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A CONTRIBUTION TO THE KNOWLEDGE OF BIOLOGY AND HARMFULNESS OF *DEPORAUS BETULAE* (L.) (COLEOPTERA, ATTELABIDAE)

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Abstract

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The paper deals with the occurrence, development and harmfulness of *Deporaus betulae* (L.). The majority of field studies was carried out at Training Forest Enterprise (TFE) Masaryk Forest in Křtiny (District Brno-venkov) in 2010 and 2011. In addition to this, the species was studied in detail also in a laboratory. It occurred mostly on *Betula pendula* and *Carpinus betulus*. Rarely, the species was found on *Alnus glutinosa* and *Corylus avellana* and only sporadically on *Fagus sylvatica*, *Quercus petraea*, *Tilia cordata* and *T. platyphyllos*. In the studied area, larvae and pupae hibernate. Beetles occur on trees from the end of April to the beginning of July, sporadically later. Females lay on average 2.5 (in the laboratory 4.4) eggs into rolls on *B. pendula*, on *C. betulus* 2.2 eggs. During two months, they damage on average 5.3 cm^2 leaves creating 14 rolls and laying 35 eggs into the rolls. Larvae consume only 1.7 cm^2 leaf blade. The development of the species takes three to four months from egg laying to the departure of larvae into soil. On leaves of *B. pendula* of an average area of 14.2 cm^2, females roll up the same area (about 11.2 cm^2) as on leaves of *C. betulus* of an area of 21.7 cm^2. Into the rolls, they lay on average the same number of eggs. The average number of eggs in rolls increases with the increased area of *B. pendula* leaf blade. Trees partly compensate for the reduction of assimilatory area also by the growth of the area of neighbouring undamaged leaves (on average by 12.7 %).

Deporaus betulae, Attelabidae, host plants, occurrence, creation of rolls, laying eggs, development, harmfulness[1]

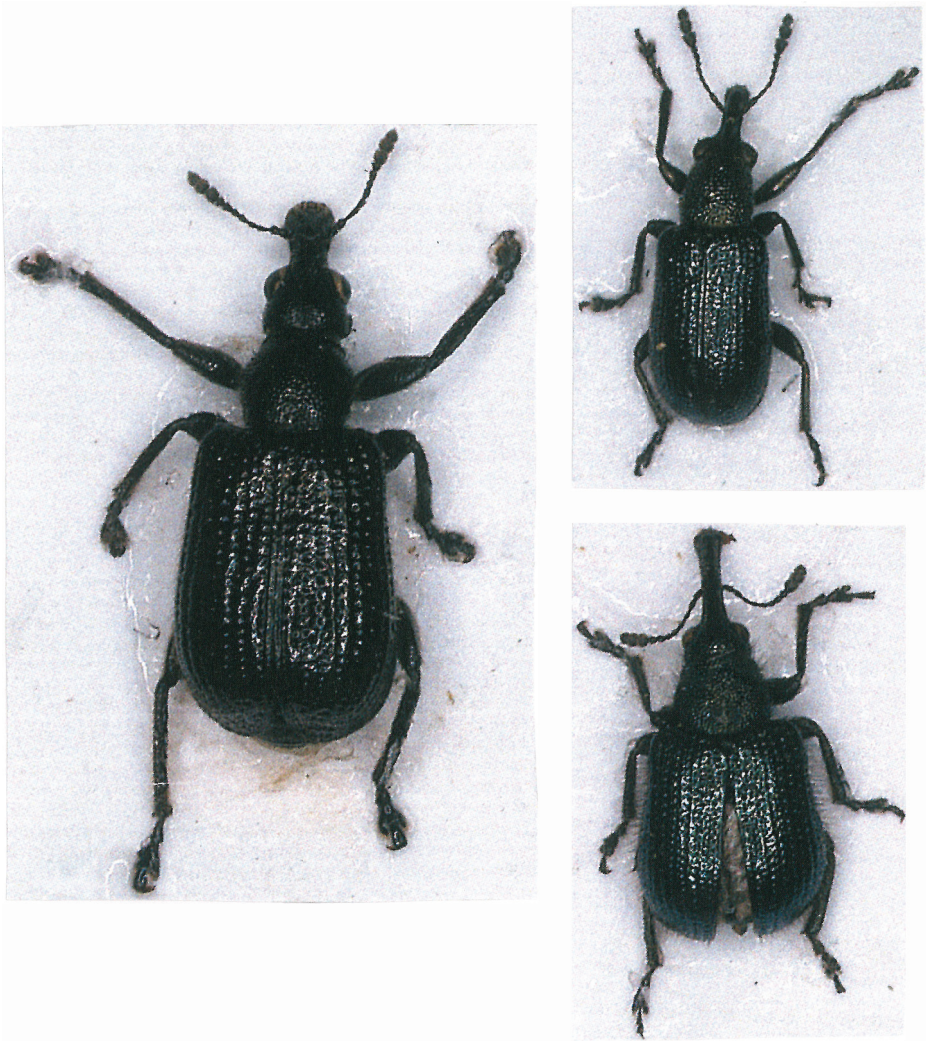
Birch leaf-roller (*Deporaus betulae* /L./) is a representative of the species- not very extensive but biologically exceedingly interesting family of leaf-rolling weevils (Attelabidae) (Curculionoidea). The majority of species of this family is characterized by the intensely developed instinct of mother care of offspring. In the course of reproduction, females make species-specific (or genus-specific) leaf rolls or develop in young shoots or fruits. At the same time, they generally disturb conducting tissues. As a consequence, plant organs or their parts gradually wilt and die back. They lay eggs into wilting tissues of plant organs or on the leaf surface into leaf bends, sporadically into leaf rolls of other species of leaf-rolling weevils. Larvae feed on dying tissues in plant organs prepared in this way. These remain joined with the plant during the growing season and sooner or later they fall to the soil surface where they rot. They pupate in the place of their development or in the soil layer. The species are characterized by univoltine or bivoltine development.

The family of Attelabidae is created by representatives of three subfamilies (Rhynchitinae, Apoderinae and Attelabinae), which are sometimes considered as separate families. On the area of the Czech Republic, the family is represented by

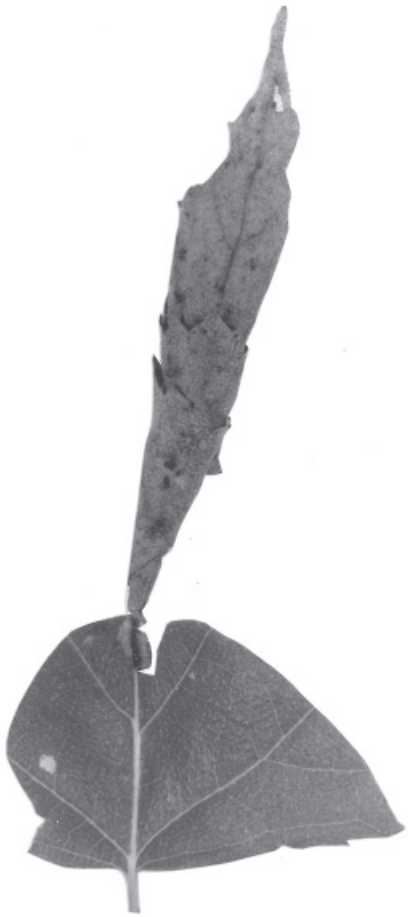
1 The paper was prepared at the Faculty of Forestry and Wood Technology, Mendel University in Brno within the MSM 6215648902 research project.

about 32 species. Morphologically, they are near beetles of the family Curculionidae. Therefore, particularly in the past, *D. betulae* was ranked among the family, namely into its species-richest subfamily Rhynchitinae (Formánek, 1911; Kuhnt, 1913; Reitter, 1916; Schaufuss, 1916; Escherich, 1923; Scheerpelz & Winkler, 1930; Dosse, 1954; Francke-Grosmann, 1974; Lohse, 1981; Horváth, 1989 etc.). Particularly recently, many authors include *D. betulae* into a separate family Rhynchitidae (Nüsslin & Rhumbler, 1922; Sawada, 1993; Hamilton, 1994; Gharadjedaghi, 1997; Shevnin, 2007; Alonso-Zarazaga, 2008; Nazarenko & Petrenko, 2008; Legalov, 2009, 2011 etc.). The systematic belonging of *D. betulae* to the family Attelabidae mention Schenkling (1903), Ter-Minasjan (1965), Mamaev *et al.* (1976), Sawada & Lee (1986), Neuvonen *et al.* (1988), Sakurai (1990), May (1993), Benz & Zuber (1993), Abbazzi (1995), Morris (1995), Opanasenko & Legalov (1996), Roper (2008), Fowles (2009), Mazur (2011), Park *et al.* (2012) etc. Thus, it is evident, that the entomological system of beetles from the family Curculionidae has not been stabilized so far.

The family Attelabidae includes important pests in agriculture, fruit growing and viticulture. *D. betulae* (Fig. 1) belongs together with *Apoderus coryli* (L.), *Attelabus nitens* (Scop.), *Byctiscus populi* (L.) and *B. betulae* (L.) to forestry remarkable but economically little important species. Females of *D. betulae* notch bilaterally leaf blades and roll the apical part of the blade (hanging on the central leaf vein) into longitudinal funnel-shaped rolls (Figs. 2 to 4). Longitudinal leaf rolls of cigarette-shape from whole leaf blades are made by *B. populi* and *B. betulae*. Both species do not cut the blade but locally damage (through punctures) leaf petioles or end parts of shoots. Leaves are unilaterally crosswise cut (including a central vein) by *A. coryli* the end part being rolled up into a cross roll. *A. nitens* cut leaves from both sides up to the central vein and rolls up the apical part of the leaf blade transversely (the leaf main vein is in the cross axis of the roll).



1: *Frequent species of Attelabidae on Betula pendula in the Brno region: Deporaus betulae (L.) (left), Caenorhinus aeneovirens (Marsh.) (right down), C. germanicus (Herbst) (right above). Photo J. Beránek (Brno).*



2: *A roll of D. betulae on a leaf of B. pendula (top view). Bílovice n. Svitavou, 17 July 2010.*

3: *A roll of D. betulae on a leaf of B. pendula (bottom view). Bílovice n. Svitavou, 17 July 2010.*

Deporaus betulae belongs to our most abundant species of leaf-rolling weevils. This paper provides results of the study of its occurrence, making rolls, development and harmfulness. The majority of examinations was carried out in 2010 and 2011 at TFE Masaryk Forest in Křtiny (District Brno-venkov).

Geographical distribution

Deporaus betulae is a broadly distributed species occurring in the boreal and subboreal zones of Eurasia (Legalov, 2009, 2011). According to Mazur (2011), its distribution reaches from the Atlantic to the Pacific. The centre of its occurrence is in Europe (Reitter, 1916; Schaufuss, 1916; Francke-Grosmann, 1974 etc.). It belongs to common species in the British Isles (e.g. Roper, 2008; Edwards & Hodge, 2009; Fowles, 2009) and in Fenoscandinavia where it often reaches behind the Arctic Circle (Fridén, 1971; Andersen & Fjellberg, 1975; Neuvonen *et al*., 1988; Saikkonen *et al*., 1996; Riihimäki *et al*., 2003; Crutsinger *et al*., 2008; Kozlov *et al*., 2012 etc.). Its natural range reaches Turkey and in Asia Mongolia and northern and eastern China. It is often mentioned from the European part of the former USSR (Ter-Minasjan, 1965; Malozemov, 1969; Mamaev *et al*., 1976; Opanasenko & Legalov, 1996; Nazarenko & Petrenko, 2008 etc.). The species was detected in the Far East (Legalov & Shevnin, 2007) and in Japan (Kôno, 1930; Sawada, 1993). Park *et al*. (2012) mention the species from northern Eurasia, from Hokkaidó (Japan) and Korea. The occurrence of D. *betulae* has not been evidently proved e.g. in Israel (Legalov & Friedman, 2007) and Iran (Legalov *et al*., 2010). In North America, only *D. glastinus* (Le Conte) occurs.

On the area of the CR, *D. betulae* belongs to abundant to very abundant and commonly distributed species. It occurs from lowlands up to mountains namely where its host species grow.

Host plants

Deporaus betulae is a polyphagous species. However, opinions on its species spectrum of host plants differ. Most often, young *Betula* spp. is mentioned (Kuhnt, 1913; Pfeffer *et al*., 1961; Forst *et al*., 1985; Koehler & Schnaider, 1972; Roper, 2008 etc.). According to Edwards & Hodge (2009), it occurs occasionally on hazel and alder, according

4: *An uncompleted roll of D. betulae on a leaf of B. pendula (top view). Bílovice n. Svitavou 17 July 2010.*

to Formánek (1911) and Schaufuss (1916) on hazel, alder and beech. Horváth (1989) mentions preferential damage to birch and rare occurrence on hazel, alder and hornbeam. According to Nüsslin & Rhumbler (1922), Escherich (1923), Salač (1924), Živojinovič (1948), Brauns (1964), Francke-Grosmann (1974) etc., hazel, alder, beech and hornbeam are attacked less then birch. However, some authors (e.g. Reitter, 1916; Ter-Minasjan, 1965 and Mamaev *et al*., 1976) consider alder in addition to birch to be the most often damaged species.

According to Reitter (1916), *Fagus*, *Corylus avellana* L., *Quercus* and *Padus avium* Mill. belong to little visited species. Roubal (1937–1941) found the species on *Betula*, *Alnus*, *Corylus*, *Quercus* and sometimes very abundantly on *Fagus*. Legalov (2009) regards (among others) *Quercus*, *Padus avium*, *Populus* and *Tilia* as occasional hosts. Older data on the occurrence of *D. betulae* on *Castanea sativa* Mill. (Gusev & Rimskij-Korsakov, 1953), *Populus* (Schenkling, 1903), *Quercus and Ulmus* (Prell, 1924), *Populus*, *Tilia* and *Ulmus* (Dosse, 1954), *Acer pseudoplatanus* L. (Kôno, 1930) etc. are rather rare. According to Buck (1952), the beetles are, however, not harmful to *Populus*, *Quercus*, *Ulmus* and *C. sativa*, damages to *P. avium* are minimal.

From the most damaged species (*Betula*) and from leaf rolls (rarely from the appearance of imagoes), names of *D. betulae* in national languages are derived. For example, in Czech, it is named as "zobonoska březová", in Slovak "nosánik brezový", in Polish "zwijacz (tutkarz) brzozowiec", in German e.g. "Trichterwickler" or "(schwarzer) Birkenblattroller", in Russian "trubkovërt berëzovyj (čërnyj)", in Hungarian "nyírfa-levélsodro", in Serbian "brezin cigaraš", in French "cigarier (rhynchite) du bouleau", in Italian "sigaraio della betulla", in Danish "birkenbladruller", in Swedish "björkrullvievel", in Norwegian "björkenbladruller", in Finnish "suppilokärsäkäs" etc.

Biology

The biology of *D. betulae* and mainly its instinct of mother care of progeny are dealt with e.g. by Prell (1924), Kôno (1930), Dichtl (1934), Lengerken (1939), Oxenov (1946), Buck (1952), Rosskothen (1964) etc. The biomathematical description of the wound shape of cut, which can explain its asymmetry, gives Horváth (1988, 1989). Sakurai (1990) deals with the suitability of leaves for rolling up, localization of cut and making rolls by females of *Deporaus* sp. The direction of rolling up the apical part of a leaf blade to the right or to the left (clockwise or anticlockwise) depends on notching leaf blades from their right or left margin. Malozemov (1969) assumes that according to this type, it is possible to specify two biological forms of *D. betulae*. According to Oxenov (1946), however, the same female can produce both right and left rolls. Therefore, the severance of such forms is not suitable.

In recent years, some research workers dealt mainly with the ecology of *D. betulae*. For example, effects of the retrogression stages of the ecosystem development on the biomass of *Betula pubescens* and abundance of *D. betulae* studied Crutsinger *et al.* (2008). Neuvonen *et al.* (1988) and Riihimäki *et al.* (2003) reported on direct and indirect interactions among dominant herbivores (including *D. betulae*) on birch. Saikkonen *et al.* (1995) dealt with the effect of endophytic fungi on relationships between tree species and insect herbivores (among others also *D. betulae* on *B. pubescens*).

Through the histological study of the imago brain of some representatives from the family Attelabidae (genera *Deporaus*, *Rhynchites*, *Attelabus* and *Apoderus*), their affinity was proved (Rossbach, 1961). Determined differences between sexes show evidently relationships to marked instincts of mother care. May (1993) dealt with the description of larvae and the system of superfamily Curculionoidea. For example, Buck (1952) and Morris (1995) dealt with the function of markedly enlarged femurs of rear legs of males.

Economic importance

Beetles *D. betulae* attack mainly young trees, advance growth and thickets or shoots up to a height of man and only rarely lower branches of older trees. During maturation and regeneration feeding, they skeletonise leaves of host trees. This feeding is mostly inconspicuous and nearly unknown so far. Roubal (1937–1941) mentions its allegedly considerable harmfulness on beech. Leaf rolls are remarkable and very noticeable. In case of the pest gradation, nearly every leaf is frequently rolled up at trees of the 1st age class. However, forest damages are not usually important and thus the pest control is not necessary (Francke-Grosmann, 1974). Escherich (1923), Brauns (1964) and Benz & Zuber (1993) consider the species to be rather an interesting than harmful species. In the following year, the damage is compensated for by larger increment and higher antiherbivorous protection (Kozlov *et al.*, 2012). Nevertheless, *D. betulae* is often ranked among pests (Forst *et al.*, 1985; Schwerdtfeger, 1970; Schimitschek, 1955; Živojinovič, 1948; Stalev, 1991 etc.). The decline of damaged trees has not been noted yet.

MATERIAL AND METHODS

The main survey was carried out in 2010 a 2011 at Forest District Bílovice nad Svitavou (TFE Masaryk Forest at Křtiny). The area of interest occurred on the Hádecká planina plateau, Forest Range Resslovka, i.e. in the vicinity of the NE part of Brno. Studied stands 380 A, 380 B and 381 B are situated at an altitude about 400 m, stand 373 D at an altitude 340 m. The average annual temperature of the area amounts to 7.7 °C, average annual precipitation 620 mm and average growing season 160 days. It referred to stands of the 1st age class, which were created by planted commercial species (mainly oak and spruce). The admixture of birch, aspen, hornbeam, hazel and goat willow was abundant. Undesirable species were removed from the stands as necessary. Self-seeding species of young age occurred also outside the studied stands (e.g. along roads, cleared boundary lines, along stand margins etc.)

Partial surveys were also carried out at Forest District Vranov close to city part Brno-Ořešín in 2011 (altitude 400 m) and in the region of Vsetín, cadastre Bystřička (altitude 400 m) and Malá Bystřice (altitude 620 m).

In 2010, field inspections were carried out in month intervals and in 2011, in week intervals, namely for the whole growing season. Imagoes of *D. betulae* were caught by simple collection and sweeping using a sweep net from 10:00 to 15:00. From some study areas, all leaf rolls were taken for laboratory examinations, from other areas only part of the rolls. At marked trees, an increase in the number of rolls and the course of their fall was monitored in week intervals. At two spatially-isolated 7-year birch trees (*B. pendula*) situated on Palacký vrch Hill in Brno-Žabovřesky, newly created leaf rolls were taken for the inspection of laying eggs every week in 2010 and 2011. In the course of field excursions, the occurrence was monitored of rolls on birch and other woody species.

Newly hatched imagoes of *D. betulae* were placed into individual or mass rearings on 10 to 15 cm long leaved terminal parts of shoots of *B. pendula*. Lower ends of shoots were inserted into vessels with water the throat of which was sealed using cotton wool. For the purpose of rearing, glass Drigalski plates of a diameter 15 to 20 cm and height 6 to 8 cm were used. Fresh food was offered to imagoes after three to four days. The damaged area of leaves and the number of leaf rolls including the number of eggs were recorded continuously. The number of defecated frass pellets was noted and their dimensions were determined by means of micrometry. The number

of non-laid eggs was examined at dead females by a microscopic dissection.

Attention was paid to the preimaginal development of *D. betulae* in rolls obtained in nature and in the laboratory. Belonging to particular instars was determined by micrometry according to the width of cranium. Rolls with full-grown larvae (taken from trees in the first half of July) were placed into pots with soil, covered with monofilament fabric and left outdoor. In the period of the start of autumn frosts, the hibernating stage of the pest was determined.

Rolls taken in nature and rolls obtained in the laboratory were analysed separately. Following parameters were measured: dimensions of rolls, dimensions and the area of a rolled up and non-rolled up part of the leaf blade. The content of every roll was examined by micrometry (e.g. the number and size of eggs and the number and size of larvae of particular instars). Leaf area damaged by larvae was determined.

RESULTS AND DISCUSSION

Host species

According to literature, it is evident that main host species of *D. betulae* are various species of *Betula* spp., above all *B. pendula* Roth. and *B. pubescens* Ehrh. According to Escherich (1923), it can also damage *B. nana* L. and according to Buck (1952) also *B. humilis* Schrank. *B. nana* is a North American species, which is cultivated in Europe for example in arboreta, *B. humilis* is a Eurasian (in the CR extinct) species. *Alnus* spp., *Corylus avellana* L., *Fagus sylvatica* L. (including *F. orientalis* Lipsky) and *Carpinus betulus* L. are often mentioned host species.

In the Brno region, rolls of *D. betulae* were mostly found on *B. pendula* and often on *C. betulus*. It occurred rather rarely on *Alnus glutinosa* Gaertn., *C. avellana* and sporadically on *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., *Tilia cordata* Mill. and *T. platyphyllos* Scop. However, in the region of Žďár (e.g. Forest District Polnička – Forest Management Administration of Dr. R. Kinský), the species was ordinarily found in 1995 to 1998 on 3 to 15-year *A. glutinosa*. However, on abundantly interspersed *A. incana* Moench., rolls were not found. Results of field studies show that *A. glutinosa* but not exactly *A. incana* is a trophicly suitable species. This statement is confirmed by Buck (1952), which found experimentally that beetles did not damage leaves of *A. incana* and died.

Host plants of *D. betulae* are only those species, which are damaged by the beetles both by maturation feeding and making leaf rolls. Based on literature findings and our research, it is possible to conclude that in the Central-European area, the pest can develop successfully in open air on *Betula pendula*, *B. pubescens*, *Carpinus betulus*, *Alnus glutinosa*, *Fagus sylvatica*, *Corylus avellana*, *Tilia cordata* and *T. platyphyllos* (the hosts are ranked according to decreasing palatability). Finds of imagoes of *D. betulae* on *Quercus* spp. (Reitter, 1916; Roubal, 1937–1941; Javorek, 1947; Schwerdtfeger, 1970; Legalov, 2009 etc.) are rather frequent. *Padus avium* Mill. (which is visited due to glands at the base of leaves), *Castanea sativa* Mill., *Salix* spp., *Populus* spp. etc. (Buck, 1952) are confuse hosts.

WINTERING AND THE OCCURRENCE OF BEETLES

Literature data on wintering stages of *D. betulae* differ. According to Escherich (1923), Salač (1924), Koehler & Schnaider (1972) and Francke-Grosmann (1974), mature larvae pupate already in autumn in earth pupal chambers and beetles hatch as late as the next year in spring. For example Brauns (1964) mentions wintering the pupae and invasion of beetles on newly foliated trees at the end of April and at the beginning of May. However, Buck (1952) found that nearby Stuttgart (Germany), larvae pupated in September and October and under favourable conditions already in August. Imagoes hatched in the same year and pupal chambers were abandoned as late as the second half of April and at the beginning of May in the next year. Also Živojinovič (1948) etc. mention the wintering of imagoes.

Beetles occur on trees from the end of April and at the beginning of May (Benz & Zuber, 1993) or in April and May (Schaufuss, 1916) or in May and June (Koehler & Schnaider, 1972; Majzlan *et al.*, 1999). At the beginning of June, the number of beetles culminates (Buck, 1952). For example, the beetles were found by Andersen & Fjellberg (1975) and Roper (2008) in May. Legalov & Shevnin (2007) mention their occurrence in July. Last beetles can occur in the open even at the end of July and at the beginning of August.

At TFE Masaryk Forest in Křtiny, the pest winters in the stage of larvae and pupae. In the winter season 2010/2011, 40% larvae and 60% pupae occurred there. In the winter season 2011/2012, 80% larvae and 20% pupae hibernated there. No mentions of wintering the larvae occur in available literature. Grown up larvae leave rolls, namely partly before their fall to the ground. At studied localities, the rolls fell from mid-July to the 20th October. In non-fallen rolls on trees, larvae were not found from mid-August. On the soil surface, rolls disintegrate early not providing any protection to larvae and pupae from unfavourable effects of weather and natural enemies (mainly predators).

In rearings, larvae usually move for a certain time on the soil substrate surface before hiding in the soil. Observations carried out from the 1st to the 4th August 2010 showed that larvae could move even on smooth glass walls of rearing vessels. After penetration into soil, they make pupal chambers with smoothed walls at a depth of 1 to 4 (in loose soil even 8) cm.

The chambers are usually oval, 3.5 to 6.0 (on average 5) mm long and 3.5 to 4.5 (on average 4) mm wide. In rearings, larvae often hided in loamy earth than in the humic garden substrate.

If only heterogeneous garden earth was used then the chambers were always localized in places with the higher content of mineral substances.

Beatles *D. betulae* hatch as late as in spring of the next year. Young beetles have temporary (so called provisional) teeth on the outer side of mandibles. After short time, beetles plough by means of mandibles from the pupal chamber out. In the Brno region, beetles were found on trees in 2011 from 25 April and in 2012 from 27 April. At the end of May and at the beginning of June, their numerical occurrence culminated. Last beetles were caught at the beginning of July and rarely as late as 15 July.

Beetles, their feeding and copulation

Males and females of *D. betulae* hatch in the rate of 1:1 occurring on trees at the same time. No significant differences were found in the size of males and females caught in the Brno region. Beetles including beak were 3.5 to 5.5 mm long, at the beak upright position only 2.6 to 4.1 mm. In literature, the length of beetles is given mostly without the beak, namely 2.5 to 4.0 mm. According to Schenkling (1903), the body length including the beak (in natural position) is 5 to 6 mm, according to Schaufuss (1916) 3.8 to 5 mm, according to Salač (1924) 3 to 5 mm and according to Legalov (2009) about 3.7 mm. The length of beetles determined by our measurements corresponds to data of the majority of older and recent authors.

After leaving pupal chambers, imagoes occur on budding and newly unfolded leaves of trees. They colonize particularly young and well-insolated shrubby advance regeneration, young-growth stands and shoots/sprouts up to the height of an adult, rarely lower branch of old trees. They do not occur inside closed older stands and often colonize nutritionally stressed woody species growing on unproductive and exposed sites (Fridén, 1971; Crutsinger *et al*., 2008 etc.).

Beetles are rather able fliers. They have well-developed membranous wings, which are twice longer than tectrices. Under warm sunny days, they often promptly fly. Under cool rainy and windy weather they hide in ground covers. They climb trees only when the air temperature exceeds 15 °C and trees dry and wind quietens. The beetles respond to approaching danger by escape, climb or fall connected with akinesis. The akinesis takes mostly only a moment (maximally 20 seconds). Tiny and inconspicuously coloured beetles in undergrowth easily lurk. Under worsened living conditions (e.g. after felling) the beetles fly over to suitable biotopes in the neighbourhood. Imagoes are heavily positively phototactic to light. Under artificial light, they sometimes wildly fly running against walls of glass rearing vessels.

Imagoes of *D. betulae* occur most often on the adaxial face of leaves, under hot sunny days often also on the abaxial face of leaves. They bite out tiny holes into leaf blades. The holes extend to opposite (as a rule lower) epidermis. Quite sporadically, they also punch the leaves. During feeding, beetles back up and rank particular holes (average dimensions 1 × 0.9 mm) into rows. Feed marks are straight (rarely slightly bent), liny. On *B. pendula* leaves, they are on average 2.0 (maximally 10) mm long and 0.9 mm wide. On leaves of *A. glutinosa*, they are on average 1.8 mm long and 0.8 mm wide. In nature, beetles skeletonise 90% from above and 10% from below. In the laboratory, beetles damaged leaves from both sides in the same way. After food consumption (taking usually only 1 to 5 minutes) rather long period of digestion always follows (taking often even more than 30 minutes).

Beetles are relatively of short age. In nature, they live 1.5 to 2.5 (on average 2) months, in rearings on average only one month. In rearings on *B. pendula*, females produced on average 300 feed-marks of average dimensions 2 × 0.9 mm. In total, they damaged 4.0 to 6.9 (on average 5.3) cm^2 leaf blades. Through the consumption of sappy tissues they obtain nutrients and water. They can also ingest water from dewdrops or rain. Indigested parts of food are defecated in the form of elongated rugged frass pellets. The frass pellets are at first dark green, later black. Females produce on average 1 464 frass pellets of a size 0.41 × 0.11 mm and volume 0.003894 mm^3 (i.e. in total 5.7 mm^3). The leaf area damaged by males is roughly half.

According to Buck (1952), beetles copulate for the first time after 8 days of feeding. According to our findings, beetles feed day and night and copulate first already after 4 to 6 days of feeding. The copulation takes 5 to 40 (on average 20) minutes. In captivity, beetles copulated during day-times and night- times, namely as many as 7 times per day. Repeated copulation with the same male and other males occurs also in nature. However, the only copulation is sufficient for the fertilization of the whole supply of eggs. In the course of copulation, females often ingest, move or notch or roll up leaves. Without food, beetles do not copulate and die within a week. Males have markedly thickened femurs of rear legs. However, the function of rear legs is not to skip but mainly gripping as well as defensive functions (Morris, 1995). Males skip rather unwillingly and to short distances only. Males often fight a battle for females and specialized rear legs serve as arms. For starting a fight copulation is not necessary. Only the presence of a female and two males on the same leave is sufficient (Buck, 1952).

Notching a leaf blade

During 5 to 7 days of maturation feeding, first eggs mature in ovaries of females. Then, fertilized females start to make leaf rolls and lay eggs. For the purpose of rolling up they search for young growing up and newly grown-up subterminal leaves (Tab. I).

I: *Localization of Deporaus betulae rolls on shoots of a 7-year Betula pendula. Bílovice nad Svitavou, 13 July 2010.*

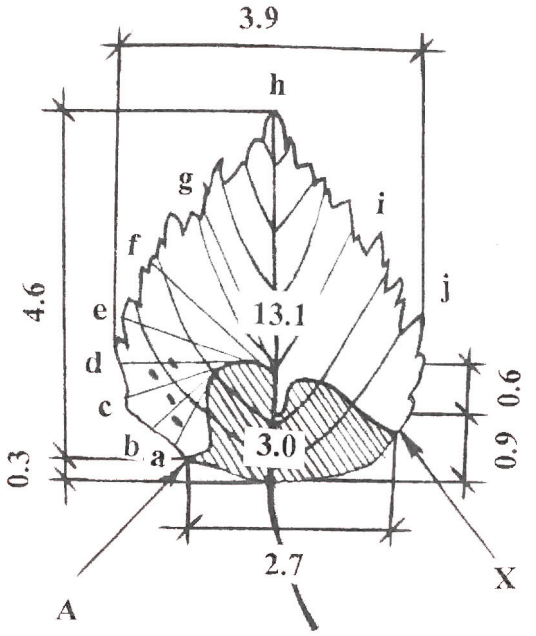
The order of leaves with rolls (from the terminal bud)	Number of rolls	(%)	The order of rolls (from the terminal bud)	Number of rolls		(%) rolls fallen on the soil surface
				total	fallen on the soil surface	
1	4	3.4	1	65	3	4.6
2	6	5.0	2	28	9	32.1
3	15	12.6	3	8	4	50.0
4	23	19.3	4	1	0	0
5	27	22.7	5	1	0	0
6	21	17.6	-	-	-	-
7	12	10.1	-	-	-	-
8	7	5.9	-	-	-	-
9	4	3.4	-	-	-	-
Total	119	100.0	Total	103	16	-
Average	(5.0)	-	Average	(1.5)	-	15.5

Before cuts, they usually carry out several rounds mainly along a main vein. In the course of the rounds, they evaluate the size of leaves and decide on the position of the initial place of cuts (Sakurai, 1990).

On *B. pendula* in the Brno region, cuts began in 51% at the left margin of the leaf blade and in 49% at the right margin of the blade, namely at its base near a petiole. On *C. betulus*, cuts began in 48% at the left margin of the leaf blade and in 52% at the right margin of the blade, namely roughly in the blade half. According to our studies and according to Oxenov (1946), the same female is able to notch leaves from both sides. On leaves (average length 4.6 cm, width 3.9 cm and area 16.1 cm^2), the beginning of a cut was placed at a distance of 0.5 to 2.5 (on average 1.2) cm from the central vein (Fig. 5). In the selected point, a female turns towards the leaf base (i.e. in parallel with the main vein) and begins to cut the leaf blade. During this activity, it occurs almost always on the adaxial face of leaves being orientated (by its longitudinal axis) upright the cut. It moves sideways, namely counterclockwise or clockwise creating the cut of a characteristic geometrical shape in the leaf blade.

The first part of the cut is of the distinct shape of a letter S. On *B. pendula*, the cut begins at the lower margin of the blade and ends at the main vein (about 1/3 of its length). The female does not cut the main vein but moves 1 to 10 mm towards the leaf petiole partly disturbing the leaf blade adjacent the main vein. In this section, it usually damages the central vein (its surface) (Tab. II). This surface feeding is often completed by shallow oblique notches. At the end of this modified section of a main vein the female bites out a distinct oblique notch (sometimes even almost longitudinal). Then, the female continues in biting through the second half of the leaf blade towards the opposite leaf margin. According to the majority of authors, this cut shows the shape of a lying letter S. In reality, the cut shape is considerably variable (mostly corrugated, rarely bow-shaped or irregularly sigmoid). At *B. pendula*, the cut usually ends at a distance of about 2 cm from the central vein and 0.7 cm from the blade base. Both cuts are markedly asymmetrical. To the central vein, they are usually joined at a various height, which significantly strengthens the connection of a future roll with the leaf base.

Contrary to *Bycticscus* spp., mandibles of females of *D. betulae* are toothed on the inner side (adapted for shearing). According to Buck (1952), making a cut takes 18 to 102 minutes. In our rearings, females cut the *B. pendula* leaf blade of an average size about 50 minutes, with one to two breaks about 70 minutes. Biting off one lateral vein takes about 5 minutes and the adjustment of a main vein and its surrounding 10



5: *The schema of a leaf of B. pendula with average dimensions (cm) and area (cm^2) of the not rounded up and rounded up part of a leaf. Bílovice n. Svitavou, 2010.*

II: *Damage to the leaf central vein of B. pendula at making rolls by females D. betulae. Bílovice nad Svitavou, 1 September 2010.*

Damage to the central leaf vein		Number of rolls	(%)	(%) total
Veins ± bitten off	Fallen off rolls	15	17.5	21.0
	Rolls on the tree	3	3.5	
Veins notched (or gnawed) (mm)	1	2	2.3	79.0
	2	5	5.8	
	3	7	8.1	
	4	11	12.8	
	5	13	15.1	
	6	13	15.1	
	7	8	9.3	
	8	6	7.0	
	9	2	2.3	
	10	1	1.2	
Total		86	100.0	100.0

to 25 minutes. After the cut termination, the female usually checks the cut and mainly the central vein adjustment for several minutes. Similarly as at the actual cut, the female moves sideways at checking.

In nature as well as in rearings, leaves with a bitten off central vein and the blade apical part hanging on one or several lateral veins occurred rather sporadically. Females often very frequently cut the leaf blade so that the blade apical part falls to the soil surface. At 7-year *B. pendula* on Palacký vrch Hill in Brno, more than 50% out of the total number of damaged leaves were cut off. These abnormally damaged leaves were also commonly found at other examined localities.

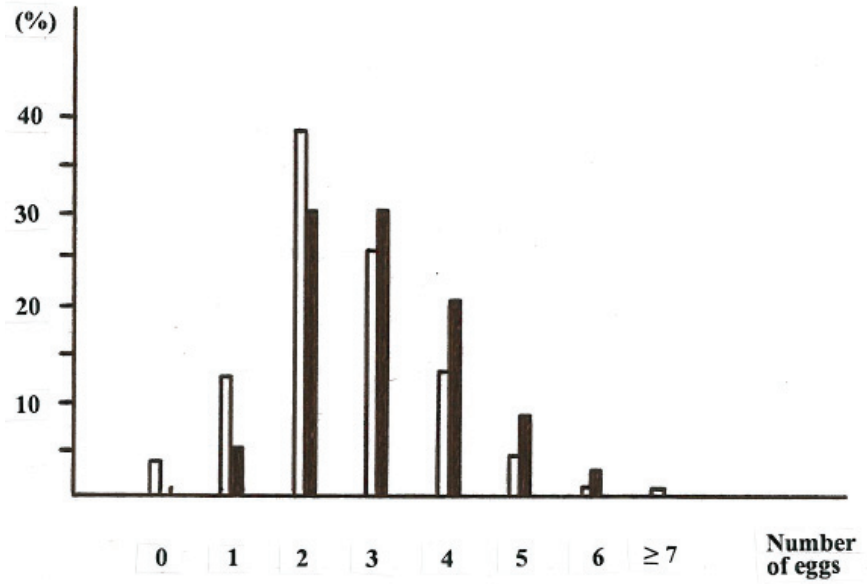
Rolling up leaves and laying eggs

A female of *D. betulae* is not able to roll up a new (fresh) leaf. Therefore, after the cut termination, it leaves temporarily the notched leaf. However, it stays nearby and is at rest, ingests or copulates. After a certain time (in the laboratory after 1 to 2 hours) the female returns to a wilted and slightly droopy apical part of a leaf. It checks the plant tissue elasticity by walking and using its beak. If the leaf blade is sufficiently supple, it begins to roll up it. It settles down on the abaxial face of the leaf blade nearby a place where it began to cut the leaf. It takes parallel position with the margin of the blade lobed projection (its head towards the main vein). By means of legs, beak and abdomen it makes first a minute fold at the leaf margin. The leaf is turned by its abaxial face inward, i.e. according to the natural tendency of rolling up drying leaves. Only sporadically, the leaf is rolled up towards the adaxial face, i.e. by its abaxial face outside. Then, it continues to roll up the first half of the leaf, i.e. the creation of a compact inner roll.

According to Koehler & Schnaider (1972) and Sakurai (1990), females lay eggs before the blade rolling up, according to Buck (1952), Dosse (1954) and Francke-Grosmann (1974) as late as during the blade rolling up. Some researchers (e.g. Klapálek, 1908; Formánek, 1911; Kôno, 1930 and Horváth, 1989) mention that females lay eggs into a ready roll. According to our findings, females lay eggs already during the creation of the inner roll. A female bites out a slotted notch of a length of about 0.8 mm in the lower epidermis before laying eggs. The notch is generally parallel with a side vein. From the notch, a minute pouch of an average length 1.14 mm and width 1.07 mm projects under loose epidermis (towards the leaf base). The female inserts a laid egg into the pouch by its rear legs. In the pouch, eggs are always orientated in parallel with the slot.

Into one leaf, the female lays according to Klapálek (1908) 3 to 4 eggs, according to Formánek (1911) 1 to 4 eggs, according to Escherich (1923) 2 to 4 eggs, according to Kôno (1930) 1 to 3 eggs, according to Dosse (1954) 2 to 5 eggs and according to Buck (1952) 1 to 6 (in the laboratory as many as 10) eggs. In the region studied by our team, females laid 1 to 7 (in case of the cooperation of two or more females rarely even 13) eggs into one leaf of *B. pendula* (Fig. 6). About in 5% rolls, no egg was laid. In 95%, one egg was placed into pouches (rarely two eggs) and about 5% pouches were empty. The pouches are localized in the inner roll, namely in a lobed projection of the blade rolled up part (5 to 30 mm from its top and at least 3 mm from margins). On average, 94% pouches occur in the free part of the leaf blade and 6% slotted holes with pouches occur below longitudinally bisected lateral veins.

Eggs of *D. betulae* are rounded-cylindrical, slightly tapered at one end. They are on average 0.87 mm long and 0.43 mm wide (Figs. 7 and 8). Newly laid eggs are yellow-green, soft, smooth, glossy and slightly sticky. After death, the eggs get yellow to brown, their chorion gets slightly stiff becoming more firm (leathery). Outlines of eggs are rather well visible through a semi-transparent and slightly protuberant epidermis.



6: *Frequency of the occurrence of rolls of D. betulae according to the number of eggs (light columns). Frequency of the occurrence of eggs according to the number of eggs in rolls (dark columns). In 340 rolls, there were 864 eggs, i.e. on average 2.5 eggs in one roll. The region of Brno and Vsetín, 2011.*

After laying eggs and completing a rather compact inner roll, female roll up also the second half of the leaf blade into a somewhat looser outer roll. Thus, a longitudinal funnel-shaped (rarely fusiform) roll originates, which is attached (at the top) to the non-rolled up basal part of the leaf blade by means of a specifically modified central vein. Females usually reinforce the roll by one (in 76%) or two punctures (in 9%) (according to Buck, 1952 even three punctures). Punctures are created by holes, which affect at least two peripheral layers of rolls. They are rather rolled back than bitten out into the leaf blade. Rather large part of rolls is without punctures (about 15%). It refers often to unfinished defect rolls.

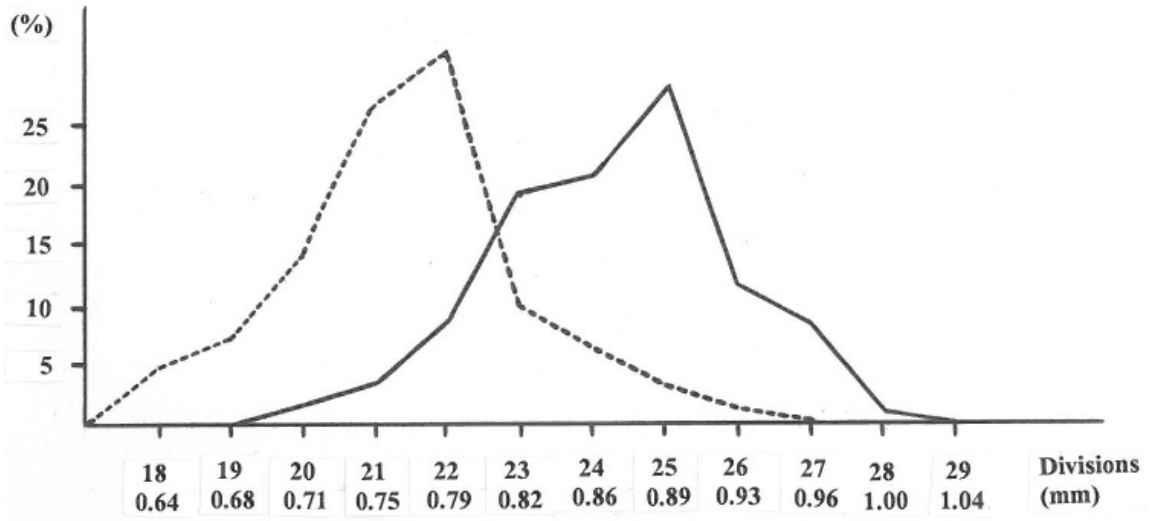
The orifice of rolls remains mostly open. Only less than 10% rolls on *B. pendula* are closed by a turned down (or coiled or rumpled) leaf tip. Closed rolls on other woody species (e.g. at hazel or other birch species) are even more scarce or are missing at all (Buck, 1952; Francke-Grosmann, 1974). Rolling up the leaves takes one to two hours (according to Horváth, 1989 30 to 60 minutes, according to Buck, 1952 at least 84 minutes). Females can interrupt the reeling and later continue again. Even two females can participate in reeling so that the work can be accelerated. Also males copulating with females even in the course of reeling are often present. Males sometimes imitate reeling movements of females but in reality, they never help to females in reeling. The rolls are made mainly during the day but even at night the reeling is not interrupted. The work is interrupted only in the period of large dew or during intense rain or wind.

During May till the first half of July, females make on average 14 (in the laboratory 6) rolls and lay on average 35 (in the laboratory 25) eggs. In leaf rolls on *B. pendula*, on average 2.5 eggs occurred and on *C. betulus* 2.2 eggs. Under laboratory conditions, eggs in ovaries mature faster and making rolls is more difficult. Therefore, in rolls obtained in rearings on *B. pendula*, on average 4.6 (at the most 9) eggs were laid. In ovaries of dead females, there were on average five non-laid eggs. The birth rate of *D. betulae* is the same as the birth rate of *Bycticscus populi* (L.) on *Populus tremula* L. (Urban, 2011).

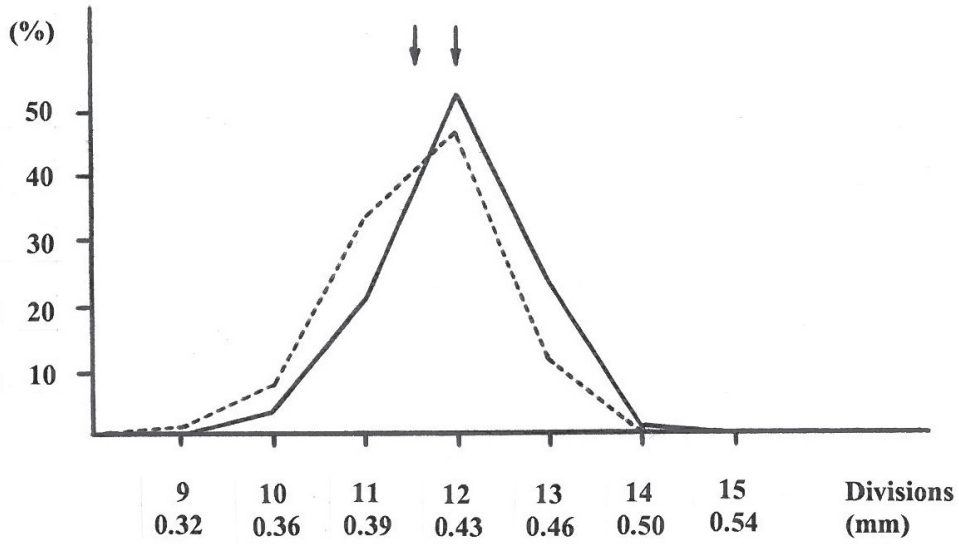
While the not rolled up basal part of the leaf blade remains green till the end of the growing season, rolls gradually get dry and brown from the periphery. In the Brno region in 2011, rolls on *B. pendula* started to brown as early as the 5th May, i.e. about a week after their making. Until the end of May, 53% rolls get brown, until the end of June 73% rolls and to mid-July 88% rolls. However, inner rolls with eggs and larvae *D. betulae* remain green for a long time. In the half of length, rolls are crated by 6 to 11 (on average 8.5) layers of the leaf blade eggs being laid into the 2nd to the 5th layer. Rain precipitation and dew contribute to preserve suitable moisture of tissues of the inner roll. From the beginning of July, rolls start to fall off and till about the 20th October all rolls are already fallen. The fall of rolls is accelerated by windy and rainy weather. Undamaged leaves begin to get yellow usually as late as the second half of October. They begin to fall as late as the first half of November, i.e. two months later than rolls.

Preimaginal development

In the Brno region in 2010, vital eggs of *D. betulae* occurred from the beginning of May till the end July (in 2011 from the end of April to mid-July). From newly laid eggs larvae of the 1st instar hatch after 2 to 3 weeks (in the laboratory after 9 to 12 days). Larvae consume first egg envelopes. Then, they bite out a longitudinal corridor of a length of 5 to 9 mm,



7: *The length of vital eggs of D. betulae (solid line) and dead eggs (dash line) (1 division = 0.0357 mm). Vital eggs were on average 0.87 mm long, dead eggs 0.77 mm. In total, 340 vital eggs and 168 dead eggs were examined. The region of Brno and Vsetín, 2011.*



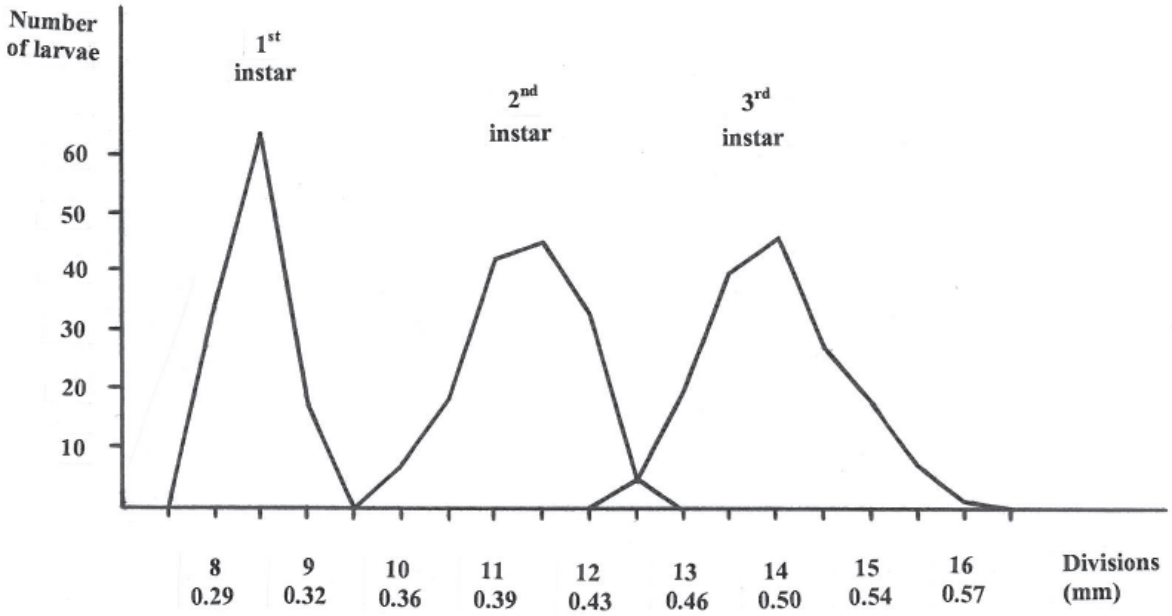
8: *The width of vital eggs of D. betulae (solid line) and dead eggs (dash line) (1 division = 0.0357 mm). Vital eggs were on average 0.43 mm wide, dead eggs 0.41 mm. In total, 340 vital eggs and 168 dead eggs were examined. The region of Brno and Vsetín, 2011.*

width 1 to 2 mm and area about 0.1 cm^2 from the place of hatching in the leaf parenchyma. During their feeding, larvae secrete funicular dark frass pellets which grow black early. The frass pellets are on average 0.2 mm long and 0.036 mm wide. After three weeks of feeding, egg larvae moult first inside leaves. Owing to the lengthily period of egg laying, larvae occurred at studied localities for a period of two months (from 10 May till 10 July).

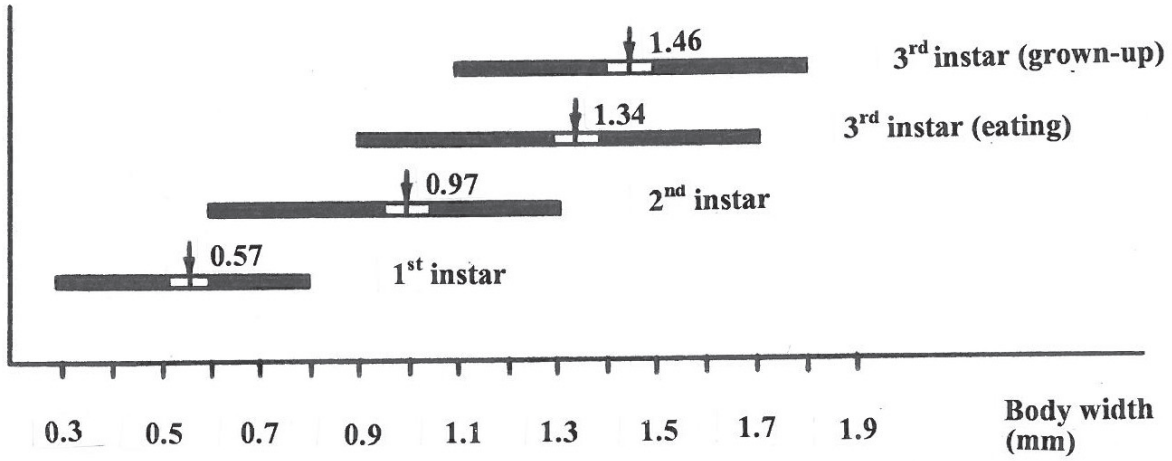
Larvae of the 2nd instar consume first exuviae. Then, they continue in feeding mines, later they irregularly punch the leaf. Larvae of this instar damage on average 0.4 cm^2 leaf blades. They produce funicular slightly strangulated frass pellets of an average length of 0.4 mm and width 0.05 mm. At examined localities, they occurred from the beginning of June to mid-July. After three weeks, larvae moult in places of feeding for the second time.

Also larvae of the 3rd instar consume exuviae first. Then, they eat up very irregularly the inner roll. They damage on average 1.2 cm^2 and produce quantities of funicular frass pellets of an average length of 0.2 (most 2.5) mm and width 0.07 mm. At examined localities, these larvae occurred in rolls on trees from 20 June to the end of August or until the beginning of September. Larvae of all three instars damage on average 1.7 cm^2 leaves *B. pendula*, i.e. 3.1 times less than beetles. The width of a head and the length and width of larvae of particular instars are depicted in Figs. 9 to 11.

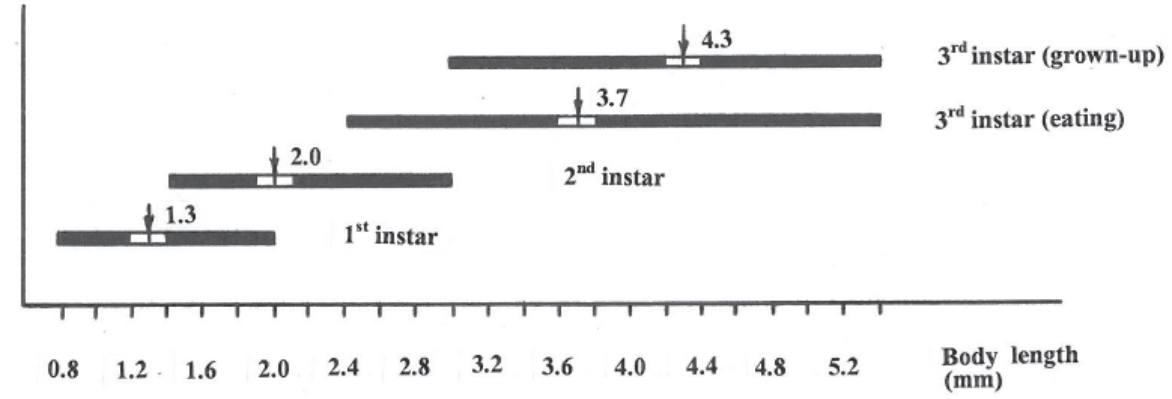
Thus, it is possible to say that vital eggs and eating larvae *D. betulae* occurred in the Brno region in rolls from May to August. Grown-up larvae of the



9: *The width of the head of larvae of the 1st to the 3rd instar of D. betulae (1 division =0.0357 mm). In total, 115 larvae of the 1st instar, 148 larvae of the 2nd instar and 161 larvae of the 3rd instar were measured. Bílovice n. Svitavou, 2010, 2011.*



10: *The length of the body of larvae of the 1st to the 3rd instar of D. betulae was measured, namely 115 larvae of the 1st instar, 148 larvae of the 2nd instar, 82 eating larvae of the 3rd instar and 79 grown up larvae of the 3rd instar. Bílovice n. Svitavou, 2010, 2011.*



11: *The width of the body of larvae of the 1st to the 3rd instar of D. betulae was measured, namely 115 larvae of the 1st instar, 148 larvae of the 2nd instar, 82 eating larvae of the 3rd instar and 79 grown up larvae of the 3rd instar. Bílovice n. Svitavou, 2010, 2011.*

last instar left rolls on trees (or rolls fallen on the soil surface) in August and September. They hid in surface soil layers where they made pupal chambers. Their development from egg laying to the departure of larvae to the ground took three to four months. Part of the population changed into pupae by the autumn, part overwintered in the stage of larvae (see Chapter "Wintering and the occurrence of beetles").

Mortality

In rolls on *B. pendula*, the bulk of the *D. betulae* population dies (Tab. III). The first dead eggs begin to occur in rolls already at the end of May. These can be differentiated from vital eggs according to their orange-yellow to rachel colouring. The proportion of dead eggs reached 70.8% at the end of June and in July 2011 (on *C. betulus* only 8%). Unlike width, the length of dead eggs considerably decreased (Figs. 7 and 8, Tab. IV). Dead eggs keep their basic shape and striking colouring also in the moist environment for a period of at least eight months. The size of vital eggs does not change during their embryonal development. At the end of July, the total mortality of the population increased to 93%. On this enormous mortality eggs participated in 75%, larvae of the 1st instar 10%, larvae of the 2nd instar 5% and larvae of the 3rd instar 3%. Eggs died probably mainly due to the effect of extremely high summer temperatures. About 8% of the population was killed by larvae of Neuroptera, about 8% larvae of Cecidomyiidae and

III: *The number and percentage of living and dead eggs and larvae of particular instars of D. betulae in leaf rolls on B. pendula and in soil. The region of Brno and Vsetín*, 2011.*

Date	Locality	Number of rolls	Number of living /dead					
			Eggs	Larvae of the 1st instar	Larvae of the 2nd instar	Larvae of the 3rd instar (eating)	Larvae of the 3rd instar (grown up)	Total
8. 5.	Bílovice n. Sv.	58	119/0	-	-	-	-	119/0
18. 5.	Bílovice n. Sv.	32	59/0	5/0	-	-	-	64/0
21. 5.	Ořešín	49	44/8	55/2	5/0	-	-	104/10
1. 6.	Bílovice n. Sv.	34	67/17	6/0	2/0	-	-	75/17
12. 6.*	Bystřička*	17	15/18	10/0	-	-	-	25/18
12. 6.*	Malá Bystřice*	12	16/1	7/0	-	-	-	23/1
15. 6.	Bílovice n. Sv.	40	59/44	9/1	3/2	-	-	71/47
22. 6.	Bílovice n. Sv.	28	3/57	8/9	2/0	2/0	-	15/66
25. 6.	Ořešín	30	2/68	6/13	6/0	1/0	-	15/81
29. 6.	Bílovice n. Sv.	30	9/48	9/0	1/0	1/0	-	20/48
13. 7.	Bílovice n. Sv.	13	1/25	0/2	5/2	2/0	-	8/29
30. 7.	Ořešín	30	0/45	0/6	1/3	0/2	3/0	4/56
	Total	373	394/331	115/33	25/7	6/2	3/0	543/373
	(%)	-	43.0/36.1	12.6/3.6	2.7/0.8	0.7/0.2	0.3/0	59.3/40.7
	(%)	-	79.1	16.2	3.5	0.9	0.3	100.0

IV: *The number and average size of living and dead eggs of D. betulae in rolls of leaves of B. pendula. The region of Brno and Vsetín*, 2011.*

Date	Number of examined eggs		Average length/width of eggs (mm)	
	living	dead	living	dead
8. 5.	108	-	0.87/0.43	-
18. 5.	52	-	0.87/0.43	-
21. 5.	40	4	0.88/0.43	0.87/0.43
1. 6.	55	10	0.84/0.41	0.80/0.41
12. 6.*	13	5	0.87/0.42	0.80/0.37
12. 6.*	16	0	0.93/0.45	-
15. 6.	51	35	0.86/0.42	0.81/0.42
22. 6.	3	40	0.81/0.42	0.75/0.41
25. 6.	1	53	0.79/0.41	0.75/0.41
29. 6.	8	32	0.83/0.43	0.75/0.41
13. 7.	1	15	0.71/0.39	0.76/0.43
Total	348	194	0.87/0.43	0.77/0.41

about 2% caterpillars of *Anacampsis populella* (Clerck) (Gelechiidae). Cocoons of larvae of Braconidae were found sporadically in the rolls.

Skuhravá (2005) reported on the occurrence of larvae of *Leptodiplosis* sp. (Cecidomyiidae) in rolls of *D. betulae*. From eggs, imagoes were brought up of *Ophineurus signatus* Ratz. (Nikolskaja & Trjapicyn, 1978) and *Trichogramma dendrolimi* Matsum. (Trichogrammatidae) (Polaszek, 2010). We have not obtained any findings on the occurrence of egg parasitoids.

Further characteristics of rolls

Basic metric data on leaves of *B. pendula* and *C. betulus* damaged by females of *D. betulae* are given in Tabs. V and VI. The length of basal (non-rolled up) part of the leaf blade was measured always upright (width in parallel) with the main leaf vein. The length of the apical (rolled up) part of the leaf blade was measured always in parallel (width always upright) to the main vein. The total length of damaged leaves is equal to the width of the non-rolled up part of the leaf blade on the main vein including the length of the rolled up part of the blade on the main vein. The

V: *Average dimensions and the area of not rolled up part of leaves of B. pendula (in the last line C. betulus) with rolls of D. betulae. The region of Brno and Vsetín*, 2011.*

Date	Number of rolls	Not rolled up part of the leaf blade		
		length/width (mm)	width on the main vein (mm)	area/area of the blade "half" with eggs (cm^2)
8. 5.	60	21.7/14.2	5.5	1.9/1.0
18. 5.	35	20.6/15.3	7.4	1.8/0.9
21. 5.	50	25.8/17.4	7.7	2.6/1.4
1. 6.	35	27.2/17.0	8.5	3.0/1.5
12. 6.*	19	18.4/14.9	6.4	1.5/0.8
12. 6.*	13	23.5/14.6	5.8	2.1/1.2
15. 6.	40	33.0/17.8	9.6	4.0/2.0
22. 6.	30	26.8/15.5	6.6	2.7/1.4
25. 6.	30	36.3/19.7	8.7	5.4/2.4
29. 6.	30	34.6/19.2	8.1	4.7/2.3
13. 7.	17	29.8/16.3	7.4	3.3/1.6
Total (*Betula*)	359	27.0/16.6	7.5	3.0/1.5
29. 6. (*Carpinus*)	24	39.3/36.3	29.0	9.7/5.4

VI: *Average dimensions of the blade rolled up part and whole leaves B. pendula (in the last line C. betulus) with rolls of D. betulae. The region of Brno and Vsetín*, 2011.*

Date	Rolled up part of the leaf blade			Damaged leaf- total	
	length/width (mm)	length on the main vain (mm)	area/area of the blade "half" with eggs (cm^2)	length/width (mm)	area (cm^2)
8. 5.	47.0/39.6	41.3	9.5/4.9	46.8/39.6	11.4
18. 5.	46.2/37.6	39.7	8.6/4.3	47.1/37.6	10.4
21. 5.	52.0/41.4	45.8	10.3/5.1	53.5/41.4	12.9
1. 6.	54.1/42.6	47.8	11.2/5.4	56.3/42.6	14.2
12. 6.*	42.5/33.2	39.8	7.0/3.4	46.2/33.2	8.5
12. 6.*	52.2/39.6	46.5	10.7/5.2	52.3/39.6	12.8
15. 6.	61.2/47.0	52.1	14.4/7.1	61.7/47.0	18.4
22. 6.	56.5/43.4	49.2	12.4/6.2	55.8/43.4	15.1
25. 6.	60.6/47.1	52.4	14.5/7.6	61.1/47.1	19.9
29. 6.	58.6/46.6	51.1	13.2/6.9	59.2/46.6	17.9
13. 7.	56.8/42.8	49.2	11.9/6.2	56.6/42.8	15.5
Total (*Betula*)	53.2/42.1	46.5	11.2/5.7	54.0/42.1	14.2
29. 6. (*Carpinus*)	58.6/38.9	50.1	12.0/5.6	79.1/38.9	21.7

VII: *Average dimensions of leaf rolls, average number of eggs in rolls and the average area of leaves of B. pendula (in the last line C. betulus) damaged by imagoes D. betulae. The region of Brno and Vsetín*, 2011.*

Date	Length/width of rolls (mm)	Number of eggs	Area of the leaf blade damaged by imagoes (mm²)			
			not rolled up part of the leaf blade	rolled up part of the leaf blade		total
				"half" with eggs	"half" without eggs	
8. 5.	39.1/5.1	2.1	1.2	3.5	0.8	5.5
18. 5.	39.3/5.0	2.0	1.2	4.0	1.3	6.5
21. 5.	44.8/5.3	2.3	1.9	3.7	1.1	6.7
1. 6.	45.3/4.9	2.7	1.8	3.5	1.3	6.6
12. 6.*	36.8/4.2	2.5	2.2	2.5	1.3	6.0
12. 6.*	45.5/5.1	2.0	1.5	1.8	1.4	4.7
15. 6.	51.8/5.7	3.0	4.0	7.3	3.0	14.3
22. 6.	48.4/5.6	2.9	0.9	3.4	1.1	5.4
25. 6.	50.9/6.1	3.2	2.5	3.4	1.8	7.7
29. 6.	50.1/6.0	2.3	2.7	4.4	2.3	9.4
13. 7.	44.0/4.8	2.8	3.7	3.6	2.0	9.3
Total (*Betula*)	45.0/5.3	2.5	2.1	3.9	1.5	7.5
29. 6. (*Carpinus*)	48.6/5.4	2.2	5.7	1.9	1.2	8.8

total width of damaged leaves is equal to the width of the rolled up part of the blade (Fig. 5).

Tabs. V and VI show that on *B. pendula*, leaves of an average area of 14.2 cm² were damaged. From this total area on average 3.0 cm² (21.1%) blade were not rolled up. On average 11.2 cm² (78.9%) leaf blade were included into rolls. On *C. betulus*, leaves of an average area of 21.7 cm² were damaged. From this area, on average 9.7 cm² (44.7%) blade was not rolled up. On average 12.0 cm² (55.3%) blade was included into rolls. Thus, it is evident that leaves of *C. betulus* were 1.5 times larger compared to *B. pendula*. It is of interest that the area of the blade rolled up part at both species was roughly of the same size (11.2 or 12.0 cm²). It is because cuts on leaves of birch are placed roughly in the basal third of the leaf blade (i.e. near the leaf petiole) whereas on leaves of hornbeam, the cuts are roughly placed in the blade half (i.e. far from the leaf petiole). The mentioned average area of the blade rolled up part evidently corresponds to the physical efficiency of females. Into rolls on both tree species, roughly the same number of eggs was laid (2.5 or 2.2) (Tab. VII). Rolls on birch and hornbeam create favourable living conditions (particularly enough suitable food and protection) for on average the same number of *D. betulae* offspring.

As it is already emphasized above, a cut, which separates the apical (rolled up) part of the leaf blade from the basal part, is markedly asymmetric. Females notch the leaf blade from the right or left margin. The first part of the cut is always of the shape of a regular standing letter S, the second half shows usually the shape of a twirl (serpentine). Eggs are laid into the blade lobed projection, which originated making a cut of the letter S shape. The total cut is always carried out in such a way that the main vein divides geometrically the blade basal part area (and the area of the blade apical part) to two equal parts (Tabs. V and VI).

In breaks (intervals) during making the rolls (or in a period before or after rolling up a leaf) imagoes skeletonise leaves from an adaxial face. At all inspections on *B. pendula*, the "half" of the blade rolled up with eggs was most damaged by feeding (average area 3.9 mm²). The basal (non-rolled up) part of the leaf blade was substantially less damaged (on average 2.1 mm²). The "half" of the blade rolled up part without eggs was damaged least (on average 1.5 mm²) (Tab. VII). Thus, it is evident that females do not interrupt their maturation feeding even during the blade rolling up. They damage the leaf blade in the inner roll, i.e. in places where they stay at laying eggs and at time-demanding rolling up blades.

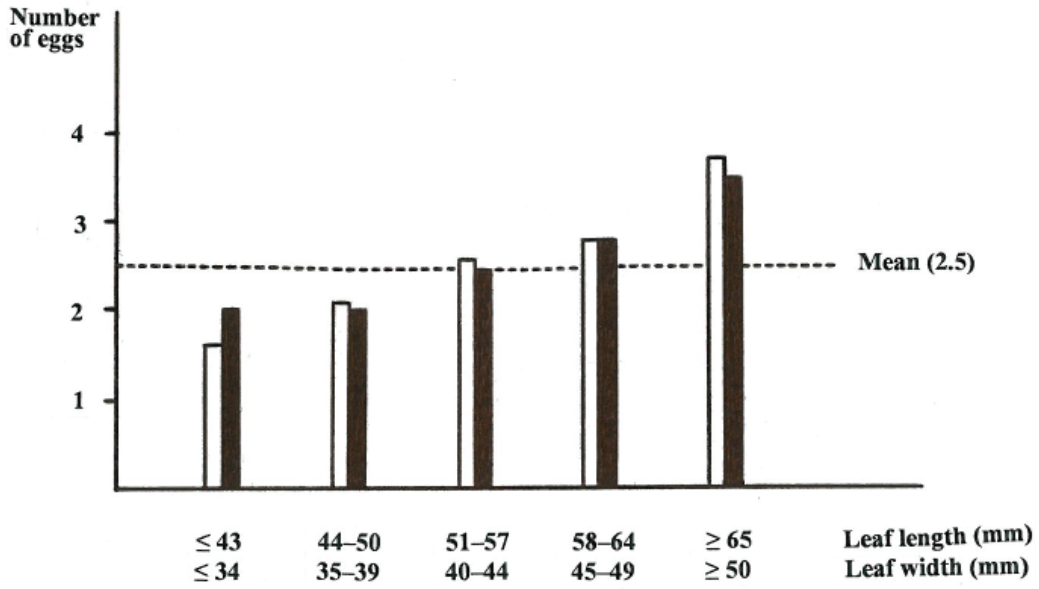
According to Sakurai (1990), females of the genus *Deporaus* sp. relate the number of laid eggs to the size of the blade rolled up area. On the other hand, Buck (1952) concludes that the size of leaves has no effect on the number of laid eggs. Nevertheless, the author admits that there are certain differences among particular host species. For example, he found on average 2.1 eggs in rolls of leaves of *Fagus sylvatica*, in rolls of *B. pendula* 2.8 (in the laboratory 4.4) eggs. In rolls of leaves of *B. pendula* in the Brno and Vsetín regions, we found on average 2.5 (in the laboratory 4.6) eggs. In rolls of *C. betulus* leaves, there were on average 2.2 eggs, i.e. roughly the same number as on birch. At other five host species, rolls of *D. betulae* occurred only rarely and, therefore, data on the number of laid eggs have virtually no information capability. Buck's supposition (1952) on

VIII: *Average number of eggs of D. betulae in rolls of leaves of B. pendula (depending on the area of the blade rolled up and not rolled up part). The region of Brno and Vsetín, 8 May to 13 July 2011.*

Number	Area of the blade not rolled up part (cm²)	Number of rolls /average number of eggs	Average area of the blade rolled up part (cm²)	Number	Area of the blade rolled up part (cm²)	Number of rolls /average number of eggs	Average area of the blade not rolled up part (cm²)
1	≤ 1.0	39/2.0	7.7	1	≤ 8.0	78/2.0	1.6
2	1.1–2.0	108/2.2	9.3	2	8.1–11.0	117/2.2	2.1
3	2.1–3.0	89/2.5	10.9	3	11.1–14.0	76/2.6	3.4
4	3.1–4.0	40/2.6	13.4	4	14.1–17.0	41/3.4	5.2
5	≥ 4.1	64/3.4	15.7	5	≥ 17.1	28/4.0	6.4
Total		340/2.5	11.2	Total		340/2.5	3.0

IX: *Average number of eggs of D. betulae in rolls of leaves on B. pendula (depending on the total area of leaves). The percentage proportion of the blade rolled up part and the blade area damaged by the feeding of imagoes. The region of Brno and Vsetín, 8 May to 13 July 2011.*

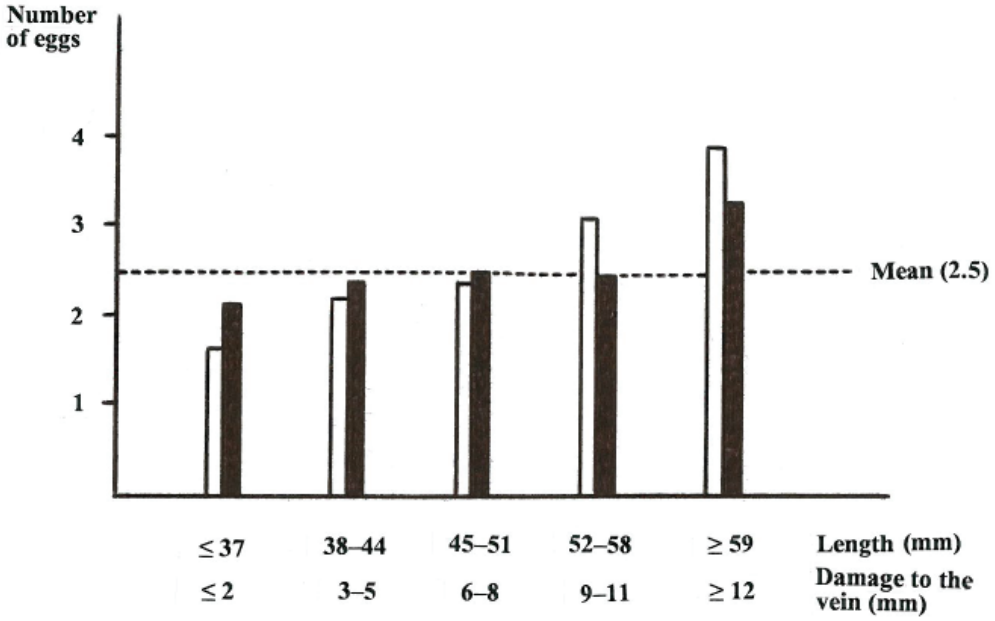
Number	Total area of leaves with rolls (cm²)	Number of rolls / average number of eggs	Average erea of leaves with rolls (cm²)	% of rolled up area /average damage caused by imagoes (mm²)
1	≤ 10.0	87/1.9	8.3	82.6/5.3
2	10.1–13.0	88/2.3	11.5	83.7/6.2
3	13.1–16.0	65/2.4	14.4	80.6/8.6
4	16.1–19.0	43/3.1	17.3	78.3/7.3
5	≥ 19.1	57/3.6	25.0	73.6/11.8
Total		340/2.5	14.2	80.4/7.6



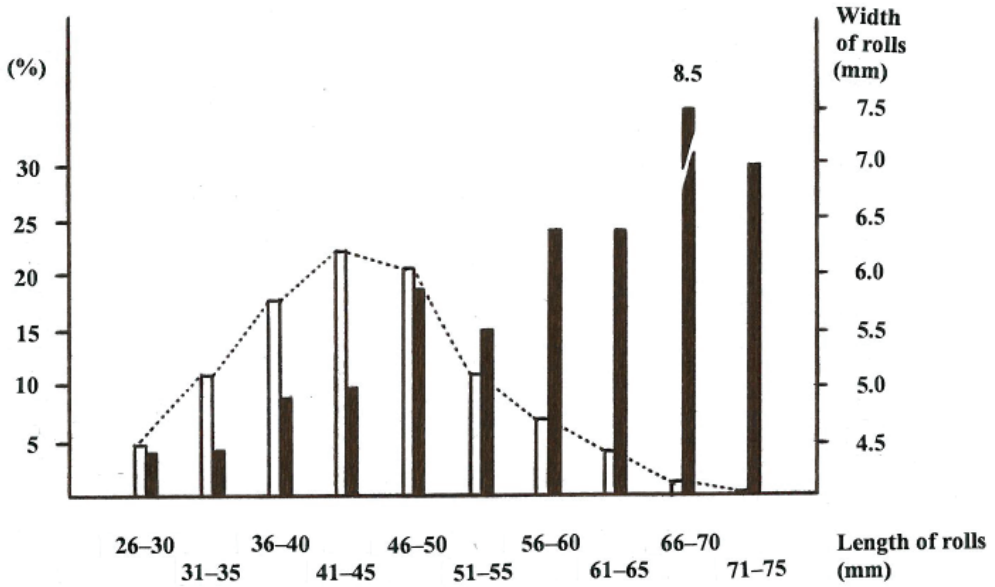
12: *Relationships between the length of leaves of B. pendula and the number of eggs of D. betulae in rolls (light columns). Relationships between the width of leaves and the number of eggs (dark columns). The region of Brno and Vsetín, 2011.*

the different number of eggs in rolls on various host woody species has not been reliably confirmed or disproved so far.

Through the study of leaves of *B. pendula* damaged by *D. betulae* in the Brno and Vsetín regions it has been found that the average number of eggs in rolls significantly increases with the increase of an area of the blade rolled up part, of a non-rolled up part and the total blade area. However, with the increase of the total area of damaged leaves the % of the rolled up area of leaves decreases (Tabs. VIII and IX). There are positive correlations between the total length (and width) of the leaf blade and the average number of eggs (Fig. 12). The average number of eggs in rolls markedly increases (as many as 2.4 times) with the increase of the length of the blade rolled up part and



13: *Relationships between the length of the rolled up part of leaves of B. pendula and the number of eggs of D. betulae in rolls (light columns). Relationships between the length of a section from the leaf base to the place of a cross damage to the central vein and the number of eggs (dark columns). The region of Brno and Vsetín, 2011.*



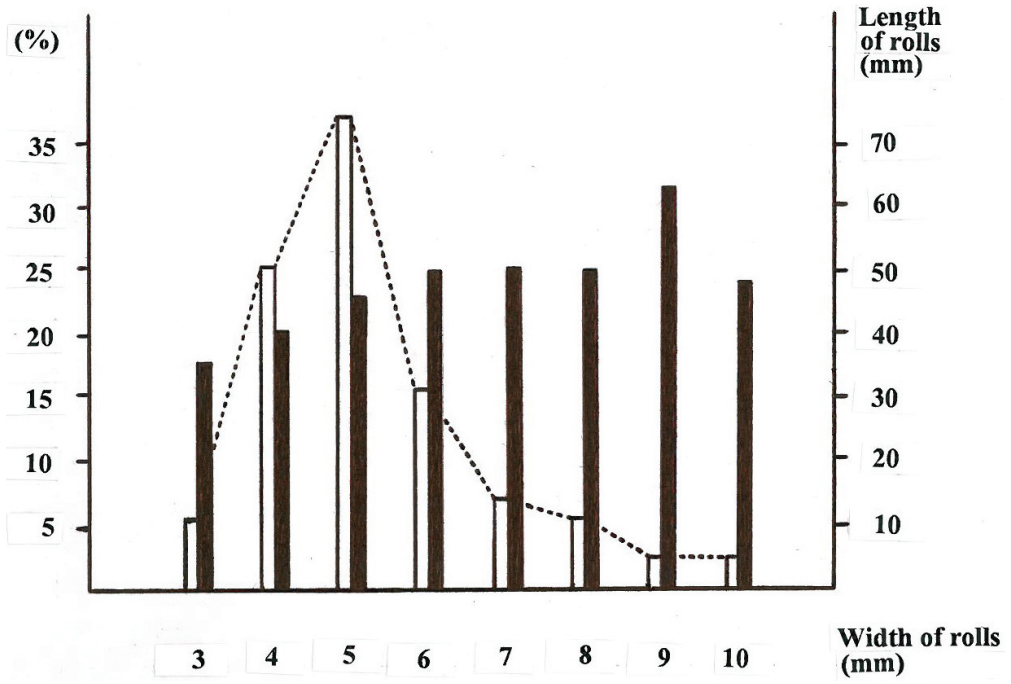
14: *Frequency of the occurrence of rolls D. betulae on leaves of B. pendula according to their length (light columns) (%). The average width of rolls in particular length categories of rolls (dark columns) (mm). In total, 340 rolls of a length of 26 to 73 (on average 45.0) mm and width 3 to 10 (on average 5.3) mm were measured. The region of Brno and Vsetín, 2011.*

the main vein length from its base to the place of its damage (Fig. 13).

D. betulae produces longitudinal (or slightly oblique) rolls from the apical part of leaves generally of the cone shape. Rolls are sometimes closed on an open end. Therefore, the resulting roll can be by several mm shorter than the length of the blade rolled up part. The width of rolls depends not only on the width but also length of rolls (Figs. 14 and 15).

Harmfulness

D. betulae is biologically interesting and a relatively well-studied species from the family of Attelabidae. It is most abundant on *Betula* spp. of the first age class, where it is a regular component of the species-rich consortium of phylophagous insects. Newly hatched beetles fly at the end of April and at the beginning of May on budding and newly flushed host trees. For a period of 1.5 to 2.5 months, they bite out inconspicuous feed marks in leaves. In our



15: *Frequency of the occurrence of rolls of D. betulae on leaves of B. pendula according to their width (light columns) (%). The average length of rolls in particular width categories of rolls (dark columns) (mm). In total, 340 rolls of a length of 26 to 73 (on average 45.0) mm and width 3 to 10 (on average 5.3) mm were measured. The region of Brno and Vsetín, 2011.*

X: *Dimensions of undamaged leaves of B. pendula and the size of leaves damaged by rolls of D. betulae. Bílovice n. Svitavou, 13–17 July 2010.*

Leaves		Blade length (mm)	Blade width (mm)	Blade area (cm²)
Undamaged rolls	under rolls	53.3	44.7	14.1
	above rolls	57.1	46.6	16.0
	average	55.2	45.4	15.0
Damaged rolls (order from terminal buds)	1st	46.7	39.3	12.8
	2nd	45.9	38.2	12.7
	3rd–5th	54.0	41.0	16.8
	average	47.0	39.1	13.1
Difference		8.2	6.3	1.9
(%)		14.9	13.9	12.7

rearings, females lived on average four (males three) weeks damaging on average 5.3 (males 2.7) cm² leaves *B. pendula*. In studied stands, this dispersive damage to leaves by maturation feeding and regeneration feeding was virtually unimportant from the aspect of forestry.

After a week feeding, females begin to make leaf rolls and lay eggs. They shear bilaterally leaves up to the main vein and damage also the main vein surface. Then, they roll up withering apical parts of the leaf blade into noticeable rolls, which hang on main veins. From May to mid- July, a female makes on average 14 rolls and lays on average 35 eggs. Leaf tissues in the roll die during the growing season and in the course of August to October, rolls fall to the ground surface. Females quite sever a rather large number of leaves (10 to 40% out of the total number of successful rolls). Apical parts of leaf blades are not rolled up because immediately after the cut they fall to the ground.

At examined localities, rolls on birch (average area 14.2 cm²) included on average 11.2 cm² (78.9%) leaf blade. The area of the blade basal part amounted to on average only 3.0 cm² (21.1% leaf blade). On leaves of hornbeam (average area 21.7 cm²), on average 12.0 cm² (55.3%) leaf blade were rolled up. The area of the blade basal part was on average 9.7 cm² (44.7% leaf blade) (Tabs. V and VI). Thus, it is evident that *D. betulae* eliminates about 79% of the *B. pendula* blade area from the assimilatory process due to making rolls and 55% of the *C. betulus* blade area. Basal (not rolled up) parts of leaves remain green fulfilling their assimilatory function till the end of the growing season (i.e. until the natural leaf-fall). As for larvae, these are indifferent or rather useful from economic aspects (unlike imagoes). Through biting out inner parts of rolls they damage on average

only 1.7 cm^2 dying or dead blades and thus they somewhat accelerate their decomposition.

During outbreak, as many as 80% leaves were damaged at some 4- to 7-year birch trees in the Brno region. The trees tolerated the damage rather well and through the creation of new leaves at the end of growing shoots they partly compensated for the assimilatory area decrease. Examinations carried out from 13 to 17 July 2010 in Bílovice nad Svitavou proved that trees responded to the loss of the assimilatory apparatus early after damage also by the growth of undamaged neighbouring leaves (as against damaged leaves) on average by 1.9 cm^2 (12.7%) (Tab. X). According to Kozlov *et al.* (2012) the damage becomes evident even in the following year, namely by the higher production of biomass (on average by 13.8%) and by the increase of herbivorous defence (i.e. fall of damage).

In conclusion, it is possible to state that *D. betulae* is not an important physiological pest from the aspect of forestry. It is ranked among remarkable species due to its frequent occurrence, distribution and the creation of complicated and remarkable leaf rolls. Nevertheless, even heavy damage does not endanger the existence of trees. Thus, only their total weakening and decrease of growth become evident. Therefore, no protection was carried out against the pest so far (Escherich, 1923; Živojinovič, 1948; Francke-Grosmann, 1974 etc.). Killing the beetles (or larvae) by insecticides decreasing attack in the next year as well as preventive collection of leaf rolls are recommended quite sporadically in the literature. The rolls have to be removed already in May and June, i.e. before hiding grown up larvae in soil.

SUMMARY

Deporaus betulae (L.) is biologically an interesting and rather well-examined species from the family Attelabidae. The presented paper brings findings concerning its occurrence, development and harmfulness. The majority of examinations were carried out at TFE Masaryk Forest in Křtiny (district Brno-venkov) in 2010 and 2011.

1. The species was most often found on *Betula pendula* and *Carpinus betulus*. It occurred rarely on *Alnus glutinosa* and *Corylus avellana* and sporadically on *Fagus sylvatica*, *Quercus petraea*, *Tilia cordata* and *T. platyphyllos*.
2. A half of its population winters there in the stage of grown up larvae and a half in the stage of pupae.
3. Beetles occur on trees from the end of April to the beginning of July, exceptionally later. They settle particularly trees of the 1st age class. From the adaxial face, they skeletonise leaves biting out in them feed marks of an average length 2 mm and width 0.9 mm. They live on average two months. Females damage on average 5.3 cm^2 (males about half of the area) and defecate on average 1 464 frass pellets of a size 0.41 × 0.11 mm.
4. After four to six days of feeding, the beetles copulate first and fertilized females begin to produce rolls and lay eggs. They cut the leaf blade from the right or left margin. The first part of the cut shows the shape of a standing letter S. The second part of the cut is attached to the main vein by 1 to 10 mm closer to the leaf petiole having usually the shape of a serpentine. The female does not sever the main vein but nibbles its surface. In the place of the connection of the second part of the cut to the main vein, the pest bites out a transverse (oblique) groove up to the vein half. The *B. pendula* leaf blade of an average area is notched within 50 minutes, with breaks after 70 minutes.
5. After one to two hours, the female begins to roll up the wilting apical part of the leaf blade. First, it makes a compact inner roll. During rolling up the leaf blade, the female lays eggs into pouches under the lower epidermis. Into a roll on *B. pendula*, the female lays on average 2.5 (in the laboratory 4.6) eggs, on *C. betulus* 2.2 eggs. After the creation of the inner roll, the female completes rolling up the second half of the leaf blade. It hardens the conical roll at its margin by one or two punctures. It does not mostly close the roll enlarged base. Rolling up the leaf blade takes one to two hours. During May to the first half of July, the female makes on average 14 rolls and lays on average 35 eggs.
6. The development from egg laying to the termination of feeding takes three to four months. Larvae develop through three instars and damage on average only 1.7 cm^2 leaf blade on a roll on *B. pendula*. In rolls at examined localities, as many as 93% population died. Eggs participated in the enormous mortality by 75%. Grown up larvae leave the rolls in August and September. They hide in soil making oval pupal chambers 5 × 4 mm at a depth of 1 to 5 cm.
7. On leaves of *B. pendula* (average area 14.2 cm^2), on average 11.2 cm^2 (78.9%) were rolled up. On leaves of *C. betulus* (average area 21.7 cm^2), on average 12.0 cm^2 (55.3%) were rolled up. At both species, the rolled up blade area was of the same size and the same average number of eggs was laid (2.5 or 2.2 pcs).

8. Females do not interrupt feeding even during rolling up the blade. They damage the leaf blade most in the inner roll where they lay eggs and carry out difficult rolling up.
9. Females lay on average the higher number of eggs into larger leaves.
10. In the Brno region, females damaged as many as 80% leaves on some birch trees. Through one roll, they destroy 79% blade area of *B. pendula* and 55% blade area of *C. betulus*. They damage many leaves (as many as 50% leaves with successful rolls) through the total abscission of the blade apical part. The blade basal part fulfils the assimilatory function until the end of the growing season. Trees respond to the assimilatory area reduction by the growth of the area of neighbouring undamaged leaves on average by 1.9 cm^2 (i.e. by 12.7%). The damage becomes evident only by the physiological weakening of the trees. The economic importance of the pest is negligible.

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