf roller's patterns is independent of leaf size and leaf shape.

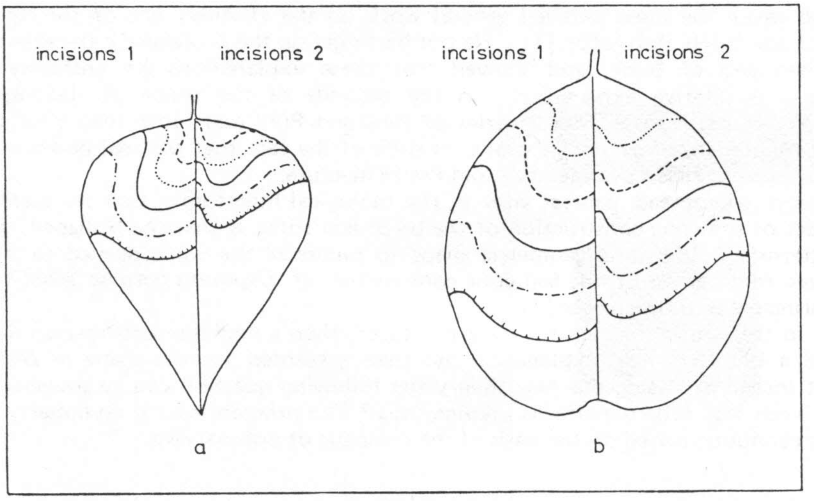

Fig. 2. First and second incisions of birch leaf roller for different leaves [1] (a) birch (*Betula*), (b) alder (*Alnus*). The differently coded lines represent the curves for leaves of different sizes. The incisions near the petiole and distant from it are characteristic of the smaller and the larger leaves, respectively

Previous descriptions of the birch leaf roller's patterns

The first mathematical description for the shape of *Deporaus betulae*' s incisions was given by Heis and Debey [2, 3]. In their opinion the first incision is the evolute of the leaf border (Heis's evolute). Heis's theory was improved by Prell, who determined an imaginary curve, and he identified the second incision with the involute of this curve (Prell's involute) [4].

The evolute-involute theory of Heis and of Prell is only a mathematical description, and Heis's evolute and Prell's involute do not agree well with the shape of the birch leaf roller's patterns. The theory of Heis and of Prell cannot explain the biophysical nor the bionic reason for the shape of the patterns.

Another theory was presented by Buck [5], he derived the shape of the incisions from the anatomy of the beetle and from the structure of the leaf. In his opinion the main arc of the patterns rises from the fact that the hindmost legs of the beetle are longer than its forefeet, so during the cutting the beetle sidles along an arc. Buck explained the smaller arcs of the incisions on the basis of the leaf structure and of the cone construction.

Rosskothen gave a new explanation for the patterns of *Deporaus betulae* [6]. He constituted the incisions from several small arcs and he derived every single arc from the roll techniques and from the structure of the leaf. In Rosskothen's opinion the beetle works out experimentally the optimal shape of the patterns through repeated cutting and rolling of some leaves. He assigned some intellectual capacity to the beetle, and he denied that the optimal shape of the patterns is genetically fixed. Nowadays this theory is a worn out conception.

Daanje wrote the most detailed general work on the ethology and on the roll techniques of the birch leaf roller [1]. He put his finger on the mistakes in the theories of Rosskothen and of Buck, and showed that these explanations are unmaintainable. He gave a qualitative explanation on the grounds of the shape of the *Deporaus. betulae's* patterns. He used the theories of Heis and Prell and their mathematical description for the shape of the incisions, in spite of the fact that the real patterns differ significantly from Heis's evolute and from Prell's involute.

The most widespread general view in the biological literature is that the mathematical aspect of the cone construction of the birch leaf roller is that the S-shaped, serpentine patterns are the ideal geometric shape to minimize the work needed to roll the leaf halves. In other words, the leaf cone construction of *Deporaus betulae·* is determined by the principle of optimal cost [7].

First, in this work this general view is refuted, then a new biomathematical description and a biomechanical explanation are then presented for the shape of *Deporaus betulae's* incisions. Using this new theory the following question can be answered: why are the birch leaf roller's patterns asymmetrical? The problem of the asymmetry of the incisions cannot be solved on the basis of the principle of optimal cost.

Calculation of the work needed to roll a leaf half

Figure 3 shows a leaf cut by the birch leaf roller. After the cutting the beetle begins to roll leaf half 1 into a leaf cone and incision 1 helps in this cone construction. After the rolling of leaf half 1, it twists leaf half 2 round this cone. Incision 2 helps this rolling and prevents the uncoiling of the twisted leaf. In this section, I calculate the work needed to roll a leaf half.

Consider the twist of a sheet with Young's modulus E and thickness a around a cone with half aperture angle α (see Fig. 4). At the examined point the neutral surface is at distance L from the surface of the cone, and the local radius of curvature is

$$R = Bx\,, \qquad B = \tan\alpha \tag{1}$$

If the functions of the borders of the rolled sheet are $r(\phi)$ and $R(\phi)$ from the peak point of the cone (the angle ϕ is measured from the midrib), then the force and torque are (see Fig. 5).

$$F = \int_r^R \frac{Ea(a-2L)}{2(Bx+L)}\,dx \tag{2}$$

$$M = \int_r^R \frac{E\left[(a-L)^3 + L^3\right]}{3(Bx+L)}\,dx \tag{3}$$

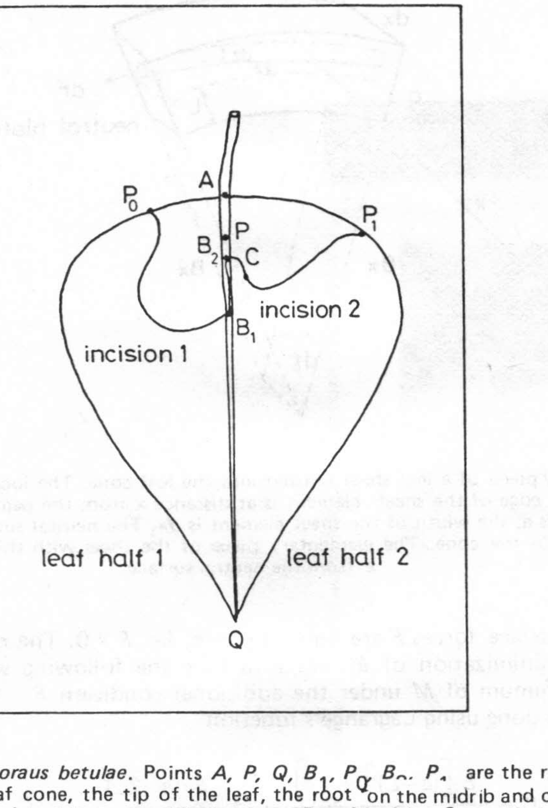

Fig. 3. Leaf cut by *Deporaus betulae*. Points A, P, Q, B_1, P_0, B_2, P_1 are the root of the petiole, the peak of the rolled leaf cone, the tip of the leaf, the root on the midrib and on the leaf edge of the first and of the second incision, respectively. Arc CB_2 of incision 2 constitutes the suspension of the completed leaf cone

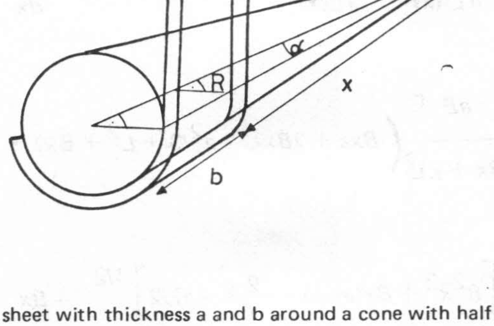

Fig. 4. Twist of a sheet with thickness a and b around a cone with half aperture angle α

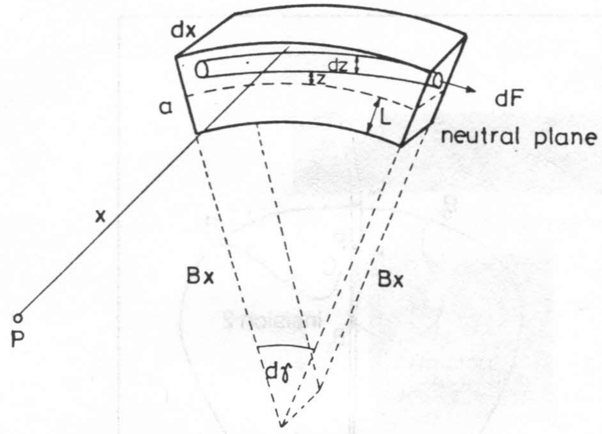

Fig. 5. Elementary piece of a leaf sheet twisted into the leaf cone. The local radius of curvature is x tanα, the nearer edge of the sheet element is at distance x from the peak of the cone, the thickness of the sheet is a, the width of the sheet element is dx. The neutral surface is at distance $L(x)$ from the surface of the cone. The elementary piece of the sheet with thickness dz is at distance z from the neutral surface.

The neutral surface forces F are equal to zero, i.e. $F = 0$. The neutral surface is determined by the minimization of M. We thus have the following variational problem. We look for the minimum of M under the additional condition $F = 0$. In this case the minimization must be done using Lagrange's function

$$\mathcal{L} = \frac{E\left[(a-L)^3 + L^3\right]}{3(Bx+L)} - \lambda \frac{Ea(a-2L)}{2(Bx+L)} \tag{4}$$

where λ is Lagrange's multiplicator. Function $L(x)$ is sought. I use for (4) the Euler–Lagrange equation

$$\frac{d}{dx}\frac{\partial \mathcal{L}}{\partial L'(x)} - \frac{\partial \mathcal{L}}{\partial L(x)} = 0\,, \qquad L'(x) \equiv \frac{dL}{dx} \tag{5}$$

Thus we get

$$\frac{\partial \mathcal{L}}{\partial L} = \frac{aE}{(Bx+L)^2}\left(-Bxa + 2BxL - a^2/3 + L^2 + Bx\lambda + \lambda a/2\right) = 0 \tag{6}$$

From here

$$L(x) = \left[B^2x^2 + Bx(a-\lambda) + a^2/3 - a\lambda/2\right]^{1/2} - Bx \tag{7}$$

We can determine Lagrange's multiplicator λ from the equation $F = 0$ using (2)

$$\frac{a}{2}\int_r^R \frac{dx}{Bx + L(x)} - \int_r^R \frac{L(x)}{Bx + L(x)}\,dx = 0 \tag{8}$$

After performing the integrations we obtain the following equation

$$\begin{aligned} F = B(R-r) &+ \left[B^2r^2 + Br(a-\lambda) + a^2/3 - a\lambda/2\right]^{1/2} \\ &- \left[B^2R^2 + BR(a-\lambda) + a^2/3 - a\lambda/2\right]^{1/2} \\ &- \frac{\lambda}{2}\log_e\left(\frac{2B^2R + B(a-\lambda) + 2B\left[B^2R^2 + BR(a-\lambda) + a^2/3 - a\lambda/2\right]^{1/2}}{2B^2r + B(a-\lambda) + 2B\left[B^2r^2 + Br(a-\lambda) + a^2/3 - a\lambda/2\right]^{1/2}}\right) = 0 \end{aligned} \tag{9}$$

The work needed to roll a leaf half is

$$W = \int_0^{\phi^*} d\phi \int_r^R \frac{E\left[(a-L)^3 + L^3\right]x}{3(Bx + L)^2}\,dx \tag{10}$$

where angle ϕ is measured from the midrib of the leaf, the origin of the system of coordinates is the peak point of the cone. Angle ϕ^* is determined by

$$r(\phi^*) = R(\phi^*) \tag{11}$$

Minimization of the work needed to roll a leaf half

I now minimize the work needed to roll a leaf half under the additional condition that the leaf surface rolled into the leaf cone is a given constant. This leads to a problem of variational calculus, which is solved in this section.

I minimize the work W needed to roll a leaf half for a given rolled leaf surface

$$T = \int_0^{\phi^*} \frac{1}{2}r^2(\phi)\,d\phi + \int_{\phi^*}^{\pi} \frac{1}{2}R^2(\phi)\,d\phi = \int_0^{\phi^*} \frac{1}{2}r^2(\phi)\,d\phi + t \tag{12}$$

From here the additional condition of the variational problem is

$$2(T-t) = \int_0^{\phi^*} r^2(\phi)\, d\phi \tag{13}$$

where the surface $2(T-t)$ is constant. Lagrange's function is

$$\widetilde{\mathcal{L}} = \int_r^R \frac{E\left[(a-L)^3 + L^3\right] x}{3(Bx+L)^2} dx - \widetilde{\lambda} r^2 \tag{14}$$

where $\widetilde{\lambda}$ is a Lagrange's multiplicator. The Euler–Lagrange equation is

$$\frac{d}{d\phi} \frac{\partial \widetilde{\mathcal{L}}}{\partial r'(\phi)} - \frac{\partial \widetilde{\mathcal{L}}}{\partial r(\phi)} = 0 \ , \qquad r'(\phi) \equiv \frac{dr}{d\phi} \tag{15}$$

I substitute (14) into (15) and obtain

$$\frac{\partial \widetilde{\mathcal{L}}}{\partial r} = 0 \ , \quad \text{from here} \quad -2r\widetilde{\lambda} = \left\{ \frac{Eax\left[a^2 - 3aL(x) + 3L^2(x)\right]}{3\left[Bx+L(x)\right]^2} \right\}_{x=r} \tag{16}$$

I introduce the following notations

$$\begin{aligned}
&h_1 = B^2 r^2 + Bar + a^2/3 \, , && h_2 = Br + a/2 \, , \\
&h_3 = -2\left(3\widetilde{\lambda} h_1 + Ea^3 + 3Ea^2Br + 3EaB^2r^2\right), && \\
&h_4 = 3h_2(2\widetilde{\lambda} + Ea) \, , && h_5 = 3Ea(a + 2Br) \, , \\
&h_6 = \frac{2h_3h_4 + h_5^2 h_2}{h_4^2} \, , && h_7 = \frac{h_3^2 - h_5^2 h_1}{h_4^2}
\end{aligned} \tag{17}$$

Lagrange's multiplicator λ can be determined using (17)

$$\lambda = -\frac{h_6}{2} \pm \left[\frac{h_6^2}{4} - h_7\right]^{1/2} \tag{18}$$

The other Lagrange's multiplicator $\tilde{\lambda}$ is determined from (16)

$$\tilde{\lambda} = \frac{-Ea\left[a^2 - 2aL(r) + 3L^2(r)\right]}{6\left[Br + L(r)\right]^2} \tag{19}$$

I solved (9) for r using Newton's tangent method, applying the following recursion

$$r_{i+1} = r_i - \frac{F(r_i)}{F'(r_i)}, \qquad F'(r) \equiv \frac{dF}{dr} \tag{20}$$

I proceed during the numerical solution in the following way. I determine F by (9) for one r_0 initial value of r using Lagrange's multiplicator λ, which is taken from (17) and (18). Then I determine the force F after which, with the application of recursion (20), I determine the next approach root r_i and repeat all these until the successive roots r_i fall within a determined error boundary.

I must still determine Lagrange's multiplicator $\tilde{\lambda}$ I cannot express $\tilde{\lambda}$ from (13) because of the extreme complexity, but $\tilde{\lambda}$ determines $r(\phi = 0) \equiv r(0)$. I choose an arbitrary $r(0)$, then solving (9) for λ by substituting $r = r(0)$, $R = R(0)$, then substituting the so-determined $\lambda(0)$ into (7), determining $L[r(0), \lambda(0)]$ and substituting it into (19), I get $\tilde{\lambda}$. λ can be determined from (9) only numerically (by Newton's tangent method, for example). I must give one λ_0 initial value, which can be estimated in the following way

$$\lambda = \frac{Br(a-2L) + a^2/3 - L^2}{a/2 + Br} \tag{21}$$

Using $0 < L < a$ I obtain

$$-a\,\frac{Br + 2a/3}{Br + a/2} \leqslant \lambda \leqslant a\,\frac{Br + a/3}{Br + a/2} \tag{22}$$

The numerical solution shows that the physically valid sign is the + in (18). In Fig. 6 some results of the calculations can be seen for birch and alder leaves. I always obtained approximate arcs for $r(\phi)$, the radius of which is $r(0)$. Since the real patterns are not arcs, the birch leaf roller does not cut its incisions on the basis of the above variational principle. Therefore the work needed to roll the leaf and the principle of optimal cost do not play a primary role in the *Deporaus betulae's* leaf twist. Furthermore the principle of optimal cost would result in symmetrical incisions because it must regard both leaf halves, however, the real patterns are asymmetrical. This contradiction and the reason for the asymmetry can be explained only by a new theory.

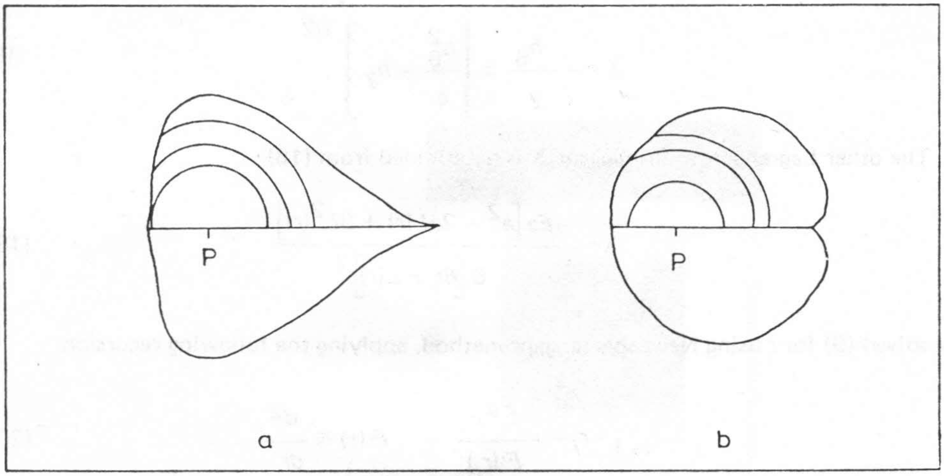

Fig. 6. Theoretically calculated incisions of the birch leaf roller for birch (a) and alder (b) leaves, if it is supposed that the beetle cuts the patterns so that the work needed to roll the leaf halves can be minimized under the additional condition that the leaf surface rolled into the leaf funnel is a given constant

New theory for the description of the birch leaf roller's incisions

After the cutting of the incisions the birch leaf roller begins to roll leaf half 1 into a leaf cone. The beetle first makes a small cone from the leaf lamina on the leaf border and it then rolls the whole of leaf half 1 around this core, a regular, slender cone is formed. A suitable microclimate can be ensured for the grubs if the peak of the cone is well closed: the peak must not have any gap. Figure 7(b) shows the situation of the leaf cone near its last stages, and Fig. 7(a) shows the situation of leaf half 1 when it is uncoiled. The external layer of the leaf cone allows the internal core to rise out easily and to close the peak of the leaf cone only if leaf half 1 forms a slanting cone section in the uncoiled stage of Fig. 7(a). Therefore *Deporaus betulae* must cut incision 1 so that after the twist of leaf half 1 the external leaf layer constitutes a slanting cone section. This can be realized if the uncoiled leaf half 1 forms a slanting cone section.

$$\rho(\delta) = y(x_o)\left[1 + 1/y'^2(x_o)\right]^{1/2} \times \frac{1 + \dfrac{\tan\beta \arctan y'(x_o) \cos\gamma}{\left\{4\pi^2 - \left[\arctan y'(x_o)\right]^2\right\}^{1/2}}}{1 + \dfrac{\tan\beta \arctan y'(x_o) \cos\left[\gamma + 2\pi\delta/\arctan y'(x_o)\right]}{\left\{4\pi^2 - \left[\arctan y'(x_o)\right]^2\right\}^{1/2}}} \tag{23}$$

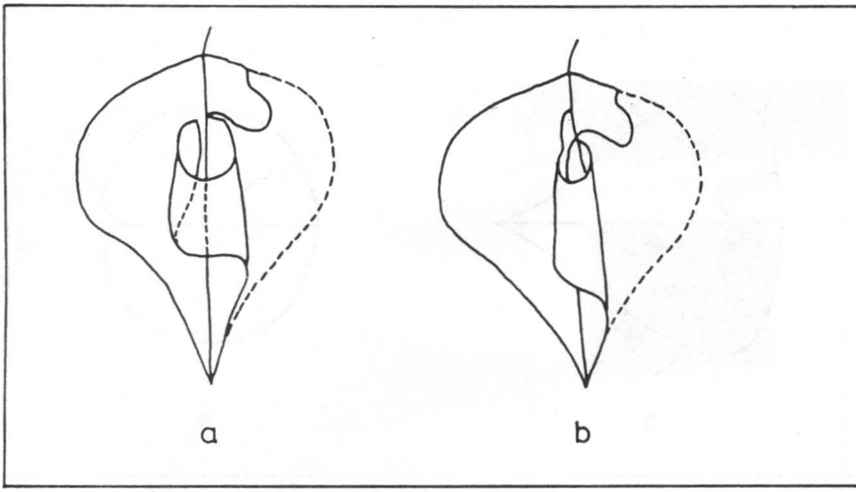

Fig. 7. (a) Such a slanting cone section can uncoil from leaf half 1 rolled by the birch leaf roller. (b) The slanting cone section in (a) ensures that the internal core of the leaf cone can rise out easily from the external layers during the leaf twist, and this internal core can form the closed peak of the leaf cone

On the basis of these, theoretical incision 1 is the curve of a slanting cone section laid out in the plane. The mathematical expression of this curve can be determined [8, 9]. (See Eq. (23).)

In (23), $y(x)$ is the function of the leaf border with Cartesian co-ordinates when axis x is parallel to the line AQ of the midrib and the origin of the system of co-ordinates is the root point A of the petiole. $y'(x) \equiv dy/dx$, and x_0 is the distance between point A and the perpendicular projection of point P_0 on the midrib. Angles β and γ characterize the slanting cone section mentioned above.

I have plotted curve $\rho(\delta)$ as a function of the parameters $y(x_0)$, $y'(x_0)$, β and γ. I sought those theoretical curves which are the most similar to incision 1 of the birch leaf roller. These curves can be seen in Fig. 8(a) and 8(b) for birch and alder leaves, respectively. It can be seen that theoretical incision 1 is very similar to the real one on both of the investigated kinds of leaf. Thus expression (23) is suitable for the description of incision 1 of *Deporaus betulae.*

After the rolling of leaf half 1 into a leaf cone the beetle twists leaf half 2 around this cone. The flexibility of the leaf lamina plays a primary role in the physics of the leaf twist, therefore consider the torque needed to roll a leaf blade around a cone with half aperture angle α. The thickness of the leaf lamina is a, the width of the rolled leaf blade along the generatrix of the cone is b. The nearer edge of the rolled leaf lamina is at distance x along the generatrix from peak P of the cone. If E is Young's modulus of the leaf blade, the torque needed to roll the leaf cone is (see Fig. 4).

$$M = \frac{Ea^3}{12 \tan \alpha} \ln (1+b/x) \tag{24}$$

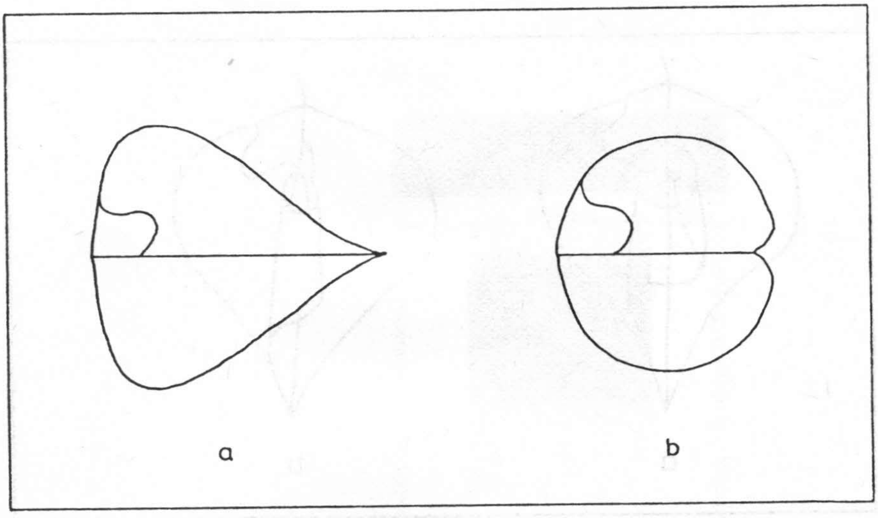

Fig. 8. These theoretically calculated curves for birch (a) and alder (b) leaves agree well with incision 1 of *Deporaus betulae*. The parameters are (a) $\alpha = 13^{o}$, $\beta = 45^{o}$, $\gamma = 60^{o}$, (b) $\alpha = 9^{o}$, $\beta = 45^{o}$, $\gamma = 60^{o}$

Cutting the midrib of the leaf causes the leaf tissue to wilt, i.e. its cells lose their normal turgor. This is a crucial factor in the strategy of the birch leaf roller because the mechanical properties of the flaccid, wilted leaf lamina are more advantageous for the leaf twist than those of the normal, turgid lamina. Young's modulus E of a wilted leaf blade is much smaller than that of a turgid blade so on the basis of (24) the torque M needed to flex a flaccid lamina is much smaller than that of a turgid one.

Furthermore it can be observed that the wilted leaf blade cutted by *Deporaus betulae* is, in itself a little twisted, and this also makes the leaf twist easier. It is important for the suitable microclimate of the grubs that the leaf tissue of the leaf cigar does not dry fully after the leaf cone is constructed, but the tissue should not regain its normal turgor after the cone construction. The upper part of the rolled leaf remains sound and turgid, and a smaller flow of tissue fluid is possible through the gnawed midrib.

We can see from (24) that *Deporaus betulae* must cut incision 2 in such a way that during the roll, distance PB_2 is not too small, because the torque needed to roll leaf half 2 would then be very great, or too large, because then little leaf mass would roll into the leaf cone. The beetle must choose a small distance PB_2 then it cuts incision 2 so that the edge of the leaf moves away quickly from point P during the twist, so x increases rapidly, M decreases rapidly, and that part of leaf half 2 near point P can be rolled.

When the beetle is ready with the twist of the leaf halves, it fastens the leaf layers of cone together with its proboscis, thus the leaf cone cannot uncoil. The last leaf layer must be tongue-shaped so that it can be fastened easily by the beetle, i.e. torque M must be small. We see from (24) that M is small if b/x is small. Consequently the last, tongue-shaped layer must be narrow and its edges must be distant from point P. Therefore *Deporaus betulae* cuts incision 2 in the leaf lamina so that the last leaf layer is a relatively narrow, long tongue far from the peak point P of the leaf cone.

Since the leaf cone nourishes the grubs, it is very important to have enough leaf mass in it, the beetle must roll as much leaf mass as possible into the leaf cigar.

Consider the angles between the borders of the lower part of leaf half 2 rolled and the generatrix of the cone. If these angles differ very much from each other during the twist, then the last leaf layer will suddenly be very wide or narrow, either one would contravene the requirement of the narrow, long, tongue-shaped last leaf layer far from the peak of the leaf cone. Therefore incision 2 must be cut in such a way that the angles between the edges of the lower part of leaf half 2 rolled and the generatrix are equal.

Referring to Fig. 3, assign polar coordinates with origin at P, and angle measured from the midrib $\overline{AQ}$ of the leaf, using function $R(\phi)$ of the leaf border, the theoretical curve of incision 2 according to the above twist method is [8, 9]:

$$r(\phi) = \frac{\overline{PQ} \cdot \overline{PB_2}}{R(\phi)} \equiv \frac{R_o r_o}{R(\phi)} \tag{25}$$

In Fig. 9(a) and 9(b), curve $r(\phi)$ is plotted as a function of r_o with a given R_o for birch (a) and alder (b) leaves, respectively. In Fig. 9(a) it can be seen that the marked theoretical curves are very similar to curve P_1C of incision 2 of *Deporaus betulae* for the birch leaf, but in Fig. 9(b) we see that for the alder leaf the theoretical curves differ significantly from the real incision 2.

There is little difference between the marked theoretical curves of Fig. 9(a) and real incisions 2. The marked theoretical curves do not have the arc CB_2 (see Fig. 3). The beetle uses arc CB_2 because thus a small distance B_1B_2 can be formed between the root point of the incisions on the midrib. This distance is very important in forming a strong suspension of the rolled leaf cone, so the completed leaf funnel cannot fall down from the midrib. In reality, peak point P of the leaf cone coincides with point B_2 of incision 2, and point C can be considered the real root point of incision 2 in respect of the rolling of leaf half 2. So expression (25) can describe the S-shaped arc P_1C of incision 2.

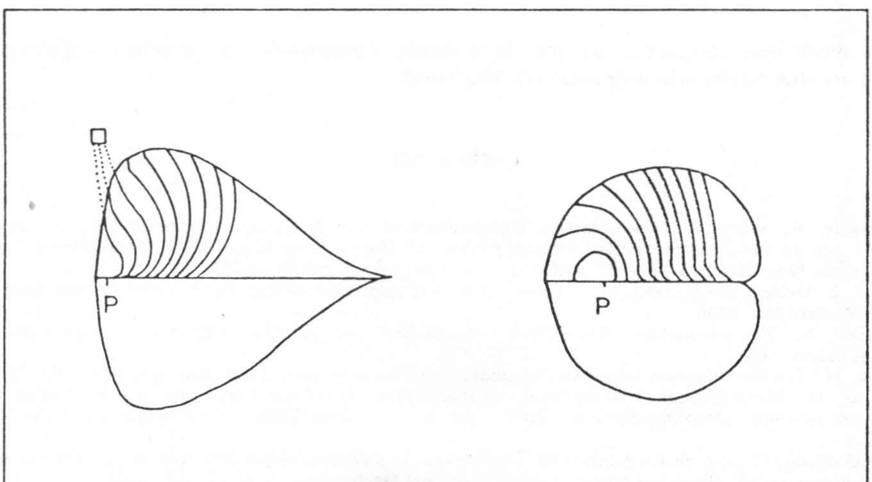

Fig. 9. Theoretically calculated curves of the birch leaf roller's incision 2 for birch (a) and alder (b) leaves. The curves marked □ agree well with real incision 2

Conclusions

The widespread view, that the leaf cone construction of the birch leaf roller is determined by the principle of optimal cost, is refuted. The asymmetry of the incisions cannot be explained on the basis of this variational principle.

The shape of *Deporaus betulae*'s patterns is independent of leaf size and leaf shape. Previously an exact biomathematical description of these patterns which could explain the biomechanical reason for the shape of the incisions did not exist. In this work a new theory is presented to describe *Deporaus betulae's* patterns.

Theoretical expression (23) for incision 1 depends only on parameters $y(x_0)$ and $y'(x_0)$ among the parameters of the leaf shape. This is only a very weak dependence on the kind of leaf, so theoretical incision 1 is almost independent of leaf shape. For some values of the parameters in (23) theoretical incision 1 agrees well with incision 1 of the birch leaf roller.

Theoretical expression (25) for incision 2 depends strongly on leaf shape. For some values of the parameters in (25) and for the shape of the birch leaf, theoretical incision 2 agrees well with the real one. However for other leaf shapes the theoretical curves differ from real incisions 2. Obviously only one shape of the incisions was fixed genetically during the evolution in the species *Deporaus betulae*, namely, that shape which belongs to the most frequently rolled leaf—the birch leaf.

The presented new mathematical expressions describe well the patterns of the birch leaf roller, and their biomechanical reasons can be justified too. The values of the parameters of those expressions, in which the theoretical patterns agree with the real ones, may be determined by the optimal, rolled leaf mass which is suitable for the nutrition of the grubs and for the muscular power of the birch leaf roller.

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