

DESCRIPTION OF THE BIRCH LEAF ROLLER'S INCISIONS FOR DIFFERENT LEAVES

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A new biomathematical description is given for the shape of the birch leaf roller's (*Deporaus betulae*) incisions. These incisions are investigated for different leaves. The theoretical patterns agree well with the real ones, and the presented mathematical expressions describe well the shape of the real incisions.

1. Introduction. The birch leaf roller (*Deporaus betulae*) rolls a regular, conical, well closed, slender leaf cigar for its offspring. 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 Rhynchitinaes the birch leaf roller cuts the most complicated incisions and this beetle rolls the most regular, closed leaf cone from the leaf. The ethology of the *D. betulae*'s care of offspring and the techniques of its leaf twist are well known (see literature).

Deporaus betulae rolls its leaf cone from birch leaves (*Betula*) and, rarely, from other leaves (*Alnus*, *Corylus*, *Carpinus*). It can be observed that the birch leaf roller always cuts the same shaped incisions 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 the size of the incisions according to the shape and size of the leaf (Daanje, 1964; Rossköthen, 1964; Lengerken, 1954; Buck, 1952). 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 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.

In Fig. 1 the incisions of the birch leaf roller can be seen for different leaf sizes and for two kinds of leaf (birch and alder) (Daanje, 1964; Rossköthen, 1964; Buck, 1952). For leaves of different sizes the incisions 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 the

larger leaves respectively. From Fig. 1 the following important conclusion can be drawn: the shape of the birch leaf roller's incisions is independent of the leaf size and the leaf shape. The incisions on other kinds of leaf (*Corylus*, *Carpinus*) also support this conclusion (Daanje, 1964; Rosskothén, 1964; Buck, 1952).

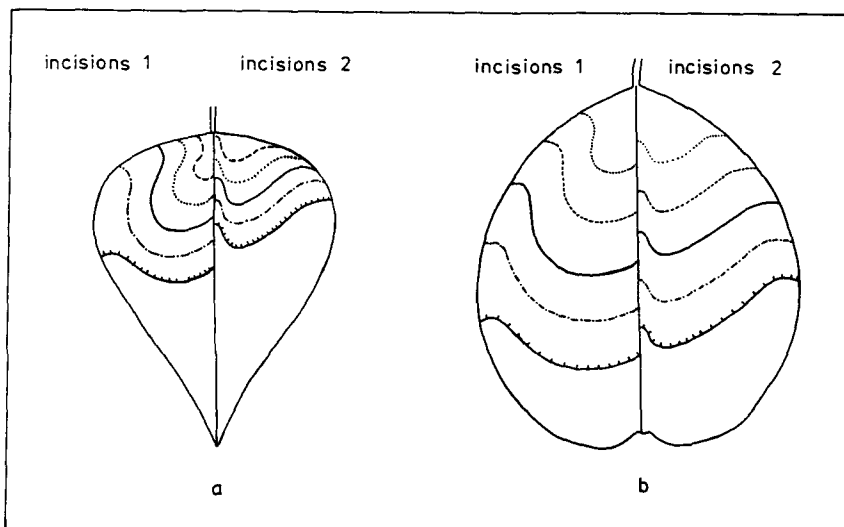


Figure 1. The incisions 1 and 2 of the birch leaf roller (Daanje, 1964; Rosskothén, 1964; Buck, 1952) for different leaves: (a) birch (*Betula*); (b) alder (*Alnus*). The differently coded lines represent the curves for leaves of different sizes. The incisions near the petiole and distant from it are characteristic of the smaller and the larger leaves respectively.

2. *Previous Descriptions and Explanations for the Shape of the Birch Leaf Roller's Incisions.* The first mathematical description for the shape of the *D. betulae*'s incisions was given by Heis and Debey (1846). In his opinion the first incision is the evolute of the leaf border (Heis' evolute), that is to say, the leaf edge is the involute of the first pattern (Heis and Debey, 1846; Debey, 1846)

Prell improved the Heis theory; he determined an imaginary curve (Prell's evolute), and he identified the second incision with the involute of this evolute (Prell's involute) (Prell, 1924; 1925).

The evolute–involute theory of Heis and Prell is widely quoted, but it is only a mathematical description; furthermore Heis' evolute and Prell's involute do not agree well with the shape of the birch leaf roller's incisions. The theories of Heis and Prell cannot explain the biophysical, bionical reason for the shape of the patterns.

Rosskothén (1949) gave another explanation for the patterns of the *D. betulae*. 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 the opinion of Rosskothén the beetle works out experimentally the optimal shape of the incisions through repeated cutting and rolling of some leaves. He thought any mathematical description of the shape of the patterns impossible and he assigned some intellectual capacity to the beetle. Rosskothén (1949; 1964) denied that the optimal shape of the patterns is genetically fixed. This theory nowadays is a worn out conception.

Buck (1952) presented a new theory; 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.

Daanje (1964) wrote the most detailed general work on the ethology and on the roll techniques of the birch leaf roller. He put his finger on the mistakes in the theories of Rosskothén and Buck, and showed that these explanations cannot be maintained. Daanje reverted to the evolute–involute theory of Heis and Prell. He gave a qualitative explanation on the grounds of the shape of the *D. betulae*'s patterns. He used the theories of Heis and Prell for the mathematical description of the shape of the incisions, in spite of the fact that the real incisions differ significantly from Heis' evolute and from Prell's involute.

Another widely quoted general view is that the optimal shape of the incisions is determined by the principle of optimal cost: the work needed to roll the leaf halves is as minimal as possible (Lengerken, 1954; Hoffmann, 1958; Schilsky, 1903; Lohse, 1981; Reitter, 1916; Rozen, 1962; Scherf, 1964). This view is refuted by the present author (1988).

Summing up, the following can be concluded: Daanje could explain qualitatively the shape of the birch leaf roller's incisions quite well; the theories of Rosskothén and Buck are refuted by Daanje; the widely quoted theory of Heis and Prell—the only mathematical theory—cannot fully describe the shape of the real patterns. A correct mathematical expression for the shape of the incisions does not exist.

In this work new biomathematical explanations and exact mathematical expressions are presented for the *D. betulae*'s patterns. Using these expressions, the shape of the incisions is investigated and compared for different kinds of leaf.

3. Mathematical Expression for the Shape of the Birch Leaf Roller's First Incision. Figure 2 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.

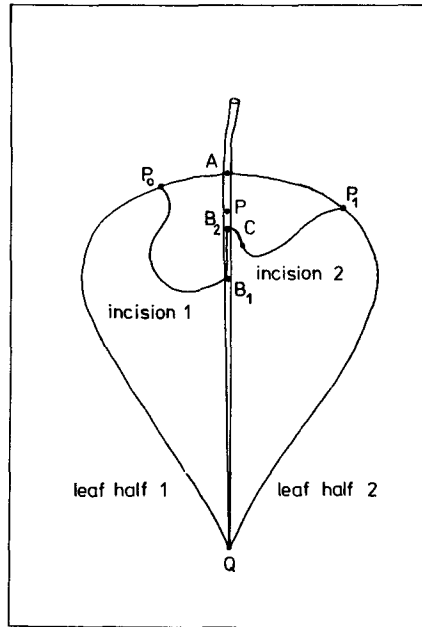


Figure 2. A leaf cut by the *D. betulae*. The points $A, P, Q, B_1, P_0, B_2, P_1$ are the root of the petiole, the peak of the rolled leaf cone, the tip of the leaf, the root on the midrib and on the leaf edge of the first and of the second incision respectively. The arc CB_2 of incision 2 constitutes the suspension of the completed leaf cone.

Deporaus betulae first makes a small cone from the leaf lamina on the leaf border and then rolls the whole of leaf half 1 around this core; a regular, slender cone is formed as in Fig. 3. 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 4b shows the situation of the leaf cone near its last stages and Fig. 4a 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. 4a. Therefore *D. betulae* cuts 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.

On the basis of the above theoretical incision 1 is the curve of a slanting cone section laid out in the plane. The expression of this curve can be determined in the following way. The leaf cone is placed in the system of coordinates of Fig. 5. The position vector of the points of the cone is:

$$\mathbf{p} = (\rho_1, \rho_2, \rho_3) = (z \tan \alpha \cos \phi, z \tan \alpha \sin \phi, -z), \quad z \geq 0. \quad (1)$$

We intersect the cone with a plane going through the point:

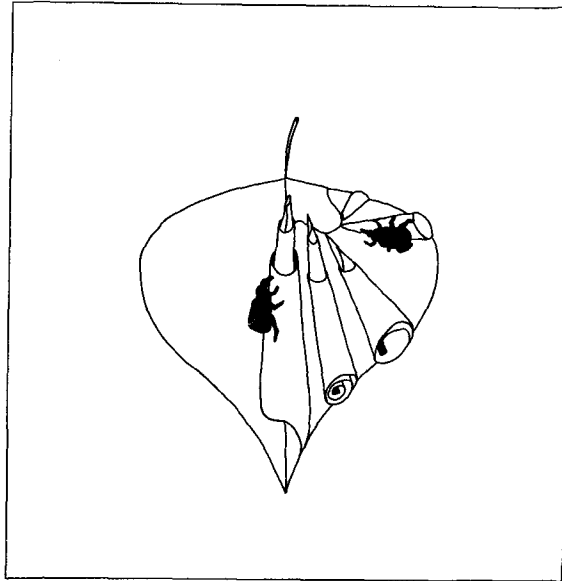


Figure 3. The birch leaf roller twists a regular, closed, slender leaf cone from leaf half 1. The back side of the leaf can be seen.

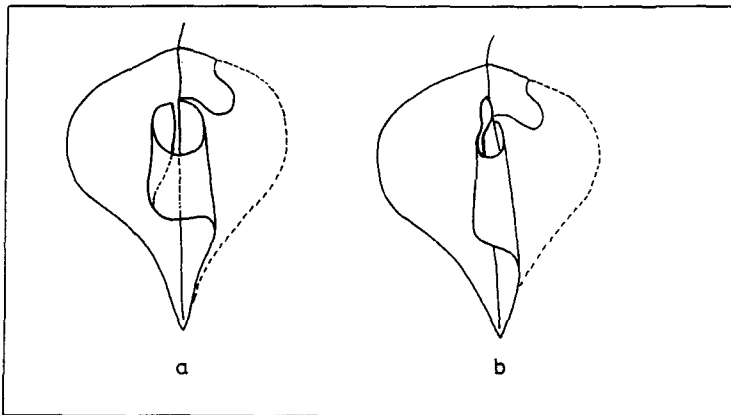


Figure 4. (a) Such a slanting cone section can uncoil from leaf half 1 rolled by the birch leaf roller. (b) The slanting cone section in (a) assures that the internal core of the leaf cone can rise out easily from the external layers during the leaf twist, and this internal core can form the closed peak of the leaf cone.

$$\mathbf{P}_0 = (x_0, y_0, z_0) = (\sin \alpha, 0, -\cos \alpha)h. \quad (2)$$

The normal vector of the plane is:

$$\mathbf{n} = (-\sin \beta \cos \gamma, \sin \beta \sin \gamma, \cos \beta). \quad (3)$$

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

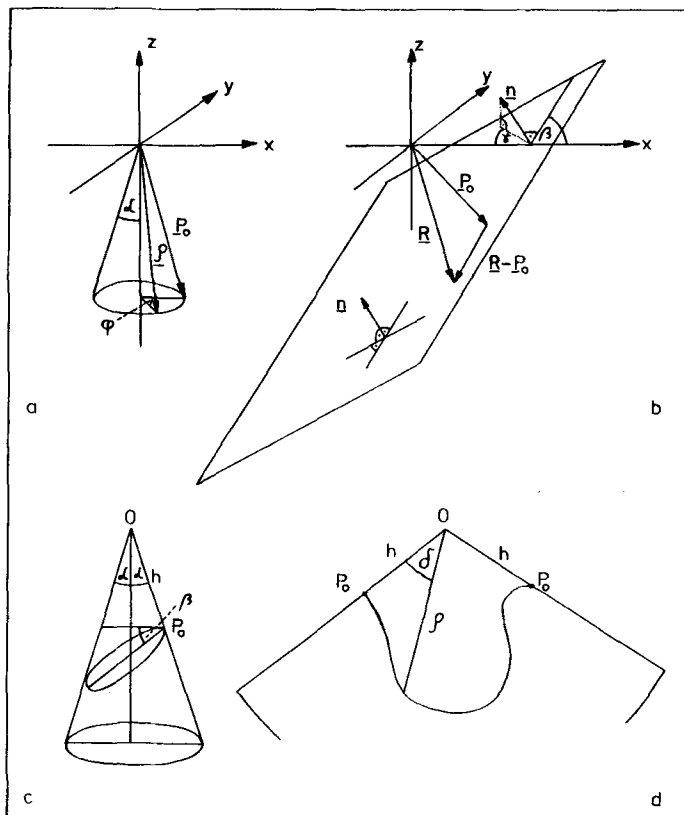


Figure 5. For the calculation of the curve of a slanting cone section laid out in the plane: (a) a cone with half aperture angle α ; (b) a plane with normal vector \mathbf{n} ; (c) a slanting section of the cone of (a) by the plane of (b); (d) the curve of the slanting cone section of (c) laid out in the plane.

$$(\mathbf{R} - \mathbf{P}_0)\mathbf{n} = 0. \tag{4}$$

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

$$\begin{aligned} R_1 = \rho_1 &= z \tan \alpha \cos \phi, \\ R_2 = \rho_2 &= z \tan \alpha \sin \phi, \\ R_3 = \rho_3 &= -z. \end{aligned} \tag{5}$$

We can write on the basis of Fig. 5:

$$\phi = \delta / \sin \alpha, \quad \rho = z / \cos \alpha. \tag{6}$$

We obtain from equations (2)–(6):

$$\rho = h \frac{1 + \tan \alpha \tan \beta \cos \gamma}{1 + \tan \alpha \tan \beta \cos(\gamma + \delta/\sin \alpha)} \tag{7}$$

We apply the above to a real leaf (see Fig. 6): h can be determined as a function of the coordinates of P_0 . The line OP_0 is a tangent of the leaf border, so we can write by Fig. 6:

$$\overline{OA} = \frac{y(x_0)}{y'(x_0)} - x_0, \quad y'(x_0) = \left(\frac{dy}{dx}\right)_{x=x_0}, \tag{8}$$

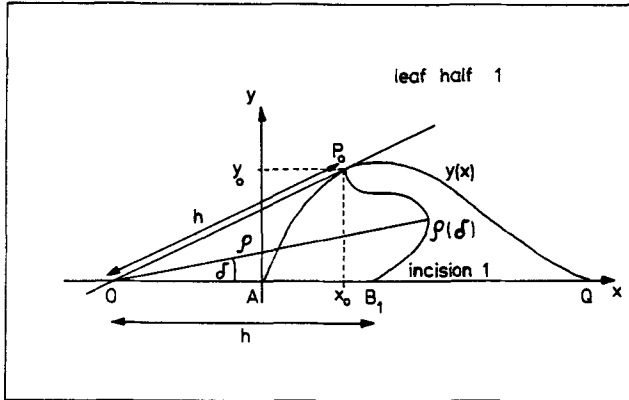


Figure 6. For the theoretical calculation of incision 1 of the birch leaf roller.

where x_0 is the distance between point A and the perpendicular projection of point P_0 on the midrib, and $y(x)$ is the function of the leaf edge. It is clear that:

$$h = [y^2 + (\overline{OA} + x_0)^2]^{1/2}. \tag{9}$$

The position of the point P_0 on the leaf edge determines the value of the angle α . Using equations (7)–(9), we get from the equation $\rho = h$:

$$\tan \alpha = \arctan y'(x_0) \{4\pi^2 - [\arctan y'(x_0)]^2\}^{-1/2}. \tag{10}$$

Using equations (7)–(10) we obtain the following expression for the theoretical incision 1 of the birch leaf roller:

$$\begin{aligned} \rho[y(x_0), y'(x_0), \beta, \gamma, \delta] &= y(x_0)[1 + 1/y'^2(x_0)]^{1/2} \\ &\times \frac{1 + \frac{\tan \beta \arctan y'(x_0) \cos \gamma}{\{4\pi^2 - [\arctan y'(x_0)]^2\}^{1/2}}}{1 + \frac{\tan \beta \arctan y'(x_0) \cos[\gamma + 2\pi\delta/\arctan y'(x_0)]}{\{4\pi^2 - [\arctan y'(x_0)]^2\}^{1/2}}}. \end{aligned} \tag{11}$$

I have plotted the curve $\rho[y(x_0), y'(x_0), \beta, \gamma, \delta]$ as a function of the leaf shape, the angles β, γ and the position of P_0 on the leaf border. I sought for those theoretical curves which are the most similar to incision 1 of the birch leaf roller. These curves can be seen in Figs 7 and 8 for birch and alder leaves respectively. The position of P_0 on the leaf edge is fixed and the angles α, β are: $\alpha = 13^\circ, \beta = 45^\circ$ for the birch leaf, and $\alpha = 9^\circ, \beta = 45^\circ$ for the alder leaf. It can be seen that the theoretical incision 1 is very similar to the real one for $60^\circ \lesssim \gamma \lesssim 90^\circ$ on both of the investigated kinds of leaf (see Figs 1, 7 and 8). Thus expression (11) is suitable for the description of incision 1 of the *D. betulae*.

4. Mathematical Expression for the Shape of the Birch Leaf Roller's Second Incision. After the rolling of leaf half 1 into a leaf cone the beetle twists leaf half 2 around this cone. Incision 2 helps this rolling and prevents the uncoiling of the twisted leaf.

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 the peak of the cone. If E is the Young's modulus of the leaf blade, the torque needed to roll the leaf cone is:

$$M = \frac{Ea^3}{12tg\alpha} \log_e(1 + b/x). \quad (12)$$

Cutting the midrib of the leaf causes the leaf tissue to wilt, that is, its cells lose their normal turgor. This is a crucial 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. The Young's modulus E of a wilted leaf blade is much smaller than that of a turgid blade, so on the basis of equation (12) the torque M needed to flex a flaccid lamina is much smaller than that of a turgid one. The concrete value of Young's modulus E of a flaccid leaf blade is of no further interest.

Furthermore, it can be observed that the wilted leaf blade cut by the *D. betulae* is a little twisted in on itself, making 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 totally after the leaf cone is constructed, but the tissue does 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 the tissue fluid is possible through the gnawed midrib.

We can see from equation (12) that the *D. betulae* must cut incision 2 in such a way that during the roll the distance PB_2 is not too small, because the torque

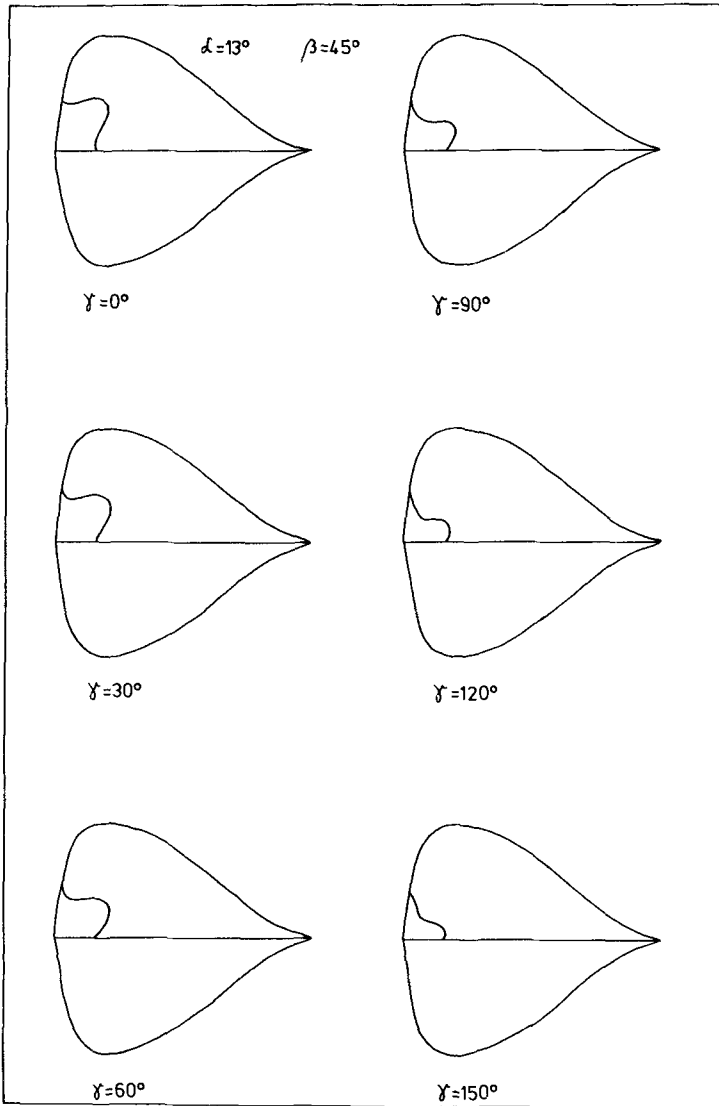


Figure 7. The theoretically calculated curves of the *D. betulae*'s incision 1 for birch (*Betula*) leaf.

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 cut incision 2 so that the edge of the leaf moves quickly from the point P during the twist, so x increases rapidly, M decreases rapidly, and the part of leaf half 2 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.

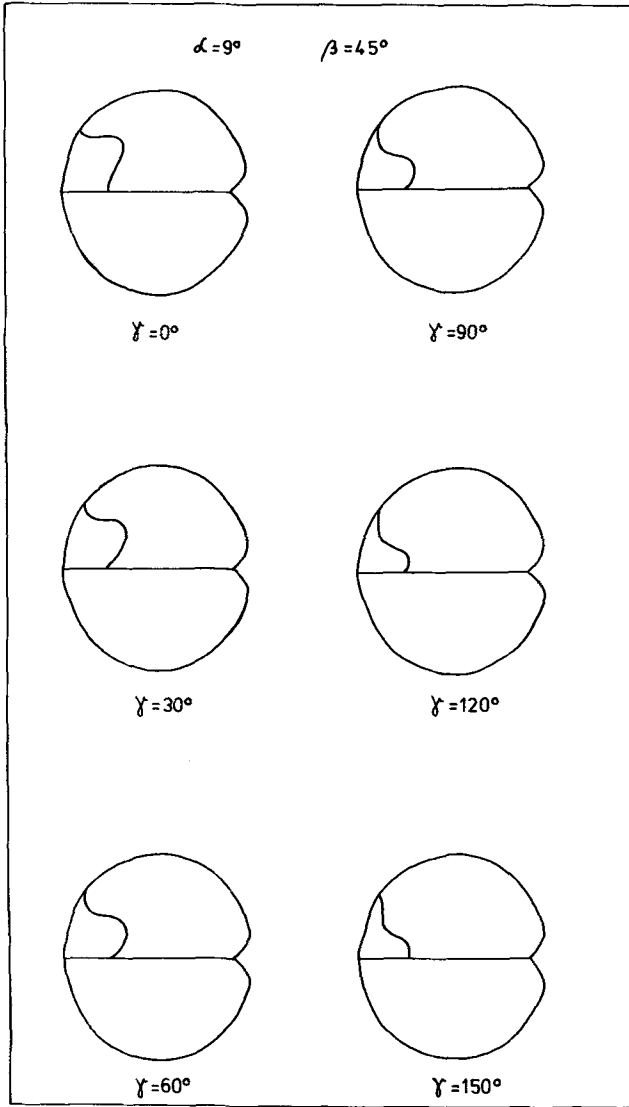


Figure 8. The theoretically calculated curves of the *D. betulae*'s incision 1 for alder (*Alnus*) leaf.

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. We see from equation (12) 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 . Therefore the *D. 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 of the leaf cone.

Since the leaf cone nourishes the grubs, it is very important to have enough leaf mass in it; the birch leaf roller 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 (the angles δ_r and δ_R in Fig. 9). If these angles differ very much from each other during the twist, then the last leaf layer will be suddenly 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.

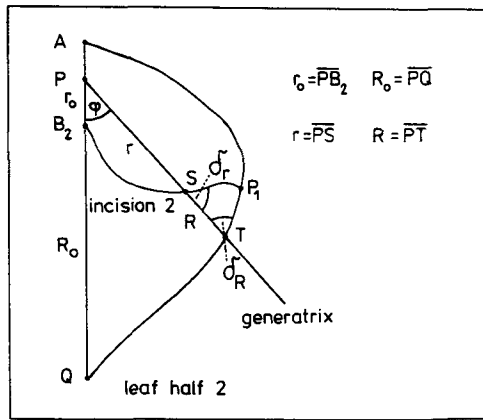


Figure 9. For the theoretical calculation of incision 2 of the *D. betulae*.

Referring to Fig. 9, assign polar coordinates with origin at P , and angles measured from the midrib AQ of the leaf. The curve of the border $R(\phi)$ is given. We want to determine the curve $r(\phi)$ (incision 2), starting at the point B_2 , for which $\delta_r = \delta_R \equiv \delta$ for every ϕ . We can write, on the basis of Fig. 9:

$$\tan \delta_r = r \frac{d\phi}{dr}, \tag{13}$$

$$\tan \delta_R = -R \frac{d\phi}{dR}, \tag{14}$$

$$\delta_r = \delta_R \equiv \delta. \tag{15}$$

We get from these:

$$\frac{r(\phi)}{r'(\phi)} = -\frac{R(\phi)}{R'(\phi)} \quad \text{or} \quad \int \frac{dr}{r} = -\int \frac{R'(\phi)}{R(\phi)} d\phi. \tag{16}$$

From equation (16) we obtain $r = c/R$, but $r = r_0$ for $R = R_0$, therefore $c = R_0 r_0$. So the theoretical curve of incision 2 according to the above twist method is the following:

$$r(\phi) = \frac{R_0 r_0}{R(\phi)} = \frac{\overline{PQ} \cdot \overline{PB}_2}{R(\phi)}. \quad (17)$$

In Figs 10 and 11 the curve $r(\phi)$ is plotted as a function of R_0, r_0 for the birch (*Betula*) and alder (*Alnus*) leaf respectively. The small perforation of the leaf border is not important in the twist of the leaf, because the teeth of the leaf edge are negligible compared with the whole leaf lamina; the perforation of the leaf edge can have little influence on the torque during the twist.

In Fig. 10 it can be seen that the marked theoretical curves are very similar to the curve P_1C of incision 2 of the *D. betulae* for the birch leaf (see Fig. 2); but in Fig. 11 we see that for the alder leaf the theoretical curves differ significantly from the real incision 2. There is a little difference between the marked theoretical curves of Fig. 10 and the real incision 2. The marked theoretical curves have not the arc CB_2 (see Fig. 2). The beetle uses the 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 the 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.

Since the mathematical description whose result is equation (17) took only the biophysics of the rolling into consideration during the calculations, equation (17) can describe only the double-S shaped arc P_1C of incision 2. In this respect the equation (17) can be viewed as correct.

5. Conclusions. The shape of the *D. betulae*'s incisions is independent of the leaf size and the leaf shape. Previously, an exact biomathematical description of these patterns which could explain the biophysical, bionical reason of the shape of the incisions did not exist. In this work two mathematical expressions are given for the description of the patterns.

Equation (11) for incision 1 does not depend on the whole leaf shape, it depends only on parameters $y(x_0)$ and $y'(x_0)$ among the parameters of the leaf shape. This is only a weak dependence on the kind of leaf, so the theoretical incision 1 is almost independent of the leaf shape. For some values of the parameters in equation (11) the theoretical incision 1 agrees well with incision 1 of the birch leaf roller.

Equation (17) for incision 2 depends on the leaf shape. For some values of the parameters in equation (17) and for the shape of birch (*Betula*) leaf the

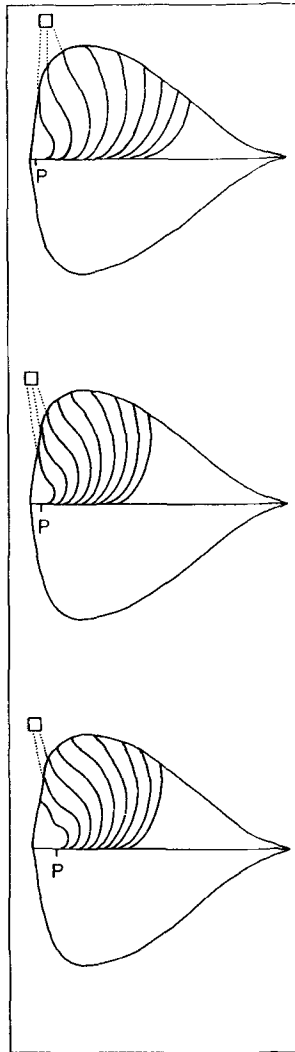


Figure 10. The theoretically calculated curves of the birch leaf roller's incision 2 for birch (*Betula*) leaf. The curves marked with □ agree well with the real incision 2.

theoretical incision 2 agrees well with the real one. For other leaf shapes equation (17) issues such theoretical curves which differ from the real incision 2. The reason for this result is that only one shape of the incisions was fixed genetically during the evolution in the species *D. betulae*; namely, that shape which belongs to the most frequently rolled leaf—the birch leaf.

In sum, the presented equations describe well the incisions of the birch leaf roller; and the biophysical, bionical reasons of these equations can be justified too. The values of parameters of the presented equations, in which the theoretical patterns agree with the real incisions, may be determined by the

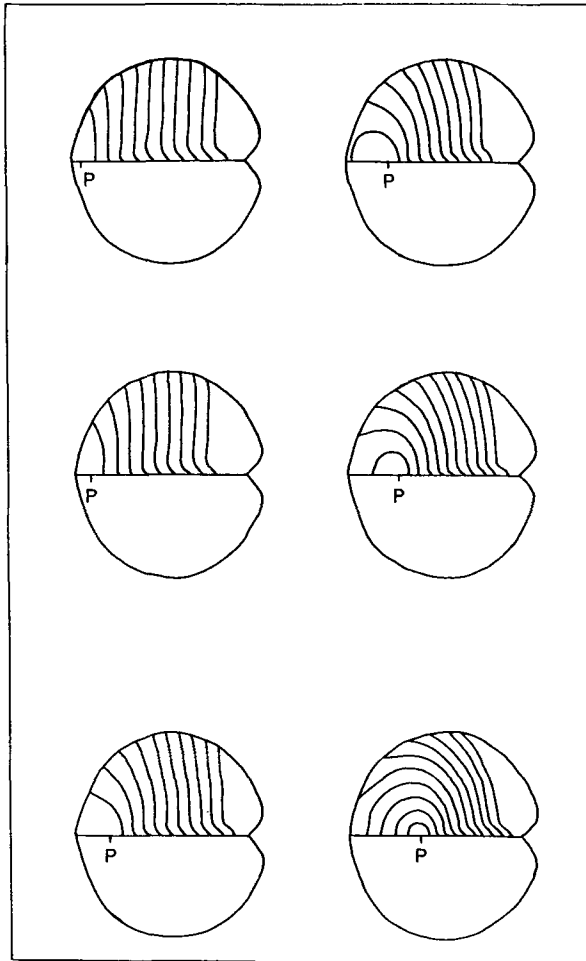


Figure 11. The theoretically calculated curves of the birch leaf roller's incision 2 for alder (*Alnus*).

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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