Bionical Investigation of the Birch Leaf Roller's Incisions

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ABSTRACT

A theoretical explanation is given for the shape of the incisions on the birch leaf cut by the birch leaf roller (*Deporaus betulae*). The theoretical predictions for the incisions agree well with the real patterns. The previous view, that the leaf cone construction is determined by the principle of optimal cost, is refuted.

1. INTRODUCTION

The Rhynchitinae provide peculiarly for their descendants. These beetles twist leaf cigars as cradles to protect and feed their grubs [1, 2]. One of the most interesting and most studied species of the Rhynchitinae is the birch leaf roller (*Deporaus betulae*). This beetle cuts S-shaped incisions on the leaf sheet before it begins rolling the leaf into a slender cone.

Deporaus betulae is very common in central Europe. In spring the 3–5 mm long female beetle makes some funnel-like leaf packs from the leaves of the birch. The female puts its eggs into these leaf cones. It twists the leaves in a definite way so that the rolled leaves will not get untied [3–14].

It may be observed that the birch leaf roller twists its cigar in the following way [15–24]. 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. Then the beetle 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.

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 3–5 points. It puts its eggs in these cuts then crawls out of the leaf funnel,

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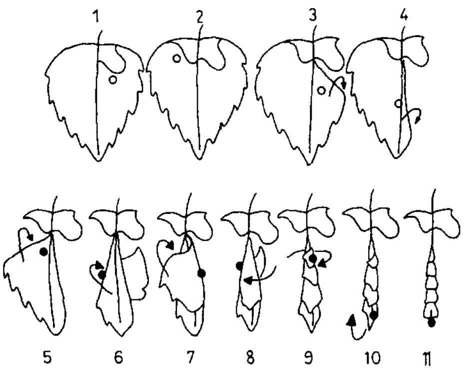

FIG. 1. The *Deporaus betulae*'s leaf twist. The front side of the birch leaf. In stages 1–2 the beetle cuts the incisions; in 3–4 it rolls the leaf cone from leaf half I. In stages 1–4 the beetle works on the back side of the leaf; in 5–9 it twists leaf half II around the leaf cone; it then works on the front side of the leaf. In stages 10–11 the beetle closes the leaf funnel below. ●, position of the beetle during the twist on the front side; ○, its position on the back side [1–24].

rolls the under edge of the cone into 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.

In a few months the wind or the rain tears the brown 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 Figure 1 we can see the main stages of the *Deporaus betulae*'s twist [5, 15, 20–24].

Only the female beetle is able to roll leaf cigars. If it is interrupted in its activity, the work does not suffer, because the female can continue the twist where it stopped [5, 7, 17, 21].

In this work I show that the second incision stands in a tight relation with the leaf edge: the incisions are placed on the leaf sheet to make it possible for the beetle to roll the relatively rigid leaf sheet easily to make a regular, slender leaf cone. I give a theoretical explanation for the shape of the incisions. This mathematical description differs from the previous geometrical explanations, which tried to describe these incisions by constructing the evolute of the leaf's shape [19, 21–24]. A widespread view in the biological literature [3–20] is that the mathematical aspect of the cone construction of the birch leaf roller is such that the serpentine incisions are the ideal geometric shape to minimize the work needed to roll the leaf halves. I refute that in the Appendix.

2. THE SHAPE OF THE SECOND INCISION OF THE BIRCH LEAF ROLLER

Figure 2 shows the birch leaf cut and rolled by the birch leaf roller. First we examine the second incision (II). The point A is the root of the peduncle of the leaf, P is the peak point of the cone, B is the root point of incision II on the midrib, and Q is the tip of the leaf.

The flexibility of the leaf sheet plays a primary role in the physics of the twist of the leaf, so consider the torque needed to roll a sheet around a cone with half aperture angle α (Figure 3). The thickness of the sheet is a; the width of the rolled sheet along the generatrix of the cone is b. The nearer edge of the rolled sheet is at distance x along the generatrix from the peak of the cone. If E is the Young's modulus of the sheet, the torque needed to bend a sheet with rectangular profile is

$$M = \frac{Eab^3}{12R}, \tag{1}$$

where a and b are the sides of the rectangle, and R is the radius of curvature. We divide the sheet into stripes with width dx and take into consideration that at distance x from the peak of the cone the radius of curvature is $R = x\tan\alpha$. The torque needed to roll the cone is

$$M = \int_x^{x+b} \frac{Eb^3\,dx'}{12x'\tan\alpha} = \frac{Eb^3}{12\tan\alpha}\log_e\left(1+\frac{b}{x}\right). \tag{2}$$

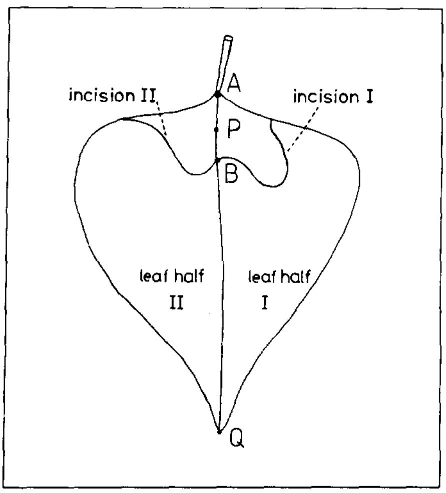

FIG. 2. The birch leaf (without perforation of the edge) cut by the birch leaf roller. The point P is the peak of the leaf cone.

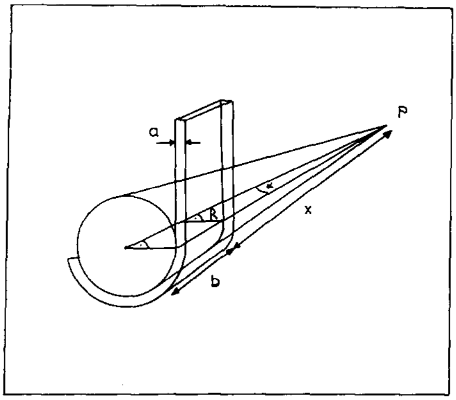

FIG. 3. Twist of a sheet with thickness a and width b around a cone with half aperture angle α. The nearer edge of the sheet is at distance x from the point P.

We can see from (2) that if $x \to 0$ then $M \to \infty$. From this we get:

Observation 1. The *Deporaus betulae* must cut incision II in such a way that during the roll the distance $\overline{PB}$ is not too small, because the torque needed to roll leaf half II 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 $\overline{PB}$; then it cuts incision II so that the edge of the leaf moves away quickly from the point P during the twist, so x increases rapidly, M decreases rapidly, and the part of leaf half II near the point P can be rolled.

When the beetle is ready with the twist of the leaf halves, it fastens the leaf layers of the 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., the torque M must be small. It can be seen from (2) 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 the point P. From this we obtain the second observation.

Observation 2. The *Deporaus betulae* cuts incision II in the leaf sheet so that the last leaf layer is a relatively narrow, long tongue far from the peak point of the leaf cone.

Since the leaf cone nourishes the grubs, it is very important to have enough leaf mass in it. From this we get the third observation:

Observation 3. The *Deporaus betulae* must roll as much leaf mass as possible into the leaf cone.

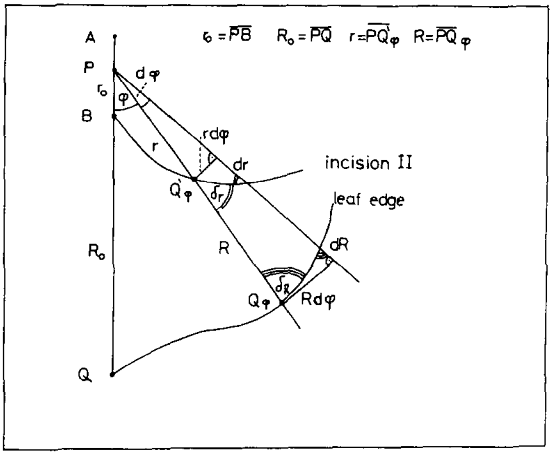

FIG. 4. For the theoretical calculation of incision II of the birch leaf roller. The points P, Q'_φ, Q_φ are on the generatrix of the cone.

So *Deporaus betulae* must balance its strategy: it uses the most leaf mass possible given that it must overcome the resistance of this mass to rolling of the leaf cone.

Consider the angles between the borders of the leaf sheet rolled and the generatrix of the cone (the angles δ_r and δ_R in Figure 4). If these angles differ very much from each other during the twist, then the last, tongue-shaped layer will be suddenly very wide or narrow; either one would contravene Observation 2. So it is useful to follow the following method in the twist of leaf half II:

Method 1. Incision II must be cut in such a way that the angles between the edges of the leaf sheet rolled and the generatrix are equal.

This method is consistent with the observations. Referring to Figure 4, assign polar coordinates with origin at P, and angles measured from the midrib AQ of the leaf. The curve of the leaf border $R(\varphi)$ is given. We want to determine the curve $r(\varphi)$ (incision II), starting at the point B, for which $\delta_r = \delta_R \equiv \delta$ for every φ. We can see in Figure 4

$$\tan \delta_r = r \frac{d\varphi}{dr}, \tag{3}$$

$$\tan \delta_R = -R \frac{d\varphi}{dR}, \tag{4}$$

$$\delta_r = \delta_R \equiv \delta. \tag{5}$$

We get from this

$$\frac{r(\varphi)}{r'(\varphi)} = -\frac{R(\varphi)}{R'(\varphi)}, \qquad \text{or} \quad \int \frac{dr}{r} = -\int \frac{R'(\varphi)}{R(\varphi)}\, d\varphi. \tag{6}$$

From (6) we obtain

$$r = c/R, \qquad \text{but} \quad r = r_0 \text{ for } R = R_0, \qquad \text{so} \quad c = R_0 r_0.$$

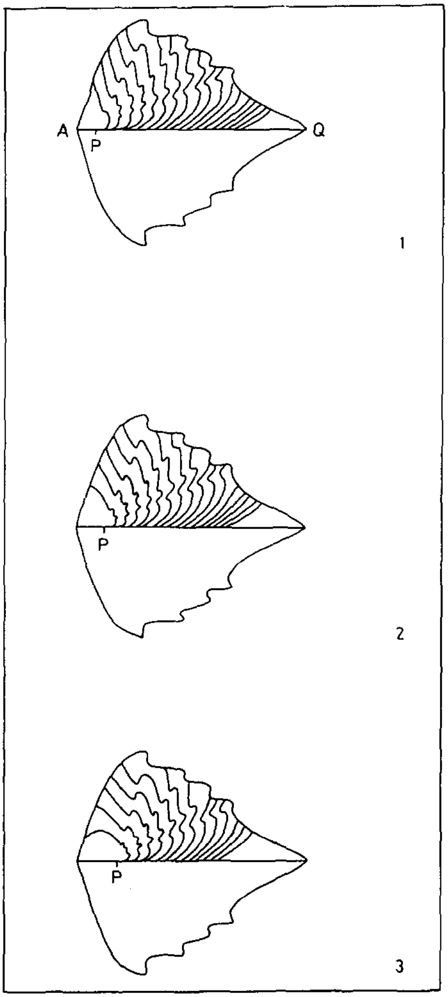

FIG. 5. The theoretically calculated incision II of the birch leaf roller if the perforation of the leaf border is taken into consideration. The free parameters of the family of curves are the distances $\overline{AP}$ and $\overline{PB}$.

So the theoretical curve of incision II according to Method 1 is the following:

$$r(\varphi) = \frac{R_0 r_0}{R(\varphi)} = \frac{\overline{PQ} \cdot \overline{PB}}{R(\varphi)}. \tag{7}$$

I determined and plotted this curve for the real shape of the birch leaf, and I got the family of curves in Figure 5. The free parameters in (7) are the distances $\overline{PQ}$ and $\overline{PB}$.

First I took the perforation of the leaf border into consideration (Figure 5). Incision II is closely connected with the leaf edge [see (7)], so the curve $r(\varphi)$ is perforated too. The real incision II of the *Deporaus betulae* is smooth; consequently the perforation of the leaf border is not important in the twist of the leaf. That is understandable, because the teeth of the leaf edge are negligible compared with the whole leaf sheet; the perforation of the leaf edge can have little influence on the torque during the twist.

A determination of the curve $r(\varphi)$ by (7) for the leaf border without perforation gives the family of curves in Figure 6. The curves marked (□) in Figure 6 resemble the real incision II of the birch leaf roller [1–24].

3. THE SHAPE OF THE FIRST INCISION OF THE *DEPORAUS BETULAE*

Deporaus betulae begins the twist of the leaf on the back side of leaf half I as in Figure 7 [17, 19, 21–24]. It first makes a small cone from the leaf sheet on the leaf border and then rolls the whole of leaf half I around this core. A regular, slender cone is formed; one of the generatrixes of this cone is the midrib of the leaf. The function of the small, initial cone can be understood using (2): the beetle decreases b in order to diminish the torque.

A suitable microclimate can be insured for the grubs if the peak of the cone is well closed: there may not be any gap on this peak. Figure 8(b) shows the situation of the leaf cone near its last stages, and Figure 8(a) shows the situation of leaf half I when it is uncoiled. It can be seen that 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 I forms a slanting cone section in the uncoiled stage of Figure 8(a).

From this we get the second method followed by the birch leaf roller:

Method 2. The Deporaus betulae cuts incision I so that after the twist of leaf half I the external leaf layer constitutes a slanting cone section. This can be realized if the uncoiled leaf half I forms a slanting cone section.

On the basis of Method 2 the theoretical incision I is the curve of a slanting cone section laid out in the plane. We place the leaf cone in the system of coordinates of Figure 9. The position vector of the points of the

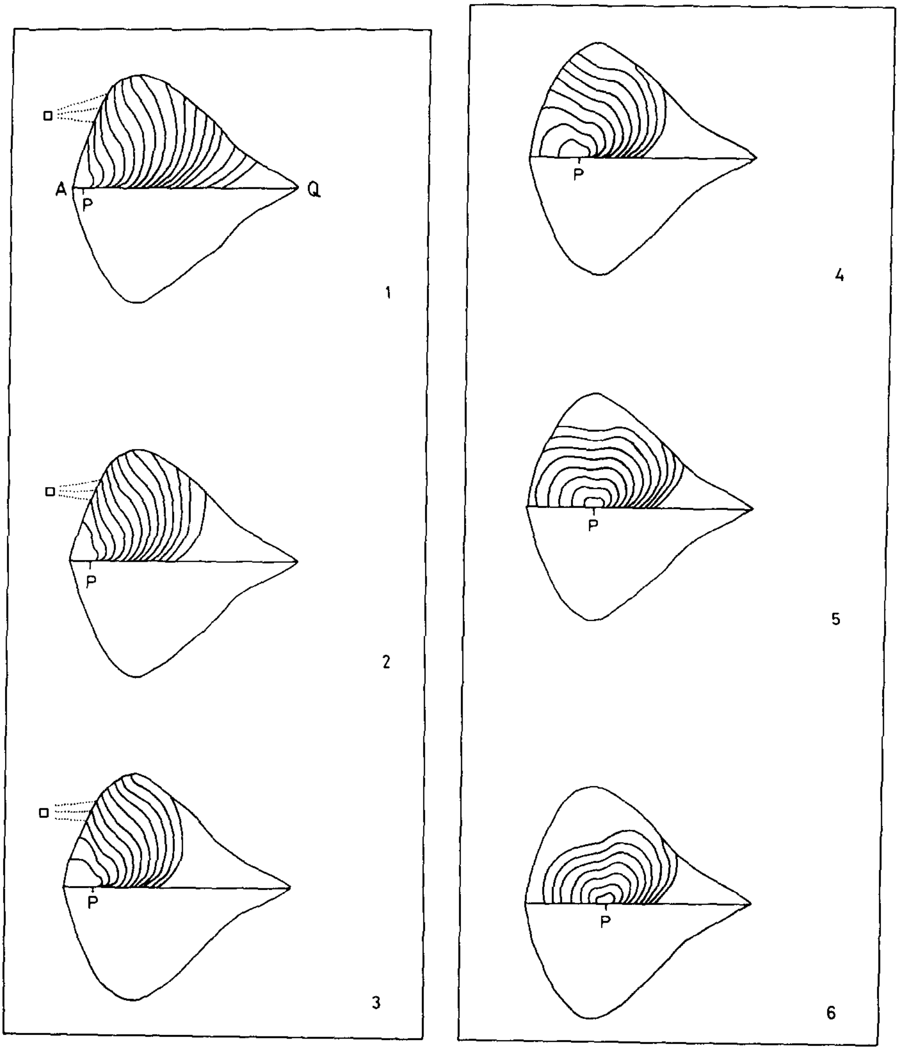

FIG. 6. As in Figure 5, but the perforation of the leaf border is not taken into consideration. The marked theoretical curves are very similar to the real incision II of the birch leaf roller.

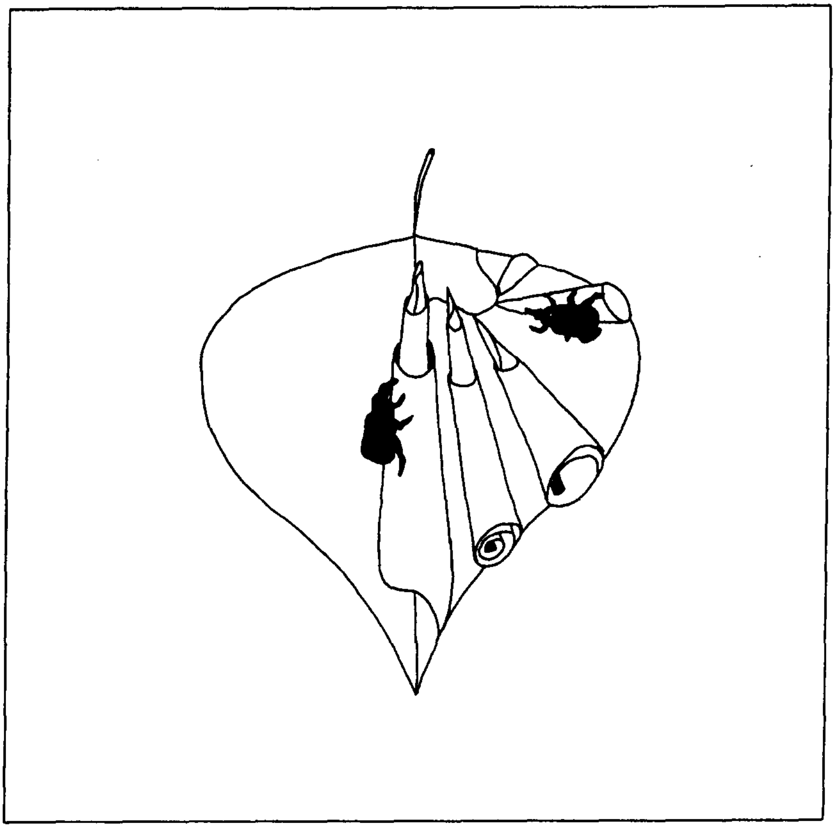

FIG. 7. The birch leaf roller twists a regular, closed, slender leaf cone from leaf half I. The back side of the leaf can be seen [17, 19, 21–24].

cone is

$$\boldsymbol{\rho} = (\rho_1, \rho_2, \rho_3) = (z \tan\alpha \cos\varphi, z \tan\alpha \sin\varphi, -z), \qquad z \geqslant 0. \tag{8}$$

We intersect the cone with a plane going through the point

$$\boldsymbol{P}_0 = (x_0, y_0, z_0) = (\sin\alpha, 0, -\cos\alpha)h. \tag{9}$$

Let the plane be parallel with the y axis, and let the angle between this plane and the x axis be β. The normal vector of the plane is

$$\boldsymbol{n} = (-\sin\beta, 0, \cos\beta) \tag{10}$$

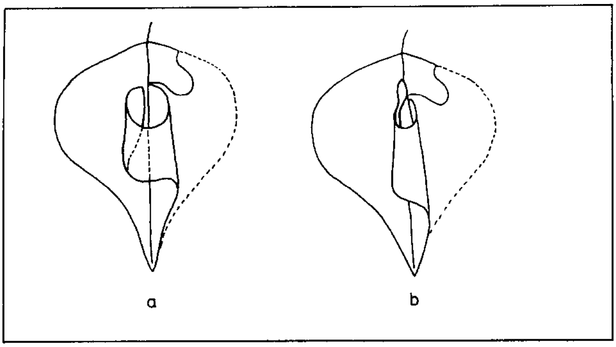

FIG. 8. (a) Such a slanting cone section can uncoil from leaf half I rolled by the birch leaf roller. (b) The slanting cone section in (a) assures that the internal core of the leaf cone can rise out easily from the external layers during the leaf twist, and this internal core can form the closed peak of the leaf cone.

The coordinates of the plane are $\boldsymbol{R} = (R_1, R_2, R_3)$; the equation of the plane is

$$(\boldsymbol{R} - \boldsymbol{P}_0)\boldsymbol{n} = 0. \tag{11}$$

The coordinates of the points of the curve which is determined by the section of the plane and the cone are

$$R_1 = z\tan\alpha\cos\varphi = \rho_1,$$
$$R_2 = z\tan\alpha\sin\varphi = \rho_2,$$
$$R_3 = -z = \rho_3,$$

and from (11),

$$-R_1\sin\beta + R_3\cos\beta = -x_0\sin\beta + z_0\cos\beta. \tag{12}$$

We get from (12)

$$z = \frac{x_0\sin\beta - z_0\cos\beta}{\cos\beta + \tan\alpha\sin\beta\cos\varphi}. \tag{13}$$

We can write on the basis of Figure 9

$$\varphi = \delta/\sin\alpha, \tag{14}$$

$$\rho = z/\cos\alpha. \tag{15}$$

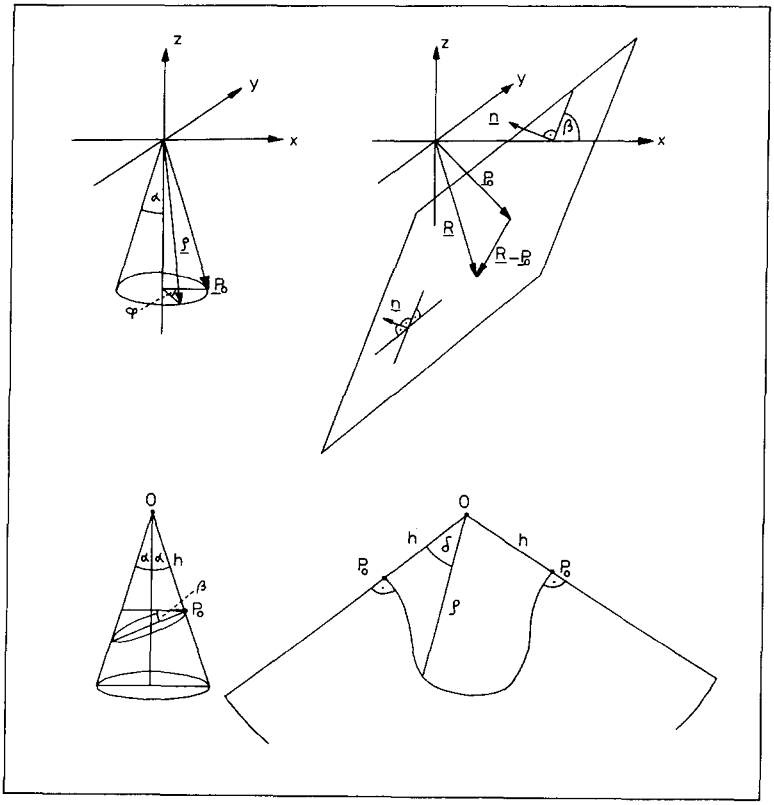

FIG. 9. For the calculation of the curve of a slanting cone section laid out flat.

The curve of the cone section is

$$\rho(h,\alpha,\beta,\delta)=h\frac{1+\tan\alpha\tan\beta}{1+\tan\alpha\tan\beta\cos(\delta/\sin\alpha)}. \tag{16}$$

We apply the above to the birch leaf (see Figure 10). h can be determined as a function of the coordinates of P_0. The line $\overline{OP_0}$ is a tangent of the leaf border, so we can write by Figure 10

$$\overline{OA}=\frac{y(x)}{y'(x)}-x,\qquad y'(x)=\frac{dy}{dx}. \tag{17}$$

It is clear that

$$h=\left[y^2+\left(\overline{OA}+x\right)^2\right]^{1/2}. \tag{18}$$

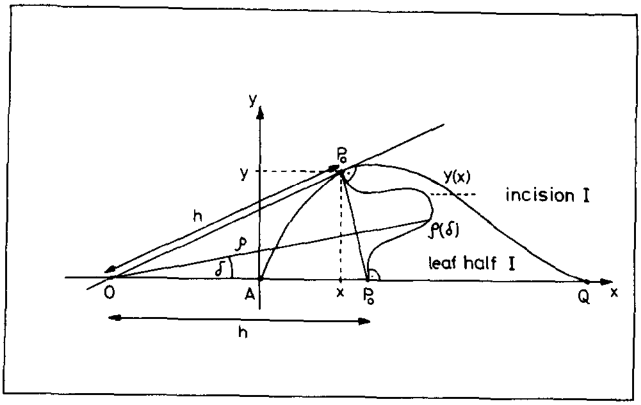

FIG. 10. For the theoretical calculation of incision I of the birch leaf roller on the basis of Method 2.

From (17), (18) we obtain

$$h = y(x)\left[1 + \frac{1}{y'^2(x)}\right]^{1/2}. \tag{19}$$

Using (16) and (17), the theoretical curve of incision I is:

$$\rho[y(x), y'(x), \alpha, \beta, \delta]$$
$$= y(x)\left[1 + \frac{1}{y'^2(x)}\right]^{1/2} \frac{1 + \tan\alpha \tan\beta}{1 + \tan\alpha \tan\beta \cos(\delta/\sin\alpha)} \tag{20}$$

The position of the point P_0 on the leaf edge determines the value of the angle α. It is known that

$$\rho = h \qquad \text{for} \quad \delta = 0 \text{ and } \delta = \arctan y'(x). \tag{21}$$

Using (20) and (21), we obtain

$$\sin\alpha = \frac{\arctan y'(x)}{2\pi},$$
$$\tan\alpha = \frac{\arctan y'(x)}{\left\{4\pi^2 - [\arctan y'(x)]^2\right\}^{1/2}}. \tag{22}$$

Using (20) and (22), we obtain the following expression for the theoretical incision I of the birch leaf roller:

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

I have plotted the function $\rho[y(x), y'(x), \beta, \delta]$ for the birch leaf in Figure 11. The position of P_0 was fixed on the leaf edge. The curves of Figure 11(b) are very similar to the real incision I of the birch leaf roller (see [1–24]).

4. CONCLUSIONS

Method 1 explains incision II of the birch leaf roller. The microstructure of the leaf edge can be disregarded. Method 2 explains incision I of the *Deporaus betulae*. The theoretically calculated incisions on the basis of Methods 1 and 2 agree well with the real patterns for some values of the free parameters.

A widespread view in the biological literature is that the birch leaf roller cuts its incisions so that the work needed to roll the leaf is minimized [3–20]. For example, J. G. Rozen writes as follows: "The arresting mathematical aspect of the cone construction is that the serpentine incisions are the ideal geometric shape to minimize the work needed to roll the leaf halves" [15]. This view is based on the principle of optimal cost.

In the Appendix I calculate the work needed to roll the whole of leaf half II and minimize this work under the additional condition that the leaf surface rolled into the leaf cone is given (constant). This leads to a problem of variational calculus. This problem can be solved.

I obtained nearly arc-shaped curves for the optimal incision II. Since the real incision II is not an arc, the birch leaf roller does not cut its patterns on the basis of this variational principle. The work needed to roll the leaf does not play a primary role in the leaf twist.

The leaf is drooped during the twist, so the work needed to roll is not large; the beetle does not do appreciable surplus work owing to not cutting the leaf sheet in an arc. Methods 1 and 2 play the primary role in the leaf twist, and these determine the optimum shape of the incisions, which prevent the uncoiling of the rolled leaf.

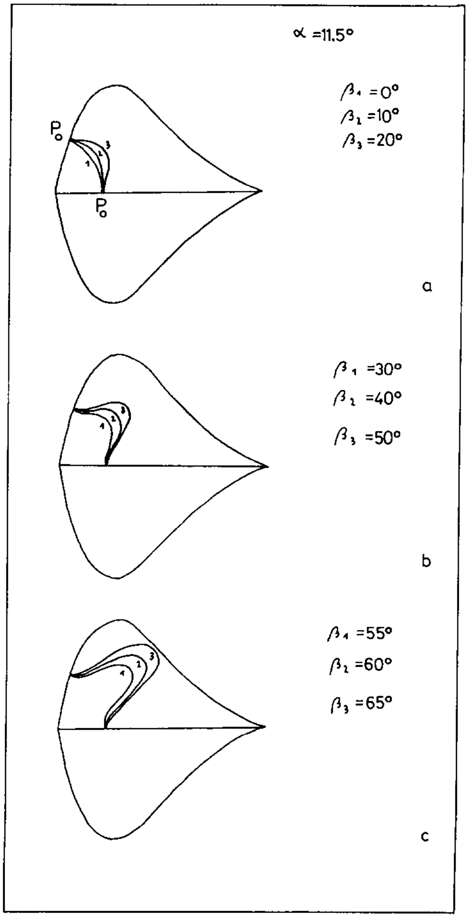

FIG. 11. The theoretically calculated incision I of the birch leaf roller. The free parameters are the angle β and the position of the point P_0 on the leaf edge. The half aperture angle of the leaf cone is $\alpha = 11.5°$, and the position of P_0 does not change. Only the angle β varies.

APPENDIX

A1. CALCULATION OF THE WORK NEEDED TO ROLL LEAF HALF II

The main radius of curvature at any point of a cone is (see Figure 9)

$$R = hB, \qquad B = \tan\alpha \tag{A-1}$$

We consider the twist of a sheet with Young's modulus E around a cone with half aperture angle α (Figure 12). At the examined point the neutral

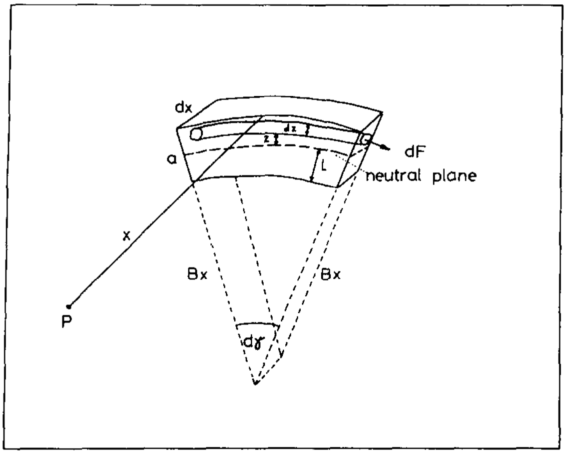

FIG. 12. Elementary piece of a leaf sheet twisted into the leaf cone. The local radius of curvature is $x \tan\alpha$, the nearer edge of the sheet element is at distance x from the peak of the cone, the thickness of the sheet is a, and the width of the sheet element is dx. The neutral surface is at 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.

surface is at distance L from the surface of the cone; the local radius of curvature is Bx. If the functions of the borders of the rolled sheet are $r(\varphi)$ and $R(\varphi)$ from the peak point of the cone, then the required force and torque are

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

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

The existence of the neutral surface requires $F = 0$. 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

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

where λ is the Lagrange multiplier. The function $L(x)$ is sought. We use for (A-4) the Euler-Lagrange equation [25]:

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

Thus we get

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

From this,

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

We can determine the Lagrange multiplier λ from the equation $F = 0$ using (A-2):

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

After performing the integrations we obtain the following equation:

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

The work needed to roll leaf half II is

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

where the angle φ is measured from the midrib of the leaf, and the origin of the system of coordinates is the peak point of the cone. The angle φ^* is determined by the following equation:

$$r(\varphi^*) = R(\varphi^*). \tag{A-11}$$

A2. MINIMALIZATION OF W

We minimize W for a given rolled leaf surface:

$$T = \int_0^{\varphi^*} \tfrac{1}{2} r^2(\varphi)\, d\varphi + \int_{\varphi^*}^{\pi} \tfrac{1}{2} R^2(\varphi)\, d\varphi \equiv \int_0^{\varphi^*} \tfrac{1}{2} r^2(\varphi)\, d\varphi + t. \tag{A-12}$$

From this the additional condition of our variational problem is

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

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

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

where $\tilde{\lambda}$ is a Lagrange multiplier. The Euler-Lagrange equation is

$$\frac{d}{d\varphi} \frac{\partial \tilde{\mathscr{L}}}{\partial r'(\varphi)} - \frac{\partial \tilde{\mathscr{L}}}{\partial r(\varphi)} = 0, \qquad r'(\varphi) = \frac{dr}{d\varphi}. \tag{A-15}$$

We substitute (A-14) into (A-15) and obtain

$$\frac{\partial \tilde{\mathscr{L}}}{\partial r} = 0, \qquad \text{whence} \quad -2r\tilde{\lambda} = \left\{ \frac{Eax\left[a^2 - 3aL(x) + 3L^2(x)\right]}{3[Bx + L(x)]^2} \right\}_{x=r} \tag{A-16}$$

We introduce the following notation:

$$\begin{gathered} h_1 = B^2 r^2 + Bar + \frac{a^2}{3}, \qquad h_2 = Br + \frac{a}{2}, \\ h_3 = -2\left(3\tilde{\lambda} h_1 + Ea^3 + 3Ea^2 Br + 3EaB^2 r^2\right), \\ h_4 = 3h_2(2\tilde{\lambda} + Ea), \qquad h_5 = 3Ea(a + 2Br), \\ h_6 = \frac{2h_3 h_4 + h_5^2 h_2}{h_4^2}, \qquad h_7 = \frac{h_3^2 - h_5^2 h_1}{h_4^2}. \end{gathered} \tag{A-17}$$

The Lagrange multiplier λ can be determined using (A-17):

$$\lambda = -\frac{h_6}{2} \pm \left(\frac{h_6^2}{4} - h_7 \right)^{1/2}. \tag{A-18}$$

The other Lagrange multiplier $\tilde{\lambda}$ is determined from (A-16):

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

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

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

We carry out the numerical solution in the following way. We determine F by (A-9) for one initial value r_0 of r using the Lagrange multiplier λ. First λ is taken from (A-17) and (A-18); then we determine the force F; then with the application of the recursion (A-20) we determine the next approximate root r_i and repeat all these steps until the successive roots r_i fall within a determined error bound.

We must still determine the Lagrange multiplier $\tilde{\lambda}$. We cannot express $\tilde{\lambda}$ as (A-13) because of its extreme complexity, but $\tilde{\lambda}$ determines $r(\varphi = 0) \equiv r(0)$. We choose an arbitrary $r(0)$; then, solving (A-9) for λ by substituting $r = r(0)$, $R = R(0)$, substituting the resulting $\lambda(0)$ into (A-7), determining $L[r(0), \lambda(0)]$, and substituting it into (A-19), we get $\tilde{\lambda}$.

λ can be determined from (A-9) only numerically (for example by Newton's tangent method). We must give one initial value of λ_0, which can be estimated in the following way:

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

Using $0 < L < a$, we obtain

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

The numerical solution shows that the physically valid sign in (A-18) is the $+$. In Figure 13 we can see some results of the calculations. I always obtained arcs for $r(\varphi)$; the radius of the arc is $r(0)$.

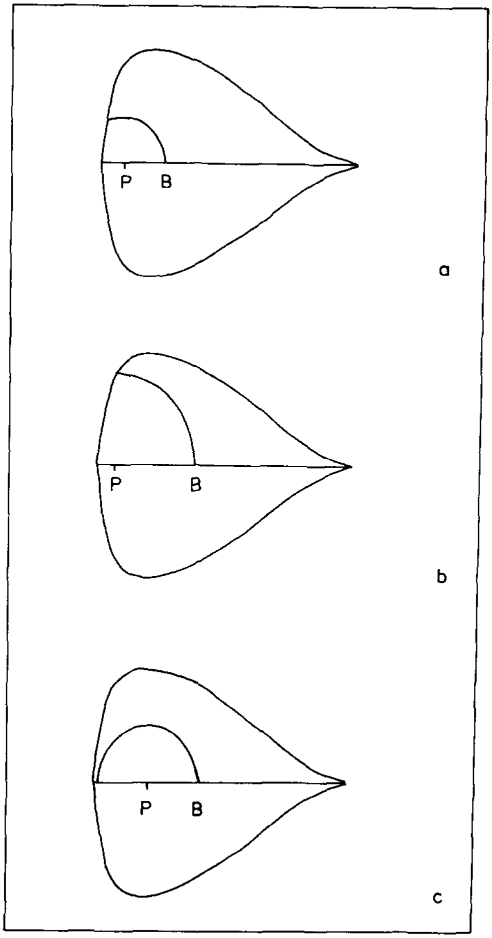

FIG. 13. The theoretically calculated incision II of the birch leaf roller, if it is supposed that the beetle cuts incision II so that the work needed to roll leaf half II can be minimized under the additional condition that the leaf surface rolled into the leaf funnel is given (constant).

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