

OCCURRENCE, DEVELOPMENT AND GALL POLYMORPHISM OF *Harmandiola cavernosa* (Rübs.) (Diptera, Cecidomyiidae)

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Abstract

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A gall midge *Harmandiola cavernosa* (Rübs.) is the second most frequent Cecidomyiidae species on *Populus tremula* in the CR. In 2007 and 2008, it occurred very abundantly in Forest District Bílovice nad Svitavou, Training Forest Enterprise Masaryk Forest in Křtiny (former Brno-venkov District). Imagoes occurred there at the end of April and at the beginning of May. Galls grew up as early as at the end of the first week in May. The formation of galls is mainly indicated by larvae of the first instar and partly larvae of the second instar. Larvae of the third instar did not participate in the creation of galls. Mature galls were on average 5.4 mm long, 4.8 mm wide and 4.7 mm high showing an inner chamber of an average length 2.4 mm and width 1.4 mm. Larvae abandoned galls from the end of May until mid-July. On average, 44% larvae completed successfully their development in galls. About 26% larvae were killed by insect parasitoids (mainly *Torymus quercinus* Boh.) and then same proportion of larvae died without any apparent exogenous causes. Insect predators and birds killed 4% larvae on average. It has been found that mortality factors markedly participated in the size, morphological, anatomical and physiognomic differentiation of galls. Gall polymorphism was analysed in detail in the paper. Galls significantly unfavourably affected the size of leaves and thus also photosynthesis.¹

Cecidomyiidae, *Harmandiola cavernosa*, occurrence, localization on leaves, development, natural enemies, gall polymorphism, harmfulness

Gall midges (Cecidomyiidae) rank among the most numerous families of the order Diptera in the CR as well as in the world. There are about 5 700 species of Cecidomyiidae in the world (GAGNÉ, 2004). In the CR, some 485 species are known (SKUHRAVÁ, 1987) and currently 549 species (SKUHRAVÁ, 2006). The majority of species (in the Palearctic region about 76%) is phytophagous (gall-forming or inquiline, gallicolous). Only about 8% are zoophagous (predacious) and mycophagous (SKUHRAVÝ, SKUHRAVÁ, 1998). Larvae of gall-forming species produce a secret from the mouth opening during sucking. The secret contains growth substances inducing the creation of galls on young developing tis-

sues of plants. In contrast to the majority of small, inconspicuous and little-known imagoes, galls of Cecidomyiidae on higher plants are usually conspicuous and species-specific. Therefore, in the past, great number of gall midges was described only according to galls. Modern internationally binding rules of zoological nomenclature require, however classification according to imagoes also in gall-forming species.

In 2007 and 2008, galls of *Harmandiola cavernosa* (RÜBSAAMEN, 1899) were found on leaves of *Populus tremula* L. at many localities in southern Moravia. Its occurrence and cecidogenesis were studied at Forest District Bílovice nad Svitavou, TFE Masa-

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ryk Forest in Křtiny (former Brno-venkov District). The paper deals with results of the field and laboratory research into this gall midge.

Systematic classification

Harmandiola (= *Harmandia*) *cavernosa* ranks among the family Cecidomyiidae, namely into its most rich and most important sub-family Cecidomyiinae. A prominent German expert professor E. H. Rüb-saamen classed it into the genus *Harmandia* Kieffer, 1896. Under this generic name the gall midge was noticed till lately. Previously, however, ROCHEBRUNE (1892) used the name *Harmandia* for members of the phylum of Mollusca. Thus, according to nomenclature principles, SKUHRAVÁ (1997) renamed the genus *Harmandia* to *Harmandiola*. In the past, this species was also rarely named as *Harmandia cristata* (Kieff.) or *Diplosis cavernosa* (Rübs.). Nevertheless, in the majority of national languages, it has not been named yet. Its former Czech name “stopečnatka důlkotvará” (VIMMER, 1931) has not been accepted. In Russian, it is named as “gallica osinovaja dvustorannaja” or “gallica dvustorannaja”.

Distribution

Harmandiola cavernosa is a widely distributed Euro-Siberian species with its centre of occurrence in Central Europe. Its abundance decreases towards south and north (SKUHRÁVÝ, SKUHRÁVÁ and BREWER, 1997). In Europe, this species is often mentioned in various dipterological, zooecidological, zoogeographical and faunistic publications.

According to SKUHRÁVÁ and SKUHRÁVÝ (1960), it occurs in the former Czechoslovakia, Poland, Austria, Hungary, Germany, Netherlands, England, former USSR, Finland, Norway and Sweden. Its galls were found also in Spain (SKUHRÁVÁ, BLASCO-ZUMETA and PUJADE-VILLAR, 2002), France (DARBOUX and HOUARD, 1901; BÉGUINOT, 2006), Luxembourg (LAMBINON, SCHNEIDER and FEITZ, 2001), former Yugoslavia (SIMOVA-TOŠIĆ and VUKOVIĆ, 1999), Lithuania (PAKALNIŠKIS et al., 2000), Latvia (SPUNĢIS and KALNIŅŠ, 2003), Kazakhstan and southern Siberia (SKUHRÁVÝ and SKUHRÁVÁ, 1998) etc. There are few actual data on the occurrence of *H. cavernosa* in regions outside Europe.

SKUHRÁVÝ and SKUHRÁVÁ (1993) records on the frequency of occurrence of Cecidomyiidae in trees in the CR, Slovakia and Austria. The authors examined more than 1200 localities and found 44 species of gall midges in 20 forest tree species. Through a representative study, they found that in trees of Central Europe, *H. cavernosa* was the eighth most numerous species of gall midges. According to VIMMER (1931), *H. cavernosa* occurred in the former Czechoslovakia where aspen grew. The author observed its numerous galls on shrubs of aspen nearby Železný Brod in Bohemia in 1901. In the area of the present CR, E. Bayer collected galls of the species at 115 localities in 1910–1946, E. Baudyš in 1916–1969 and F. Černík in 1925 (SKUHRÁVÁ,

1994b). At other 217 localities, SKUHRÁVÁ (1994b) found *H. cavernosa* in 1957–1982. In the CR, galls of *H. cavernosa* were found at 332 localities, viz. at altitudes from 162 (nearby Neratovice – central Bohemia) to 1070 m (Pláně in the Bohemian Forest).

According to SKUHRÁVÁ (1994b) and SKUHRÁVÝ, SKUHRÁVÁ and BREWER (1997), *H. cavernosa* is most abundant in regions at an altitude from 300 (400) to 600 m. Thus, it refers to a hilly (collinous) species, which penetrates from hilly locations both to lowlands and piedmont (submontane) up to mountain (montane) regions. Within the zoogeographic study of Cecidomyiidae in the CR, SKUHRÁVÁ (1994b) ranked the species among the fifth frequency group (out of six groups), ie among very numerous species. A map and a diagram (Fig. 1) show the horizontal and vertical occurrence of *H. cavernosa* in the CR.

Host species and bionomics

The main and highly preferred host plant of *H. cavernosa* is *Populus tremula* L. (DARBOUX and HOUARD, 1901; KIEFFER, 1913; RÜBSAAMEN and HEDICKE, 1925/1939; VIMMER, 1931; MOESZ, 1938; BARNES, 1951; WAHLGREN, 1951; BAUDYŠ, 1954, 1956; TURČEK, 1956; AMBRUS, 1957; SKUHRÁVÁ and SKUHRÁVÝ, 1960, 1963, 1973, 1974, 1998; SKUHRÁVÁ, 1994a,b, 1998; SKUHRÁVÝ and SKUHRÁVÁ, 1998; MAMAEV, 1969; SKRZYPCZYŃSKA, 1999, 2004; LAMBINON, SCHNEIDER and FEITZ, 2001; PERSSON, 2002; BÉGUINOT, 2006 etc.). It occurs abundantly on *P. tremula* and rarely on “silver” poplars (BUHR, 1965). GUSEV and RIMSKIJ-KORSAKOV (1953) mention rather broad spectrum of host species (*P. tremula*, *P. alba* L., *P. nigra* L., *P. nigra* L. var. *italica* Dur. and *P. laurifolia* Ledeb.). POSTNER (1982) considers *H. cavernosa* to be sporadically abundant species on *P. tremula* and rare on *P. alba* and *P. × canescens* (Ait.) Smith (= *P. alba* × *P. tremula*). Also according to ROSS (1911) and PFEFFER et al. (1954), galls of *H. cavernosa* occur on *P. tremula* and *P. alba*.

According to the minority opinion of AFONIN (2005), the species damages poplars (*Populus* spp.) being, however, able to attack also willows (*Salix* spp.). *P. tremula* is trophicly, topicly and otherwise very attractive species for *H. cavernosa* (TURČEK, 1956). The author relates this fact particularly to the chemistry of aspen and its broad ecological valence and thus also considerable spatial dispersion.

SKUHRÁVÝ et al. (1997) carried out valuable studies of the trophic affinity of gall-forming species of Cecidomyiidae in relation to domestic *P. tremula*, N. American *P. tremuloides* Michx. and their hybrid *P. tremula* × *P. tremuloides*. Out of seven species of Cecidomyiidae, the most abundant was *H. cavernosa*. Its galls were most numerous on *P. tremula*, rare on *P. tremuloides* and very sporadic on their hybrid. Authors also mention that 18 species of gall midges were described on poplars (*Populus* spp.) in the Palearctic region; out of them 17 were cecidogenic. In Europe, the development of 13 species is related to poplars.

The majority of them produce galls on leaves or shoots, one species on leaf petioles and two species are inquiline in galls of other species (SKUHRAVÝ and SKUHRAVÁ, 1998). In the CR, 11 cecidogenic and one inquiline species (SKUHRAVÁ, 1994a,b) were found on *P. tremula* (more rarely *P. alba*). According to frequency, *H. cavernosa* on *P. tremula* is the second most abundant species of Cecidomyiidae in the CR after *Dasineura populeti* (RÜBSAAMEN, 1889; SKUHRAVÝ and SKUHRAVÁ, 1993).

There are few concrete data in literature on the bioeconomics of *H. cavernosa*. Papers concerning the development of *H. cavernosa* and gall-forming polymorphism evidently do not exist.

MATERIAL AND METHODS

Harmandiola cavernosa was studied in Forest District Bílovice nad Svitavou (Training Forest Enterprise Masaryk Forest in Křtiny, former Brno-venkov district) in 2007 and 2008. The forest district occurs in the Moravský kras Protected Landscape Area. Main research was carried out in the Resslervka Forest Range, viz. in well lighted self-seeding shrubby formations (aged 5 to 15 years) of *P. tremula* along cleared boundary lines, roads, power transmission lines and at edges of stands. Stands under investigation occur about 2 km north of Brno, terrain elevation Hády (altitude about 420 m). Mean annual temperature is 7.7 °C, annual precipitation 620 mm and growing season 160 days. Inspections were usually carried out in week intervals, namely throughout the growing season. In 2007 and 2008, 25 samplings at 50 galls and 20 samplings at 25 galls, respectively were carried out. Occasionally, the gall midge was studied at other five localities in southern Moravia.

In the laboratory, the length and width of leaf blades were measured and the leaf blade area was determined using planimetry. The length, width and height of a gall were measured (including the gall height at the adaxial face of leaves). The gall wall thickness (on the adaxial and abaxial side of a leaf) and dimensions (length and width) of the inner chamber were measured using micrometry. The chamber content was evaluated, namely the size and health condition of larvae of *H. cavernosa* and insect parasitoids. The physiognomies of galls including their colour were monitored. Insect parasitoids were reared in the laboratory until the stage of imagoes, which were sent to Dr. P. Janšta (Charles University, Prague) for determination.

RESULTS AND DISCUSSION

The occurrence of imagoes and oviposition

In Forest District Bílovice nad Svitavou, imagoes of *H. cavernosa* occurred at the end of April and at the beginning of May. In temperature and precipitation-favourable years 2007 and 2008, the period of flight of *H. cavernosa* came about during one week. After copulation, females lay eggs on unfolding

leaves of aspen. Aspen buds unevenly and thus, females find leaves usually in the suitable stage of unfolding. At localities under monitoring, aspen trees began to burst into leaf about 25 April and females laid eggs as early as about 28 April. At the beginning of the period of oviposition, leaves of early-flushing aspen reached about ¼ their final size and at the end of oviposition about ½ final sizes. Late-flushing aspen trees were not attacked by *H. cavernosa* at all.

Females lay eggs nearly exclusively on the adaxial side of young fast-unfolding leaves. They place eggs quite sporadically (0.2%) on the abaxial face of leaves. The females lay one to five eggs (Fig. 2). Warm and sunny weather shortens the period of reproduction, on the contrary, cold and rainy weather extends it.

According to SKUHRAVÝ and SKUHRAVÁ (1998), imagoes fly at the beginning of May. Their active flying possibility is rather limited (LINKOWSKI, 2000). They fly only for a short term and short distance. Wind markedly affects spatial distribution of adults (WITHERS and HARRIS, 1997).

P. tremula grows on various places scattered in the landscape. Particular stands can be characterized by the various degree of isolation for the gall midge. The spatial dispersion and the occurrence frequency of actively spreading cecidogenic species (including *H. cavernosa*) living on *P. tremula* in the boreal zone of Sweden is not, however, substantially affected by the isolation of stands (PERSSON, 2002).

Cecidogenesis

Early after hatching, egg larvae settle nearby leaf veins and begin to ingest. During sucking, they let out the secret of salivary glands from their mouth opening. The secret chemically disturbs the nutritive substrate and irritates young leaf tissues. Thin-walled parenchymatous cells of leaves fast enlarge and divide. The larvae penetrate through the upper cuticula into the leaf palisade parenchyma. A narrow input fissure (about 0.8 mm long and 0.2 mm wide) is soon closed behind larvae in the lower part. Galls increase quickly at first at both faces of leaves, later only on the abaxial faces (Figs. 3 and 4).

The period of gall formation is very short. Usually at the end of the first week in May, galls mature. Dimensions of galls virtually do not change during the growing season. The growth of galls is induced of about ¾ by larvae of the first instar, which develop on average four days. Larvae of the second instar participate in only ¼ the creation of galls. Larvae of the third instar appear in galls as late as from mid-May to the end of May (at the most till mid-July). Larvae of this last instar virtually do not affect the size of galls.

In the first two days of sucking, larvae are confined by proliferous gall tissues and, thus, part of larvae is subject to the pressure of surrounding tissues. As early as the beginning of May, a large cavity is created in fast-growing galls. At the end of the first week in May, the chambers (cavities) are on average 2.4 mm long and 1.4 mm wide. Since this time, the size of chambers does not change. In these chambers, lar-

vae of the gall midge or its insect parasitoids develop. Part of chambers is empty because of mortality factors. The galls are always single-chamber and only one larva of *H. cavernosa* develops.

On 31 May 2007, two large dead larvae of *H. cavernosa* (2.3 mm long) were found in a gall of above-average size (length 6 mm, width 5 mm, height 5.2 mm) and a living larva of a parasitoid (size $0.53 \times 0.18 \times 0.11$ mm). This rarity find proves that two larvae of *H. cavernosa* can successfully develop in one chamber under favourable conditions.

Galls and their position on leaves

Galls of *H. cavernosa* are obvious on both sides of leaves. According to DARBOUX and HOUARD (1901), they are hemispherical, slightly elongated, 4 to 5 mm in size. The gall walls are very thick and about one third of their volume rises above the adaxial surface of a leaf blade. BUHR (1965) mentions that galls are longitudinally oval and usually 5 mm in size. They are mostly localized beside leaf veins. Input openings are parallel with veins and surrounded with a liplike wall. SKUHRAVÝ and SKUHRAVÁ (1998) mention that galls have the form of a hemisphere on their lower side and on their upper side (where a slotted opening occurs), they rise above the leaf level. POSTNER (1982) argues that galls are spherical and on the abaxial face of leaves, they rise twice to threefold more than on the adaxial face of leaves.

In the region of Brno in 2007, grown up galls were on average 5.1 mm long, 4.6 mm wide and 4.4 mm high (Tab. I). They rose above the leaf blade on average only 0.75 mm, i.e. 3.5 to 4.5 times less under the leaf blade. In 2008, galls were on average 5.7 mm long, 5.0 mm wide and 5.0 mm high (Tab. II). Above the leaf blade, they rose on average 0.9 mm, i.e. 3.4 to 4.1 times less than under the leaf blade. Dimensions of grown up galls ranged from $1 \times 0.8 \times 0.7$ mm to $8 \times 7.5 \times 7.5$ mm. The mean size of galls slightly increased with the increasing area of leaf blades (Tab. III) or did not nearly change (Tab. IV).

Galls of *H. cavernosa* are green or yellow-green, lightly reddish from above (rarely also unilaterally from below). The gall walls are very thick. On the adaxial face of leaves (close to slits), they are thick on average 1.7 mm. During May–October, this thickness gradually slightly increases (from 1.6 to 1.8 mm). On the abaxial face of leaves, walls of galls are on average always thinner (about 1.3 mm). In the course of May–October, the thickness significantly decreases (from 1.5 to 1.1 mm) (Fig. 5). Galls are similar to galls of a relative species *Harmandiola populi* Rüb. Galls of *H. populi* are, however, localized only on the abaxial face of leaves. They are nearly spherical and substantially minute (diameter about 2.5 mm). The gall walls are exceptionally thin (0.15 to 0.2 mm).

At studied localities, usually only one gall (in 80%) was presented on leaves (at the most five galls). With the increasing area of the leaf blade the mean number of galls on leaves generally decreased (Fig. 6).

In 2007, leaves with galls reached on average a size of 9.2 cm². The area of leaves with one gall amounted to on average 9.4 cm², with two galls 8.7 cm², with three galls 8.6 cm² and with four to five galls 8.1 cm². In 2008, leaves with galls reached on average 10.8 cm². The area of leaves with one gall amounted to on average 11.0 cm², with two galls 9.9 cm² and with three galls 9.6 cm². Data mentioned above prove that galls show significant effects on the growth of leaves and thus also on their assimilation.

The majority of galls (about 87%) are localized in the basal (proximal) third of the leaf blade. About 12% galls are created in the central (medial) third of the blade and about 1% in the apical (distal, peripheral) third of the leaf blade (Fig. 7, Tab. V). With the increasing area of the leaf blade the proportion of galls localized in the basal third significantly decreases and the proportion of galls localized in the central and apical third of the leaf blade increases (Tab. VI).

With negligible exceptions, galls are created in the immediate contact with the leaf venation. A slit on the adaxial face of a gall is only 0.1 to 2 mm from the gall edge (on average 0.76) (Fig. 8). In the immediate vicinity of a gall, veins are usually more or less tumid and slightly arc-bent. It has been found that the absolute majority of galls (about 53%) are placed along lateral veins. Considerable part of galls (about 38%) occurs in axils between main and lateral veins. Close to main veins, only about 9% galls are created. Galls show direct contact with leaf venation only quite sporadically (0.1%) (Tab. V, Fig. 9). With the increasing area of a leaf blade the proportion of galls placed nearby main veins and between main and lateral veins significantly decreases. On the other hand, the proportion of galls placed close to lateral veins evidently increases (Tab. VII). Close to main veins, galls in the basal third of the leaf blade are relatively least numerous creating about 6% galls. In the central third of the leaf blade, there are on average 28.5% galls close to main veins and in the apical third of the blade about 39% galls (Fig. 10). These interesting trends in the localization of galls are undoubtedly related to the dispersion of egg larvae at searching for suitable places for sucking as well as to the considerable importance of venation (particularly the thickness of veins) for cecidogenesis and development of *H. cavernosa*.

The growing up of larvae and abandoning the galls

Larvae of the third instar complete their development in galls at the end of May and in June (Figs. 11 and 12). Grown up larvae are 2.5 to 4 (on average 3.2) mm long, 1.1 to 1.4 (on average 1.2) mm wide and 0.8 to 1 (on average 0.9) mm high. On the ventral side of the first thoracic segment of larvae, there is a characteristic spatula sternalis (RÜBSAAMEN and HEDICKE, 1925–1939). According to SKUHRAVÝ and SKUHRAVÁ (1998), larvae are 4 mm long and orange, according to VIMMER (1931), they are cinnamon.

At first, inconspicuous gall input slots (dimensions 0.8×0.2 mm) increase "liplike" in the second half of May and in June (Tabs. I and II). At the end of the development of larvae, the chambers gradually open. Grown up larvae abandon the galls and fall on the soil surface. They hide in soil and pupate there in spring of the next year. A trophic tissue on walls of open chambers gradually dies and the chambers become brown or even grow black. Abandoned galls persist on leaves (Figs. 13, 14 and 15) and at the end of the growing season they fall together with leaves on the soil surface.

Larvae develop only in spring in the period of leaf unfolding and fast growth of host species. During the growing season, only one generation of *H. cavernosa* develops. In 2007, vital larvae in galls were usually found from 28 April to 20 June (ie for a period of 54 days). In 2008, vital larvae in galls were usually found from 1 May to 30 June (ie for a period of 61 days). A mean period of the development of larvae in galls was, however, substantially shorter (four to seven weeks).

The development of larvae in galls is uneven and the period of leaving the galls is considerably long. In 2007, the first galls abandoned by larvae were found already at the end of May. The majority of larvae abandoned galls in a period from 10 to 20 June. In mid-July, the process of leaving the galls was finished (Tab. VIII). In 2008, the first abandoned galls were found not until mid-June. The majority of larvae abandoned galls in a period between 20 and 30 June and in mid-July, the process of leaving galls was finished. Two living grown-up larvae were found in galls even in the first half of August (Tab. IX). Nevertheless, there is no more detailed explanation for this abnormal occurrence of larvae.

According to BUHR (1965), larvae of *H. cavernosa* occur in galls in May and June. Findings obtained in the region of Brno approach the findings of POSTNER (1982). According to the author, larvae leave galls at the end of May and in June.

Natural enemies

The population density of *H. cavernosa* fluctuates considerably in the course of time. Changes in the abundance are mostly affected by weather as well as by predators during the overwintering of larvae and spring reproduction. Many larvae in galls is significantly reduced by insect parasitoids from the superfamily Chalcidoidea. Many of them die due to endogenous factors and defensive and covering activities of gall tissues. After the death of *H. cavernosa*, the gall ceases to grow because dead larvae of the gall midge (as well as living and dead larvae of parasitoids) are not able to induce the creation of galls. Thus, control factors are the main cause of the size and shape differentiation of galls.

Considerable attention was paid to the health condition of larvae of *H. cavernosa* in galls (as well as to the related gall polymorphism). In 2007, on average 32.5% larvae successfully completed their development in galls (and abandoned them). One third

of larvae (33.3%) died owing to parasitoids (Fig. 16) and less than one third (29.7%) due to defensive activities of plant tissues and endogenous causes. Insect predators killed 1.8% (and birds 2.2%) larvae of *H. cavernosa* (Tab. VIII). In 2008, on average 54.2% larvae abandoned galls. On average 18.7% larvae were killed by parasitoids, 22.2% died without obvious causes, 2.7% larvae were killed by insect predators and 0.9% by birds (Tab. IX).

Eggs of insect parasitoids occurred only in mature galls, namely from the end of the first decade of May until mid-June. During the second and third decades of May, the number of parasitized galls increased culminating at the turn of May and June (Tabs. VIII and IX). The embryonic development in eggs of parasitoids takes place rather slowly and thus, the first larvae of parasitoids appeared in galls not until about 20 May. Egg larvae of parasitoids search for larvae of *H. cavernosa* and settle on their body. After the attack of a parasitoid, larvae of *H. cavernosa* still live for several days. For example, about 10 May 2007, 90% larvae of the midge lived in parasitized galls. About 20 May, 50% *H. cavernosa* survived, about 30 May 25%, about 10 June 20% and about 20 June 10%. Since the end of June, no living larvae of *H. cavernosa* were found in galls with parasitoids.

The occurrence of particular developmental stages of insect parasitoids in galls of *H. cavernosa* is given in Tabs. X–XII. Larvae of parasitoids grow up about 4 weeks after oviposition. In 2007, the first pupae of parasitoids were found on 13 June, the last one on 18 July. Imagoes hatch after the week period of pupae. Imagoes abandon the galls through a circular emergence hole on the adaxial face of a gall (Fig. 17). It is of interest that parasitized galls open only though a small slot opening or the slot opening does not create at all. Imagoes of parasitoids either extend naturally originated slots or gnaw out a small emergence hole quite outside the slot.

Results of analyses of galls and laboratory rearing show that only part of parasitoids pupates and hatches in the same year. In 2007, imagoes of parasitoids emerged from 54.5% parasitized galls. In 14.5% parasitized galls, larvae of parasitoids overwintered. Considerable proportion of parasitoids (about 19.5% larvae, 3% pupae and 8.5% imagoes) died in galls (Tab. X). For example, in October 2007, living larvae of parasitoids occurred in 4% out of the total number of galls and in 11.3% galls, dead larvae of parasitoids. Dead pupae of parasitoids occurred in 2% galls and dead adults in 4.7% galls. Parasitoids flew out from 18.7% all galls (Tab. XII). At monitored localities, *Torymus quercinus* Boh. (family Torymidae) was a highly dominant parasitoid. Imagoes of *Mesopolobus* sp. (family Pteromalidae) and *Eupelmus* sp. (family Eupelmidae), hatched less abundantly from galls.

Gall polymorphism

Galls of *H. cavernosa* are leaf chemomorphoses originating by the chemical action of secretes produced by larvae. The creation of galls is particularly induced by the first instar of larvae and to a smaller

extent also the second instar. The third instar of larvae does not participate in the growth of galls. Inside a gall, there is one chamber where only one larva of *H. cavernosa* develops (with small exceptions). The galls are of characteristic size, form and inner structure. On the gall surface, there is a covering layer (cuticular). Under the layer, there is a very thick parenchymatous layer and a plain sclerenchymatous layer within it. The layer creates a protective case around the inner cavity where the gall-forming insect lives. The cavity is covered with the layer of large thin-wall parenchymatous cells rich in nutrients, which serve for the nutrition of *H. cavernosa*. Galls of normal size and physiognomy are formed when the development of larvae is not disturbed. If the death of a larva occurs the gall ceases to grow. The sooner a larva dies the more the gall differs (as for size, morphology and anatomy) from a gall where the gall midge finished its development.

Basic data on the size of galls with the undisturbed and disturbed development of a gall midge gives Tab. XIII. In 2008, galls were on average 0.5 mm larger than in 2007. Galls with the undisturbed development of larvae of *H. cavernosa* were largest. These galls were on average 5.6 mm long, 5.0 mm wide and 4.9 mm high. Galls with insect parasitoids were on average slightly smaller ($5.5 \times 4.9 \times 4.8$ mm). It follows that parasitoids affect the growth of galls only minimally. It is because they kill the gall-forming species only after the termination of the gall growth. On the other hand, however, the death of larvae owing to the defensive and covering activities of plant tissues (or due to "endogenic" factors) shows significantly negative effects on the growth of galls. Therefore, these galls were on average only 4.9 mm long, 4.5 mm wide and 4.3 mm high. At the death of a larva in the early stage of development, a gall is formed of about 1 mm in size.

Because of "factors of the environment resistance", also the inner structure of galls is modified to a great extent. In 2007, the mean thickness of galls was on average 1.7 mm on the adaxial face and only 1.3 mm (ie 19% less) on the abaxial face. The abaxial wall of galls gradually became thinner from June (when it reached its maximum 1.5 mm) to October (when it reached its minimum 1.1 mm) (Fig. 5). Galls with living and abandoned larvae of *H. cavernosa* showed the thickest abaxial wall (about 1.6 mm) in June. Between July and October, this wall gradually decreased down to 1.0 mm. Parasitized galls showed nearly the same abaxial wall thickness (about 1.5 mm) also in June. In the course of July to October, this thickness gradually decreased down to 1.2 mm. Galls with naturally dead larvae of *H. cavernosa* showed the thinnest walls (about 1.3 mm) in June. This thickness was virtually constant during July to October (about 1.2 mm) (Tab. XIV).

The size of the inner cavity in galls is also dependent on the health condition of the gall midge. At studied localities in 2007, chambers were on average 2.4 mm long and 1.4 mm wide. In 2008, galls were on average 0.5 mm larger and chambers were on average

2.5 mm long and 1.5 mm wide. Chambers with abandoned larvae of *H. cavernosa* were largest (about 2.7×1.6 mm). Chambers in galls with parasitoids were evidently smaller (about 2.45×1.4 mm). The smallest chambers (about 2.15×1.2 mm) occurred in galls with naturally dead larvae of *H. cavernosa*. Dimensions of chambers did not change from mid-May till the end of the growing season (Tab. XV).

Galls of particular categories usually differ with one another also in their appearance. Galls (or chambers) abandoned by larvae of *H. cavernosa* were always quite open in 2007 (in 2008 some 98%). Galls with insect parasitoids were quite open in 2007 and 2008 in 44 and 28%, respectively. It is of interest that these galls were open only until August and in September and October, the galls closed. In 2007, galls with naturally dead larvae were open in 30% and in 2008 only in 20%. These galls opened only till June and later they closed. Out of the total number of full-grown galls, about 59% galls were open by a slot reaching the chamber (Tab. XVI, Fig. 18). Galls with pupae (or imagoes) of parasitoids were open nearly in 58% whereas galls with larvae of parasitoids only in less than 38% (Tab. XVII).

The mean size of the slot opening (at the gall circumference) is in the causal dependence with particular categories of galls and age of galls. Galls abandoned by larvae of *H. cavernosa* are characterized by the largest slots (mean length 2.25 mm and width 1.2 mm). Galls with parasitoids show slots of a mean length 1.5 mm and width 0.65 mm. Galls with naturally dead larvae show the smallest slots of a mean length 1.35 mm and width 0.6 mm. The mean size of slots in galls of particular categories increases from May until October (Tab. XVIII, Fig. 19). In galls settled with parasitoids, the size of a slot is dependent on the developmental stage of a parasitoid. Small slots (about 1.3×0.5 mm) occur in galls with the parasitoid egg. Larger slots (about 1.5×0.6 mm) occur in galls with larvae and pupae of parasitoids. The largest slot (about 1.7×0.8 mm) occurs in galls with imagoes of parasitoids (Tab. XIX).

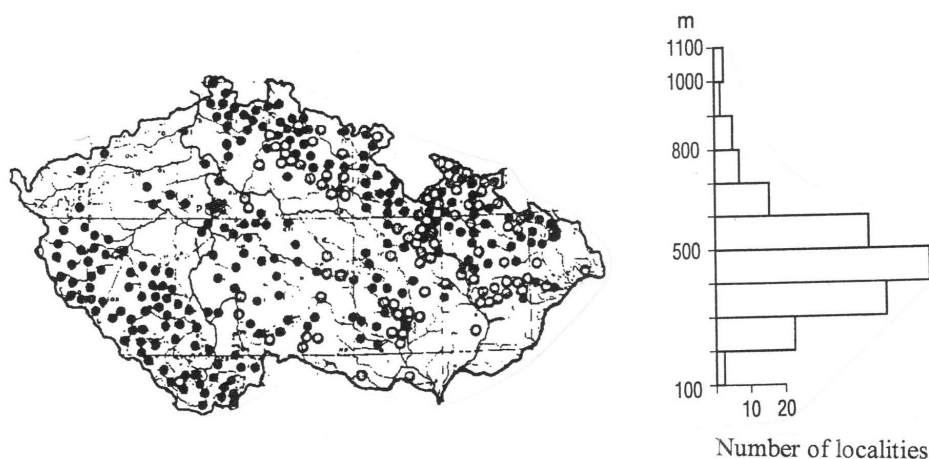
Originally green galls colour in May and in the first half of June. The adaxial face of galls is often reddish owing to insolation. On the abaxial face, galls are green or unilaterally faintly reddish. The inner walls of a crateriform slot are yellow-green. From mid-June, galls begin to brown and blacken. In open galls, also inner walls of chambers gradually darken. Galls with the undisturbed development of *H. cavernosa* darken first and most intensively. Galls with naturally dead larvae of *H. cavernosa* darken at the latest and least. Galls with abandoned *H. cavernosa* were black in 47% in July 2007 and in 96% in October. Parasitized galls were black in July in 12% and in October in 75%. Galls with naturally dead larvae of *H. cavernosa* were black in July in 9% and in October in 51% (Tab. XVI). The general course of the die-back of gall tissues is shown in Fig. 20. Tissues round the slot die usually first. Since the end of July, also leaf tissues in the surroundings of black (rarely also green) galls sometimes die. For example, in the first

half of October 2007, the surroundings of 85% galls with the abandoned larva of *H. cavernosa* were darkly edged, 40% parasitized galls and 27% galls with naturally dead *H. cavernosa*. Leaf tissues died up to a distance of 1 to 3(10) mm from the gall. The surface of dead galls is slightly warped; however, their size is not significantly changed.

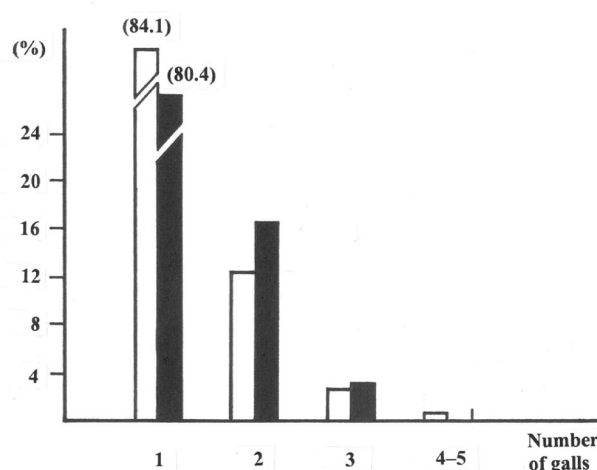
Damage and importance

In Central Europe, *H. cavernosa* ranks among the most abundant cecidogenic species of Cecido-

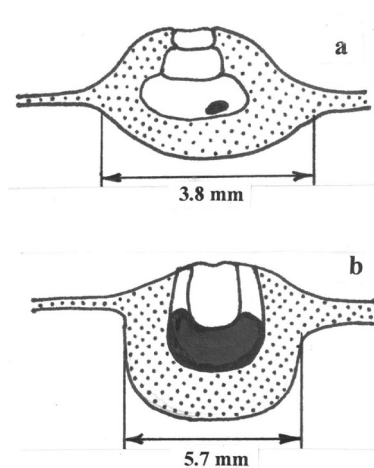
myiidae. Its galls often occur in large numbers on well insulated advance growth and young-growth stands of *P. tremula*. Leaves with galls do not die prematurely showing, however, significantly smaller area than leaves without galls. According to our findings, *H. cavernosa* reduces the assimilatory area of leaves and thus also the increment of young trees. In any case, however, it is not necessary the gall midge to be ranked among economically important forest pests (SKUHRAVÝ, SKUHRAVÁ and BREWER, 1997).



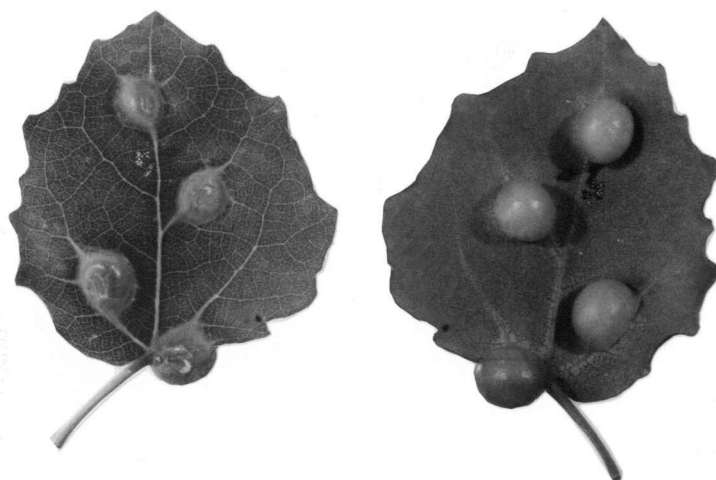
1: The occurrence of galls of *Harmandiola cavernosa* (Rübs.) on *P. tremula* in the Czech Republic. Light circles – finds of E. Baudyš and E. Bayer; dark circles – finds of V. Skuhravý and M. Skuhravá (SKUHRAVÝ and SKUHRAVÁ, 1998)



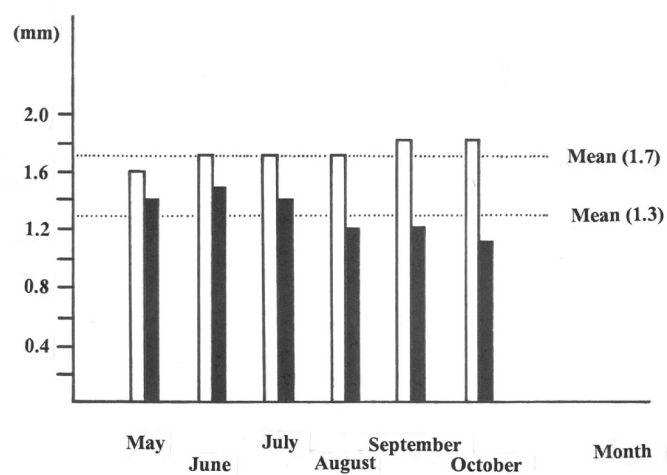
2: Frequency of the occurrence of galls of *H. cavernosa*. 2007 (light columns), 2008 (dark columns)



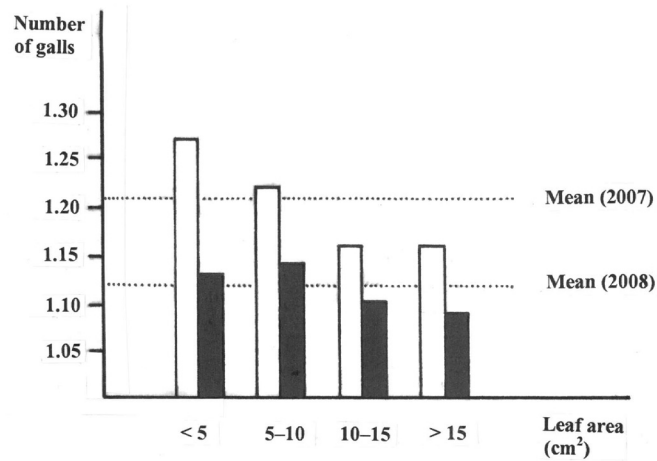
3: Longitudinal cut (a) through a growing gall of *H. cavernosa* (2 May 2007), (b) through an abandoned gall of *H. cavernosa*. 13 June 2007



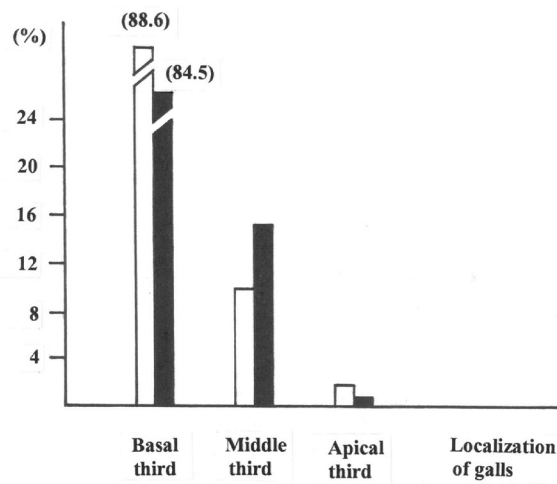
4: A leaf of *P. tremula* with galls of *H. cavernosa*. Left – top view, right – bottom view. 13 May 2007



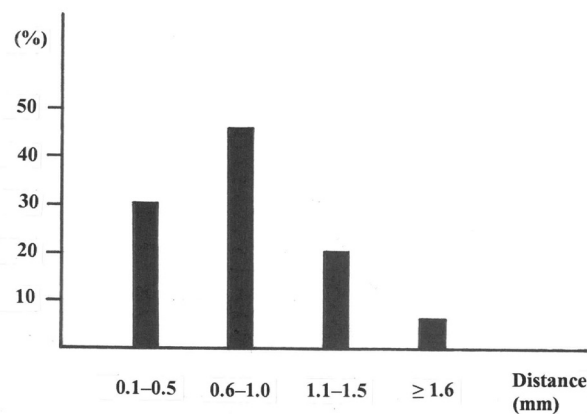
5: The mean thickness of the upper wall of galls (light columns) and the lower wall of galls of *H. cavernosa* (dark columns) (2007)



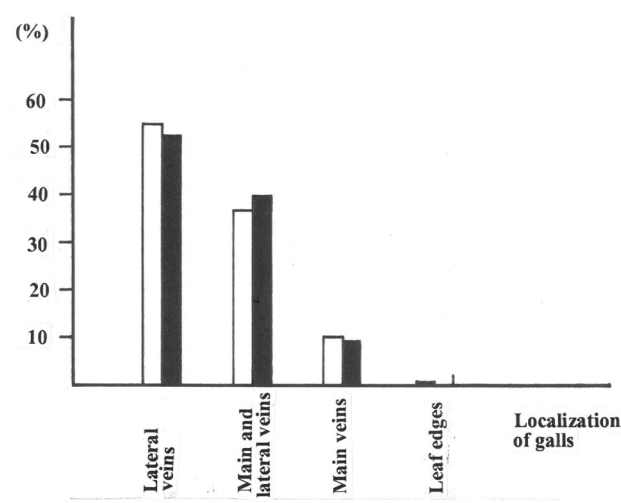
6: The mean number of galls of *H. cavernosa* divided into four area categories. 2007 (light columns), 2008 (dark columns)



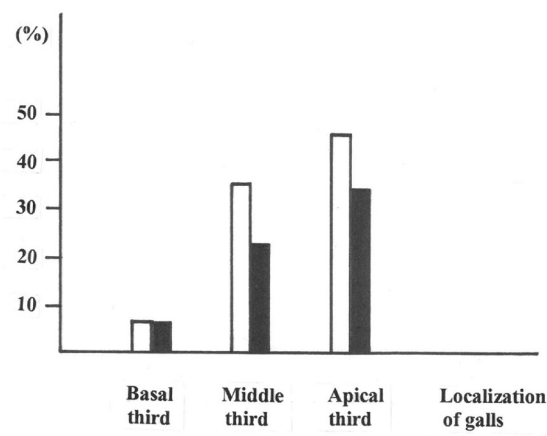
7: Localization of galls of *H. cavernosa* in particular thirds of the leaf blade (% of the total number of galls). 2007 (light columns), 2008 (dark columns)



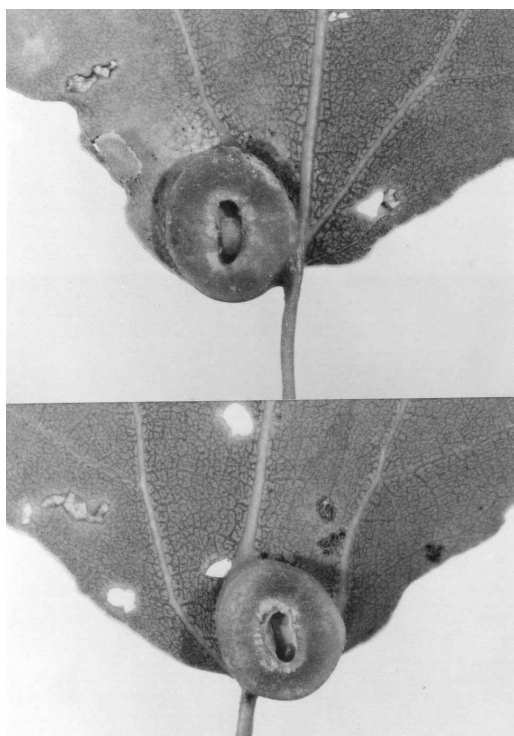
8: A distance of the slot centre in galls of *H. cavernosa* from the edge of leaf veins (2007)



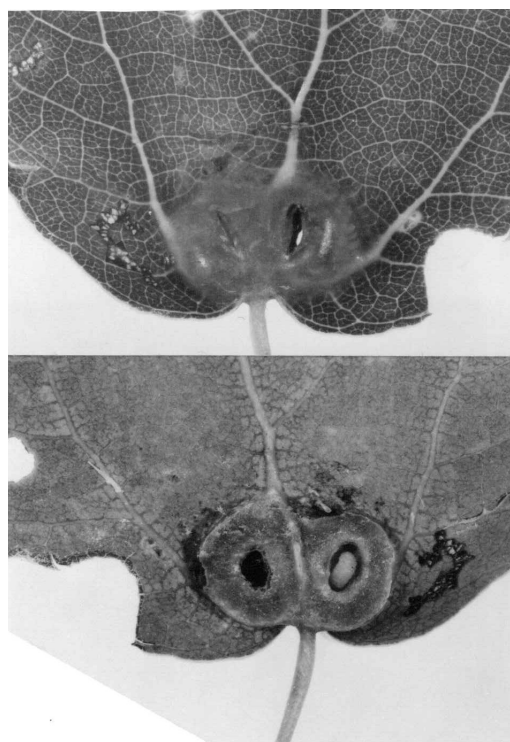
9: Localization of galls of *H. cavernosa* on the leaf blade (% of the total number of galls). 2007 (light columns), 2008 (black columns)



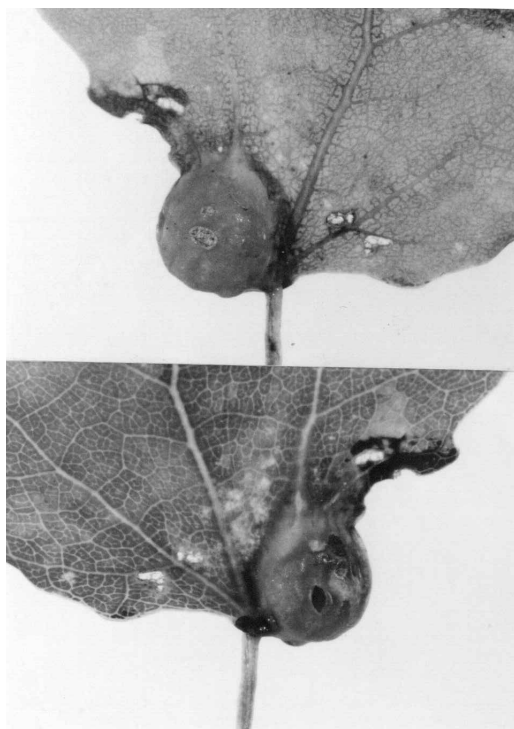
10: Localization of galls of *H. cavernosa* close to the main vein in particular parts of the leaf blade (the percentage of the number of galls in particular thirds of the leaf blade). 2007 (light columns), 2008 (dark columns)



11: A tangential cut through the gall of *H. cavernosa* with a larva of *H. cavernosa* (top) and with a parasitized larva of *H. cavernosa* (bottom). 30 May 2007



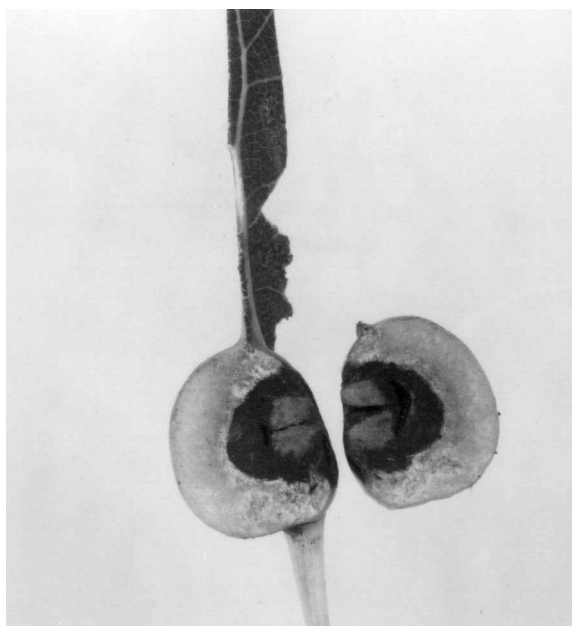
12: Top – adaxial face of the leaf with two galls of *H. cavernosa* (left, a gall with a larva of *H. cavernosa*; right, a gall abandoned by the larva of *H. cavernosa*). Bottom – abaxial face of a leaf with two galls in a tangential cut (left, a gall abandoned by the larva of *H. cavernosa*; right, a gall with the grown up larva of *H. cavernosa*). 30 May 2007



13: A view of the abandoned gall of *H. cavernosa* from the adaxial face of a leaf (top) and from the abaxial face of a leaf (bottom). 21 June 2007



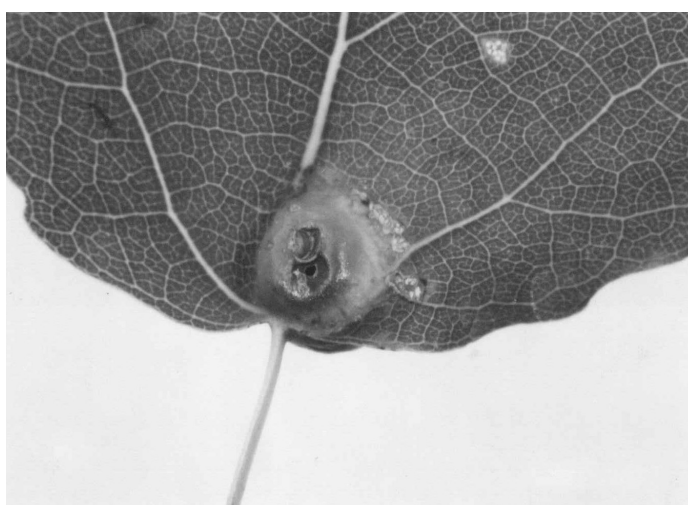
14: Top – adaxial face of a gall with an abandoned larva of *H. cavernosa*. 21 June 2007. Bottom – adaxial face of a gall with the dead larva of *H. cavernosa*. In the slot corner, there is the oval emergence hole of a parasitoid. 13 August 2007



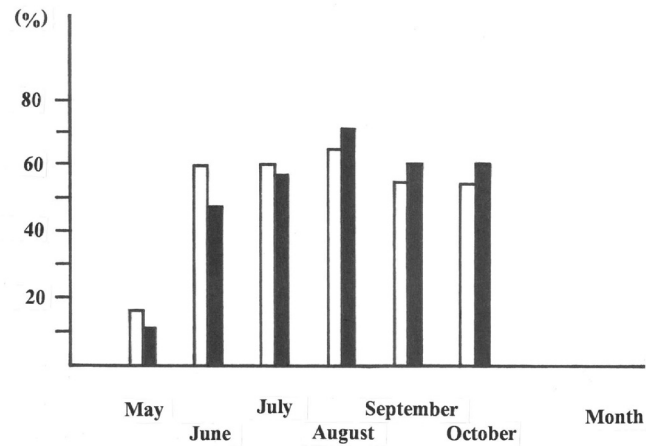
15: A longitudinal cut through the gall of *H. cavernosa*. The gall was yellow-green from an abaxial face and in cut; the inner chamber was black. 13 August 2007



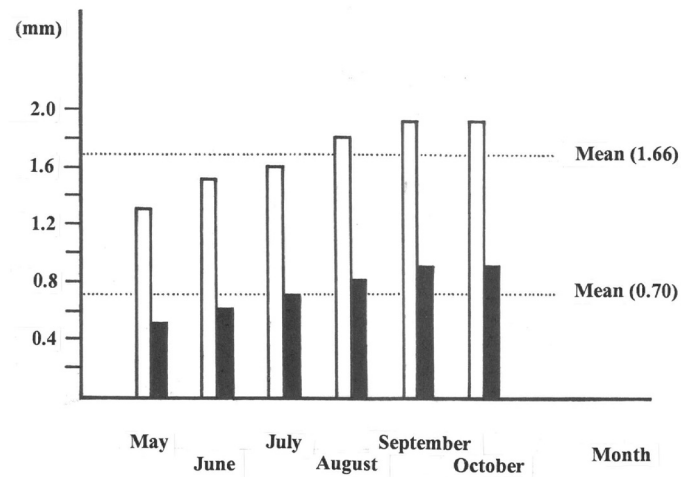
16: A longitudinal cut through the gall of *H. cavernosa* with the larva of a parasitoid. 13 August 2007



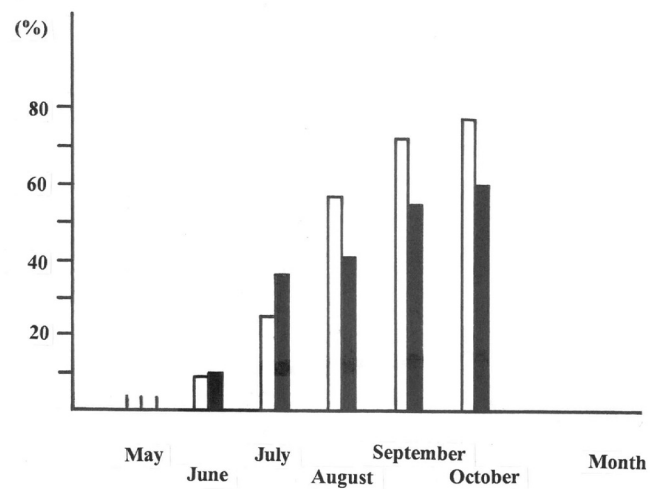
17: Adaxial face of the leaf with the gall of *H. cavernosa*. Next to the closed oval slot, there is a dark sunken facet with the oval emergence hole of a parasitoid. 13 August 2007



18: The percentage proportion of open galls of *H. cavernosa* in particular months. 2007 (light columns), 2008 (dark columns)



19: The mean length of a slot (light columns) and width of a slot in galls of *H. cavernosa* in particular months (dark columns) (2007)



20: The percentage proportion of brown and black galls of *H. cavernosa* (the percentage of darkened surface of galls in particular months). 2007 (light columns), 2008 (dark columns)

I: Mean dimensions of the leaf blade of *P. tremula* (cm) and of galls of *H. cavernosa* (mm). In each of the dates, 50 galls were analysed. Laboratory examination, 2007.

Date	Leaf length/width	Gall length/width/height	Gall height above the leaf blade	Gall wall thickness		Chamber length/width	Slot length/width
				from above	from below		
1/5	3.1/2.6	4.8/4.1/3.7	0.8	1.4	1.2	2.1/1.1	1.0/0.2
13/5	3.5/2.9	6.0/5.3/5.1	0.9	1.7	1.8	2.7/1.6	1.3/0.4
21/5	3.3/3.1	5.0/4.3/4.1	0.7	1.6	1.2	2.3/1.3	1.3/0.4
23/5	3.5/3.1	4.8/4.3/4.2	0.7	1.5	1.3	2.3/1.4	1.3/0.5
31/5	3.7/3.2	5.0/4.4/4.4	0.9	1.6	1.4	2.2/1.4	1.3/0.6
7/6	3.3/3.0	5.1/4.5/4.5	0.8	1.7	1.5	2.4/1.3	1.4/0.5
13/6	3.6/3.3	4.8/4.3/4.5	0.8	1.6	1.5	2.3/1.4	1.4/0.6
20/6	3.5/3.3	4.8/4.3/4.4	0.8	1.7	1.3	2.2/1.4	1.5/0.7
27/6	3.3/2.9	5.5/5.0/4.9	0.7	1.7	1.6	2.7/1.6	1.8/0.7
4/7	3.6/3.3	5.2/4.7/4.9	0.9	1.8	1.5	2.3/1.6	1.6/0.7
11/7	3.6/3.3	5.1/4.6/4.5	0.8	1.7	1.3	2.2/1.5	1.6/0.6
18/7	3.1/2.7	5.1/4.6/4.5	0.6	1.6	1.4	2.4/1.5	1.6/0.8
25/7	3.5/3.4	5.1/4.5/4.6	0.8	1.8	1.3	2.5/1.5	1.8/0.8
1/8	4.2/3.7	5.0/4.3/4.2	0.7	1.7	1.2	2.4/1.3	1.7/0.7
8/8	3.9/3.8	4.7/4.2/3.9	0.6	1.5	1.1	2.2/1.3	1.5/0.6
15/8	4.0/3.7	5.4/4.9/4.5	0.7	1.8	1.3	2.5/1.4	1.9/0.9
21/8	4.3/4.0	5.1/4.5/4.4	0.7	1.7	1.3	2.3/1.4	1.7/0.7
28/8	3.9/3.6	5.2/4.7/4.4	0.8	1.8	1.2	2.5/1.4	2.0/1.0
4/9	3.9/3.6	5.1/4.6/4.4	0.7	1.9	1.2	2.4/1.3	2.0/0.9
11/9	3.8/3.5	5.0/4.5/4.4	0.9	1.8	1.2	2.3/1.4	2.0/1.0
18/9	3.7/3.4	5.1/4.7/4.3	0.7	1.7	1.2	2.4/1.4	1.9/0.9
25/9	3.7/3.5	5.0/4.5/4.3	0.7	1.8	1.2	2.4/1.3	1.8/0.8
2/10	4.0/3.6	5.2/4.6/4.4	0.7	1.8	1.2	2.5/1.4	1.7/0.8
9/10	3.5/3.2	5.2/4.7/4.3	0.7	1.8	1.1	2.5/1.4	2.1/1.1
16/10	4.0/3.8	5.2/4.7/4.3	0.7	1.7	1.2	2.4/1.4	1.9/0.9
Mean Total	3.7/3.3	5.1/4.6/4.4	0.75	1.7	1.3	2.4/1.4	1.6/0.7

II: Mean dimensions of the leaf blade of *P. tremula* (cm) and galls of *H. cavernosa* (mm). In each of the control dates, 25 galls were analysed. Laboratory examination, 2008.

Date	Leaf length/width	Gall length/width/height	Gall height above the leaf blade	Gall wall thickness		Chamber length/width	Slot length/width
				from above	from below		
2/5	2.6/2.3	3.2/2.6/2.5	?	0.7	0.5	1.4/0.7	0.9/0.3
26/5	4.0/3.7	6.1/5.5/5.1	0.8	2.1	1.7	2.6/1.4	1.1/0.4
6/6	4.7/4.2	5.4/4.8/4.6	0.8	1.8	1.6	2.3/1.2	1.4/0.6
12/6	4.4/3.8	6.1/5.5/5.6	0.9	2.0	2.0	2.5/1.5	1.6/0.8
19/6	4.3/3.8	6.1/5.3/5.6	0.9	2.0	2.1	2.6/1.6	1.9/0.9
26/6	4.1/3.8	5.7/5.2/5.0	0.9	1.7	1.8	2.5/1.5	1.7/0.8
3/7	4.1/3.9	5.3/4.7/4.7	0.9	1.8	1.5	2.5/1.5	1.9/0.9
10/7	4.3/4.0	5.7/5.2/4.9	0.8	1.8	1.6	2.5/1.4	1.5/0.6
17/7	4.5/4.2	6.0/5.3/5.2	0.8	2.0	1.8	2.7/1.4	1.7/0.6
24/7	4.3/3.8	5.6/4.9/4.6	0.9	1.8	1.4	2.7/1.5	2.0/0.9
31/7	4.0/3.6	5.6/4.9/4.9	1.0	1.9	1.6	2.6/1.4	2.0/1.0
7/8	3.8/3.6	5.4/5.0/5.1	1.0	2.1	1.6	2.7/1.5	2.1/1.4
14/8	4.6/4.0	5.2/4.7/4.7	0.9	1.9	1.5	2.3/1.2	1.7/0.8
21/8	4.2/3.5	5.9/5.3/4.7	0.9	1.6	1.6	2.7/1.4	1.9/0.9

Date	Leaf length/width	Gall length/width/height	Gall height above the leaf blade	Gall wall thickness		Chamber length/width	Slot length/width
				from above	from below		
28/8	4.3/3.7	5.5/4.9/5.4	1.0	1.9	1.7	2.5/1.7	1.7/0.9
4/9	4.8/4.6	5.4/4.7/4.7	0.9	1.8	1.5	2.5/1.4	1.9/0.9
11/9	3.9/3.5	5.5/5.0/4.8	0.9	1.8	1.7	2.4/1.4	1.8/0.8
18/9	4.4/3.9	5.6/4.9/5.1	0.9	1.8	1.6	2.5/1.7	2.1/0.9
25/9	3.6/3.3	5.8/5.1/5.0	0.9	1.9	1.6	2.6/1.5	1.9/0.9
2/10	4.5/4.0	5.5/4.8/4.9	0.9	1.8	1.5	2.4/1.6	1.9/1.0
Mean Total	4.2/3.8	5.5/4.9/4.9	0.9	1.8	1.6	2.5/1.4	1.7/0.8
Mean from 26/5 to 2/10	4.2/3.8	5.7/5.0/5.0	0.9	1.9	1.7	2.5/1.5	1.8/0.8

III: Mean dimensions of galls of *H. cavernosa* on grown up leaves in relation to the leaf blade area. The height of galls on the adaxial face of the leaf blade (% of the mean height of galls). Leaves with one gall (in a numerator) and leaves with more galls (two up to five) were examined separately (in a denominator). 13/5–11/9/2007.

Leaf area (cm ²)	Number of galls	Number of galls/leaf	Gall dimensions (mm)				Gall height above the leaf blade (%)
			length	width	height	Gall height above the leaf blade	
< 5	85/63	1.27	4.9/4.9	4.4/4.3	4.4/4.2	0.65	15.1
5–10	298/164	1.22	5.2/4.9	4.7/4.3	4.6/4.3	0.75	16.7
10–15	171/64	1.16	5.2/5.0	4.7/4.4	4.6/4.3	0.81	18.0
> 15	66/31	1.16	5.3/5.0	4.7/4.5	4.6/4.4	0.76	16.9
Total	620/322	1.21	5.2/4.9	4.7/4.3	4.6/4.3	0.75	16.7

IV: Mean dimensions of galls of *H. cavernosa* on grown up leaves in relation to the leaf blade area. The height of galls on the adaxial face of the leaf blade (% of the mean height of galls). 26/5–2/10/2008.

Leaf area (cm ²)	Number of galls	Number of galls/leaf	Gall dimensions (mm)				Gall height above the leaf blade (%)
			length	width	height	Gall height above the leaf blade	
< 5	44	1.13	5.8	5.1	5.0	0.85	17.0
5–10	159	1.14	5.7	5.1	5.0	0.94	18.8
10–15	179	1.10	5.6	5.0	4.9	0.90	18.4
> 15	93	1.09	5.6	5.0	5.0	0.91	18.2
Total	475	1.12	5.7	5.0	5.0	0.91	18.2

V: Localization of galls of *H. cavernosa* on the leaf blade. 13/5–16/10/2007 (in a numerator) and 26/5–2/10/2008 (in a denominator).

Gall localization		Number of galls	(%)	(%)
At the basal edge of the leaf blade	between the lateral and main vein	436/189	36.3/39.0	53.0/55.9
	at a lateral vein	201/82	16.7/16.9	
In the basal third of the leaf blade (except the basal edge)	at the main vein	66/24	5.5/4.9	35.7/28.6
	at a lateral vein	360/115	30.0/23.7	
	at the leaf blade edge	2/0	0.2/0.0	
In the central third of the leaf blade	at the main vein	41/16	3.4/3.3	9.7/14.9
	at a lateral vein	76/56	6.3/11.6	
In the apical third of the leaf blade	at the main vein	9/1	0.7/0.2	1.6/0.6
	at a lateral vein	11/2	0.9/0.4	
Total		1 202/485	100.0/100.0	100.0/100.0

VI: Localization of galls of *H. cavernosa* in the basal, central and apical part of the leaf blade divided into four area categories (in % of the number of galls in each of the area category of leaves). Results of examinations carried out from 13/5 to 16/10/2007 are given in a numerator (in total 1 202 galls examined). In a denominator; results of examinations carried out from 26/5 to 2/10/2008 (in total 485 galls examined) are given.

Leaf area (cm ²)	Leaf blade part			Total (%)
	basal	central	apical	
< 5	91.2/91.3	8.2/8.7	0.6/0.0	100.0
5–10	89.7/88.3	9.1/11.1	1.2/0.6	100.0
10–15	87.6/83.7	10.5/16.3	1.9/0.0	100.0
> 15	81.4/73.1	12.8/26.9	5.3/0.0	100.0
Total	88.6/83.9	9.7/15.9	1.7/0.2	100.0

VII: Localization of galls of *H. cavernosa* with respect to venation on leaves divided into four area categories (in % of the number of galls in the each area category of leaves). Results of examinations from 13/5 to 16/10/2007 are given in a numerator (in total 1 202 galls examined). In a denominator; results examinations carried out from 26/5 to 2/10/2008 (in total 485 galls examined) are given.

Leaf area (cm ²)	Localization of galls				Total (%)
	Nearby the main vein	Nearby a lateral vein	Nearby the main vein and lateral vein	Nearby the leaf blade edge	
< 5	14.0/13.0	42.1/34.8	43.9/52.2	-	100.0
5–10	9.1/8.6	49.8/41.4	41.1/50.0	-	100.0
10–15	8.9/7.1	60.6/60.9	29.9/32.0	0.6/0.0	100.0
> 15	8.0/8.6	75.2/64.5	16.8/26.9	-	100.0
Total	9.6/8.5	53.9/52.6	36.3/38.9	0.2/0.0	100.0

VIII: Health conditions of *H. cavernosa* in galls. The number of galls is given in a numerator; % of the proportion of galls in particular inspections is given in a denominator. Laboratory examination, 2007.

Date	Galls with the undisturbed development of <i>H. cavernosa</i>		Galls with the disturbed development of <i>H. cavernosa</i>				Galls with the undefined content	Galls in total
	Living larvae	Abandoned larvae	Insect predators	Naturally dead larvae	Larvae bitten out by insect	Larvae pecked out by birds		
1/5	49/98	-	-	1/2	-	-	-	50/100
13/5	43/86	-	6/12	1/2	-	-	-	50/100
21/5	36/72	-	6/12	8/16	-	-	-	50/100
23/5	27/54	-	17/34	6/12	-	-	-	50/100
31/5	11/22	3/6	23/46	12/24	1/2	-	-	50/100
7/6	17/34	6/12	17/34	9/18	1/2	-	-	50/100
13/6	5/10	8/16	18/36	18/36	-	1/2	-	50/100
20/6	3/6	7/14	22/44	18/36	-	-	-	50/100
27/6	6/12	25/50	13/26	6/12	-	-	-	50/100
4/7	1/2	22/44	15/30	12/24	-	-	-	50/100
11/7	1/2	11/22	15/30	23/46	-	-	-	50/100
18/7	2/4	24/48	16/32	8/16	-	-	-	50/100
25/7	-	16/32	13/26	19/38	2/4	-	-	50/100
1/8	-	16/32	14/28	18/36	2/4	-	-	50/100
8/8	-	11/22	12/24	25/50	2/4	-	-	50/100
15/8	-	21/42	17/34	12/24	-	-	-	50/100
21/8	-	16/32	9/18	21/42	1/2	3/6	-	50/100
28/8	-	14/28	17/34	18/36	-	-	1/2	50/100
4/9	-	12/24	19/38	17/34	1/2	1/2	-	50/100
11/9	-	24/48	12/24	10/20	1/2	3/6	-	50/100
18/9	-	20/40	20/40	8/16	1/2	1/2	-	50/100
25/9	-	15/30	19/38	12/24	1/2	3/6	-	50/100

Date	Galls with the undisturbed development of <i>H. cavernosa</i>		Galls with the disturbed development of <i>H. cavernosa</i>				Galls with the undefined content	Galls in total
	Living larvae	Abandoned larvae	Insect predators	Naturally dead larvae	Larvae bitten out by insect	Larvae pecked out by birds		
2/10	-	12/24	17/34	19/38	1/2	1/2	-	50/100
9/10	-	16/32	27/54	7/14	-	-	-	50/100
16/10	-	18/36	17/34	11/22	1/2	1/2	2/4	50/100
Total	201/16.1	317/25.4	381/30.5	319/25.5	15/1.2	14/1.1	3/0.2	1 250/100
Mean (August–October)	-	195/32.5	200/33.3	178/29.7	11/1.8	13/2.2	3/0.5	600/100

IX: Health conditions of *H. cavernosa* in galls. In a numerator, the number of galls is given in particular inspections, in a denominator, their % proportion. In each of the inspection data, 25 galls were analysed. Laboratory examination, 2008.

Date	Galls with the undisturbed development of <i>H. cavernosa</i>		Galls with the disturbed development of <i>H. cavernosa</i>				Galls with the undefined content	Galls in total
	Living larvae	Abandoned larvae	Insect parasitoids	Naturally dead larvae	Larvae bitten out by insect	Larvae pecked out by birds		
2/5	22/88	-	-	2/8	-	-	1/4	25/100
26/5	14/56	-	8/32	3/12	-	-	-	25/100
6/6	4/16	-	5/20	15/60	1/4	-	-	25/100
12/6	12/48	3/12	7/28	2/8	1/4	-	-	25/100
19/6	12/48	4/16	4/16	3/12	1/4	1/4	-	25/100
26/6	5/20	9/36	4/16	5/20	2/8	-	-	25/100
3/7	2/8	10/40	3/12	7/28	2/8	1/4	-	25/100
10/7	1/4	10/40	4/16	9/36	1/4	-	-	25/100
17/7	-	10/40	7/28	7/28	1/4	-	-	25/100
24/7	-	12/48	6/24	7/28	-	-	-	25/100
31/7	-	18/72	3/12	4/16	-	-	-	25/100
7/8	1/4	15/60	8/32	1/4	-	-	-	25/100
14/8	1/4	7/28	5/20	12/48	-	-	-	25/100
21/8	-	15/60	4/16	6/24	-	-	-	25/100
28/8	-	17/68	1/4	5/20	2/8	-	-	25/100
4/9	-	11/44	6/24	7/28	-	1/4	-	25/100
11/9	-	14/56	2/8	8/32	1/4	-	-	25/100
18/9	-	15/60	5/20	4/16	1/4	-	-	25/100
25/9	-	15/60	6/24	2/8	2/8	-	-	25/100
2/10	-	13/52	5/20	5/20	-	1/4	1/4	25/100
Total	74/14.8	198/39.6	93/18.6	114/22.8	15/3.0	4/0.8	2/0.4	500/100
Mean (August–October)	2/0.9	122/54.2	42/18.7	50/22.2	6/2.7	2/0.9	1/0.4	225/100

X: The occurrence of particular developmental stages of insect parasitoids in galls of *H. cavernosa*. In a numerator, the number of galls with parasitoids is given, in a denominator their % proportion. In each of the inspection data, 50 galls were analysed. Laboratory examination, 2007.

Date	Eggs	Larvae		Pupae		Imagoes		Total
		living	dead	living	dead	flown out	dead	
1/5	-	-	-	-	-	-	-	-
13/5	6/100	-	-	-	-	-	-	6/100
21/5	6/100	-	-	-	-	-	-	6/100
23/5	15/88	2/12	-	-	-	-	-	17/100
31/5	2/9	19/82	2/9	-	-	-	-	23/100
7/6	5/29	11/65	1/6	-	-	-	-	17/100
13/6	2/11	14/78	1/5	1/6	-	-	-	18/100
20/6	-	14/64	2/9	4/18	-	2/9	-	22/100
27/6	-	8/61	4/32	1/7	-	-	-	13/100
4/7	-	3/20	6/40	2/13	-	3/20	1/7	15/100
11/7	-	3/20	1/7	7/46	-	4/27	-	15/100
18/7	-	7/44	1/6	1/6	-	6/38	1/6	16/100
25/7	-	5/38	3/23	-	-	4/31	1/8	13/100
1/8	-	3/21	1/7	-	-	10/72	-	14/100
8/8	-	4/33	2/17	-	-	6/50	-	12/100
15/8	-	4/23	1/6	-	1/6	9/53	2/12	17/100
21/8	-	2/22	2/22	-	-	4/45	1/11	9/100
28/8	-	2/12	2/12	-	-	13/76	-	17/100
4/9	-	1/5	2/11	-	-	15/79	1/5	19/100
11/9	-	2/17	3/25	-	1/8	5/42	1/8	12/100
18/9	-	5/25	4/20	-	-	8/40	3/15	20/100
25/9	-	-	5/26	-	1/5	11/58	2/11	19/100
2/10	-	2/12	4/23	-	2/12	8/47	1/6	17/100
9/10	-	3/11	7/26	-	-	15/56	2/7	27/100
16/10	-	1/6	6/35	-	1/6	5/29	4/24	17/100
Total	36/9.5	115/30.2	60/15.7	16/4.2	6/1.6	128/33.6	20/5.2	381/100
Mean (August–October)	-	29/14.5	39/19.5	-	6/3.0	109/54.5	17/8.5	200/100

XI: The occurrence of particular developmental stages of insect parasitoids in galls of *H. cavernosa*. In a numerator, the number of galls with parasitoids is given, in a denominator their % proportion. In each of the inspection data, 25 galls were analysed. Laboratory examination, 2008.

Date	Eggs	Larvae		Pupae		Imagoes		Total
		living	dead	living	dead	flown out	dead	
2/5	-	-	-	-	-	-	-	-
26/5	6/75	1/13	1/12	-	-	-	-	8/100
6/6	2/40	3/60	-	-	-	-	-	5/100
12/6	1/14	6/86	-	-	-	-	-	7/100
19/6	-	3/75	1/25	-	-	-	-	4/100
26/6	-	3/75	1/25	-	-	-	-	4/100
3/7	-	3/100	-	-	-	-	-	3/100
10/7	-	3/75	1/25	-	-	-	-	4/100
17/7	-	5/71	2/29	-	-	-	-	7/100
24/7	-	4/67	2/33	-	-	-	-	6/100
31/7	-	2/67	-	-	-	1/33	-	3/100
7/8	-	4/50	3/38	1/12	-	-	-	8/100
14/8	-	3/60	2/40	-	-	-	-	5/100
21/8	-	1/25	3/75	-	-	-	-	4/100

Date	Eggs	Larvae		Pupae		Imagoes		Total
		living	dead	living	dead	flown out	dead	
28/8	-	-	1/100	-	-	-	-	1/100
4/9	-	3/50	2/33	-	-	1/17	-	6/100
11/9	-	1/50	1/50	-	-	-	-	2/100
18/9	-	2/40	1/20	-	-	2/40	-	5/100
25/9	-	5/83	-	-	-	1/17	-	6/100
2/10	-	2/40	3/60	-	-	-	-	5/100
Total	9/9.7	54/58.0	24/25.8	1/1.1	-	5/5.4	-	93/100
Mean (August–October)	-	21/50.0	16/38.1	1/2.4	-	4/9.5	-	42/100

XII: The occurrence of particular developmental stages of insect parasitoids in galls of *H. cavernosa*. In a numerator, the number of galls with parasitoids is given, in a denominator, their % proportion. Laboratory examination, 2007.

Month	Eggs of parasitoids	Larvae of parasitoids		Pupae of parasitoids		Imagoes of parasitoids		Parasitized in total	Analysed in total
		living	dead	living	dead	flown out	dead		
May	29/14.5	21/10.5	2/1.0	-	-	-	-	52/26.0	200/100
June	7/3.5	48/24.0	7/3.5	6/3.0	-	2/1.0	-	70/35.0	200/100
July	-	19/9.5	10/5.0	10/5.0	1/0.5	17/8.5	2/1.0	59/29.5	200/100
August	-	15/6.0	8/3.2	-	1/0.4	42/16.8	3/1.2	69/27.6	250/100
September	-	8/4.0	14/7.0	-	2/1.0	39/19.5	7/3.5	70/35.0	200/100
October	-	6/4.0	17/11.3	-	3/2.0	28/18.7	7/4.7	61/40.7	150/100
Total	36/3.0	117/9.7	58/4.8	16/1.3	7/0.6	128/10.7	19/1.6	381/31.7	1 200/100

XIII: Dimensions of galls of *H. cavernosa* in relation to the health condition of larvae. Mean height of galls on the adaxial face of leaves (% of the mean height of galls). 13/5–11/9/2007 (in a numerator) and 26/5–2/10/2008 (in a denominator).

Larvae of <i>H. cavernosa</i>	Number of galls	Gall dimensions (mm)				Height of galls above the leaf blade (%)
		Length	Width	Height	Height of galls above the leaf blade	
Living (present)	153/52	5.3/6.0	4.7/5.4	4.6/5.4	0.80/0.89	17.4/16.5
Abandoned	239/182	5.3/5.8	4.8/5.1	4.7/5.1	0.80/0.92	17.0/17.6
Parasitized	259/90	5.2/5.8	4.7/5.2	4.6/5.1	0.72/0.91	15.6/17.8
Naturally dead	275/110	4.7/5.2	4.2/4.7	4.1/4.5	0.71/0.89	17.3/19.8
Total	926/434	5.1/5.7	4.6/5.1	4.5/5.0	0.75/0.91	16.7/18.2

XIV: Mean thickness of the gall wall of *H. cavernosa* (divided according to the health condition into four categories) above the leaf blade (in a numerator) and under the leaf blade (in a denominator) (mm). In particular months of the growing season 2007, on average 200 galls were analysed. For the purpose of comparison, the last line gives the mean thickness of the gall wall analysed in week inspections from 26/5 to 2/10/2008 (in total 432 galls examined).

Month	Galls				
	with living larvae of <i>H. cavernosa</i>	abandoned by larvae of <i>H. cavernosa</i>	with insect parasitoids	with naturally dead larvae	total
May	1.6/1.5	(1.9/1.3)	1.7/1.5	1.4/1.2	1.6/1.4
June	1.7/1.6	1.7/1.6	1.8/1.5	1.6/1.3	1.7/1.5
July	(1.4/1.4)	1.7/1.4	1.8/1.4	1.6/1.3	1.7/1.4
August	-	1.7/1.2	1.8/1.2	1.7/1.2	1.7/1.2
September	-	1.7/1.1	1.8/1.2	1.8/1.3	1.8/1.2
October	-	1.8/1.0	1.8/1.2	1.8/1.2	1.8/1.1
Total mean (2007)	1.6/1.5	1.7/1.2	1.8/1.3	1.7/1.2	1.7/1.3
Total mean (2008)	2.0/1.9	1.8/1.6	2.0/1.7	1.8/1.5	1.9/1.6

XV: Mean length/width of chambers in galls of *H. cavernosa* (divided according to the health condition into four categories) in particular months of the growing season 2007 (mm). In each of the months, on average 200 galls were analysed. For the purpose of comparison, the last line gives the mean size of chambers in galls analysed in 2008 (in total 453 galls examined).

Month	Length/width of the inner cavity of galls				
	with living larvae of <i>H. cavernosa</i>	abandoned by larvae of <i>H. cavernosa</i>	with insect parasitoids	with naturally dead larvae	total
May	2.5/1.4	2.4/1.5	2.4/1.4	2.1/1.2	2.4/1.4
June	2.5/1.4	2.8/1.6	2.3/1.4	2.1/1.2	2.4/1.4
July	2.3/1.4	2.6/1.7	2.5/1.6	2.0/1.2	2.4/1.5
August	-	2.6/1.5	2.5/1.3	2.2/1.1	2.4/1.3
September	-	2.5/1.5	2.4/1.2	2.3/1.2	2.4/1.3
October	-	2.7/1.5	2.5/1.3	2.2/1.2	2.5/1.3
Total mean (2007)	2.5/1.4	2.6/1.6	2.4/1.4	2.1/1.2	2.4/1.4
Total mean (2008)	2.6/1.6	2.8/1.6	2.5/1.4	2.2/1.2	2.5/1.5

XVI: The course of opening and darkening the galls of *H. cavernosa* (divided according to the health condition into four categories) in particular months of the growing season 2007. In a numerator, the mean percentage is given of galls with slots reaching the inner cavity. In a denominator, the mean percentage is given of the browned or blackened surface of galls. In each of the months, on average 200 galls were analysed. For the purpose of comparison, the last line gives mean results of an examination from 6/6 to 2/10/2008 (in total 429 galls examined).

Month	Galls				
	with living larvae of <i>H. cavernosa</i>	abandoned by larvae of <i>H. cavernosa</i>	with insect parasitoids	with naturally dead larvae	total
May	11.8/0.0	100.0/0.0	17.8/0.0	17.6/0.0	17.3/0.0
June	36.0/0.0	100.0/22.7	49.3/5.7	56.5/4.1	59.4/8.3
July	50.0/0.0	100.0/47.2	52.5/12.4	20.6/9.4	59.6/23.7
August	-	100.0/82.1	63.8/58.5	35.5/29.0	64.7/54.3
September	-	100.0/93.6	33.8/65.7	19.1/45.7	55.0/71.4
October	-	100.0/95.9	39.3/75.3	21.6/51.0	54.2/75.7
Total mean (2007)	25.3/0.0	100.0/69.5	44.1/37.3	30.1/23.7	55.3/35.9
Total mean (2008)	39.5/11.6	98.0/60.4	27.7/16.6	20.0/13.1	59.2/35.5

XVII: The percentage proportion of open galls of *H. cavernosa* with particular developmental stages of insect parasitoids (of the total number of galls with parasitoids in the given month). In each of the months, about 200 galls were analysed. Laboratory examination, 23/5–16/10/2007.

Month	Galls				
	with eggs of parasitoids	with larvae of parasitoids	with pupae of parasitoids	with imagoes of parasitoids	with parasitoids in total
May	10.5	23.0	-	-	17.8
June	0.0	51.8	66.7	100.0	49.3
July	-	44.8	40.0	70.0	52.5
August	-	26.1	0.0	86.7	63.8
September	-	21.7	100.0	37.0	33.8
October	-	39.1	100.0	31.4	39.3
Total	7.7	37.8	59.1	56.1	44.1

XVIII: The mean length and width of a slot in galls of *H. cavernosa* divided according to the health condition of *H. cavernosa* into four categories (mm). In particular months of the growing season 2007, on average 200 galls were analysed. For the purpose of comparison, the last line gives mean dimensions of a slot in galls analysed in week inspections from 26/5 to 2/10/2008 (in total 453 galls examined).

Month	Galls				
	with living larvae of <i>H. cavernosa</i>	abandoned by larvae of <i>H. cavernosa</i>	with insect parasitoids	with naturally dead larvae	total
May	1.3/0.4	1.5/0.8	1.3/0.5	1.2/0.5	1.3/0.5
June	1.3/0.5	2.1/1.0	1.4/0.6	1.3/0.5	1.5/0.6
July	1.2/0.5	2.1/1.0	1.5/0.6	1.3/0.5	1.6/0.7
August	-	2.3/1.2	1.7/0.7	1.4/0.6	1.8/0.8
September	-	2.3/1.3	1.7/0.7	1.6/0.7	1.9/0.9
October	-	2.3/1.3	1.7/0.7	1.6/0.7	1.9/0.9
Total mean (2007)	1.3/0.5	2.2/1.2	1.6/0.7	1.4/0.6	1.7/0.8
Total mean (2008)	1.4/0.7	2.3/1.2	1.4/0.6	1.3/0.6	1.8/0.7

XIX: The mean length and width of a slot in galls of *H. cavernosa* settled with particular stages of insect parasitoids (mm). In each of the months, about 200 galls were analysed. Laboratory examination, 23/5–16/10/2007.

Month	Number of galls with parasitoids	Galls				
		with eggs of parasitoids	with larvae of parasitoids	with pupae of parasitoids	with imagoes of parasitoids	with parasitoids in total
May	45	1.3/0.5	1.3/0.5	-	-	1.3/0.5
June	70	1.3/0.5	1.4/0.6	1.4/0.5	(1.6/0.8)	1.4/0.6
July	59	-	1.5/0.6	1.4/0.4	1.5/0.7	1.5/0.6
August	69	-	1.5/0.6	1.5/0.6	1.8/0.8	1.7/0.7
September	70	-	1.6/0.6	1.4/0.9	1.8/0.8	1.7/0.7
October	61	-	2.0/0.9	2.4/1.1	1.7/0.7	1.9/0.8
Total	374	1.3/0.5	1.5/0.6	1.5/0.6	1.7/0.8	1.6/0.7

SUMMARY

A gall midge *Harmandiola cavernosa* (Rübs.) is the second most frequent Cecidomyiidae species on *Populus tremula* in the CR. In 2007 and 2008, it occurred very abundantly in Forest District Bílovice nad Svitavou, Training Forest Enterprise Masaryk Forest in Křtiny (former Brno-venkov District). Imagoes occurred there at the end of April and at the beginning of May. Galls grew up as early as at the end of the first week in May. The formation of galls is mainly indicated by larvae of the first instar and partly larvae of the second instar. Larvae of the third instar did not participate in the creation of galls. Mature galls were on average 5.4 mm long, 4.8 mm wide and 4.7 mm high showing an inner chamber of an average length 2.4 mm and width 1.4 mm. Larvae abandoned galls from the end of May until mid-July. On average, 44% larvae completed successfully their development in galls. About 26% larvae were killed by insect parasitoids (mainly *Torymus quercinus* Boh.) and then same proportion of larvae died without any apparent exogenous causes). Insect predators and birds killed 4% larvae on average. It has been found that mortality factors markedly participated in the size, morphological, anatomical and physiognomic differentiation of galls. Gall polymorphism was analysed in detail in the paper. Galls significantly unfavourably affected the size of leaves and thus also photosynthesis.

SOUHRN

Výskyt, vývoj a hálkový polymorfismus *Harmandiola cavernosa* (Rübs.) (Diptera, Cecidomyiidae)

Bejlmorka *Harmandiola cavernosa* (Rübs.) je v ČR druhým nejpočetnějším cecidogenním druhem na *Populus tremula*. V letech 2007 a 2008 se velmi hojně vyskytovala na polesí v Bílovicích n. Svitavou, ŠLP Masarykův les ve Křtinách (bývalý okres Brno-venkov). Imaga se tam objevovala koncem dubna a začátkem května. Háčky dorůstaly již koncem prvního týdne v květnu. Tvorbu hálek indukují hlavně larvy prvního instaru a částečně i larvy druhého instaru. Larvy třetího instaru se na tvorbě hálek nepodílejí. Dorostlé háčky byly průměrně 5,4 mm dlouhé, 4,8 mm široké a 4,7 mm vysoké s vnitřní ko-

můrkou o průměrné délce 2,4 mm a šířce 1,4 mm. Larvy opouštěly hálky od konce května do poloviny července. Vývoj v hálkách úspěšně dokončilo průměrně 44 % larev. Kolem 26 % larev zahubili hmyzí parazitoidi (hlavně *Torymus quercinus* Boh.) a stejný podíl larev uhynul bez zjevných exogenních příčin. Hmyzí predátoři a ptáci zahubili průměrně 4 % larev. Bylo zjištěno, že mortalitní faktory se výrazně podílejí na velikostní, morfologické, anatomické a fyziognomické diferenciaci hálek. Hálkový polymorfismus byl v práci podrobně analyzován. Hálky průkazně negativně ovlivňovaly velikost listů a tím i fotosyntézu.

Cecidomyiidae, *Harmandiola cavernosa*, výskyt, lokalizace na listech, vývoj, přirození nepřátelé, hálkový polymorfismus, škodlivost

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