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CONTRIBUTION TO THE KNOWLEDGE OF INCIDENCE, DEVELOPMENT AND GALLS OF THE BISEXUAL GENERATION OF *BIORHIZA PALLIDA* (HYMENOPTERA: CYNIPIDAE)

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Abstract

The research study deals with the occurrence, cecidogenesis and development of the bisexual generation of *Biorhiza pallida* in the Brno region. Galls were found most frequently on *Quercus petraea* and on *Q. robur.* At the end of the winter season, females deposited 2–290 (on average 83.6) eggs, mainly into the above average sized buds on last-year's shoots. Larvae came to age in May in the 3rd instar, in the extremely warm and dry growing period of 2015 already in the 2nd instar. Adult individuals were leaving galls from the end of May to the end of July. Females were 3–4.5 – times superior to males in numbers. Females, males and individuals of both sexes emerged from 64.3%, 21.4% and 14.3% of galls, respectively. Galls were created from the beginning of April. In the second half of April (or at the beginning of May) they were 3–35 (on average 15.2) mm high and 3–45 (on average 20.2) mm wide. The percentage of buds infestation, average number of deposited eggs and average size of galls were increasing with the increasing mean diameter of shoots. Parasitoids (incl. parasitoid inquilines) killed 30–100 (on average 65) percent of gall wasp population. We found as many as 40% and 10% of galls with the developing *Curculio villosus* (Curculionidae) and *Synergus* spp. (Cynipidae), respectively. In the spring of 2016, nearly the whole gall wasp population in Brno-Komín was killed by late frosts. The pest infests mid-aged woody plants, sporadically also young growths and epicormic shoots of old oak trees.

Keywords: *Biorhiza pallida*, Cynipidae, occurrence, development, galls, regulating agents, significance

INTRODUCTION

Gall wasp *Biorhiza pallida* (Olivier, 1791) (Cynipidae) is the only representative of its genus in the Czech Republic. This valid species name (and other 11 synonyms) holds for its bisexual generation developing in conspicuous multiple-cell bud galls on *Quercus* spp. Less known is the unisexual (parthenogenetic) generation, referred to under four synonyms, most often as *Biorhiza aptera.* This generation develops in small single-cell galls on low-diameter roots of oak trees.

The two generations regularly alternate during the life cycle. The intraspecific morphological variability, cyclic heterogony and hidden mode of life reflect into the relatively poor knowledge of the species biology.

Our research work brings results of studying the incidence, cecidogenesis and development of the bisexual generation of *B. pallida* in the Brno region. The objective was to examine the physiological fecundity of females, number of eggs deposited into buds, creation of galls and the course of larvae development.

Geographical distribution

Gall wasp *B. pallida* is a Palaearctic species with the centre of occurrence in Europe (Stone *et al.*, 2002; Gauss, 1982). Its natural range extends from North Africa to southern Scandinavia and from Western Europe to Asia Minor. Before the disclosure of its complicated life cycle, both its generations were considered as the self-contained species of *B. pallida* and *B. aptera*. This is why e.g. Giraud, Darboux and Houard (1907) still mention their occurrence separately. According to them, *B. pallida* occurs in the former Austria-Hungary, Germany, Denmark, in the Netherlands, Belgium, England, France, Portugal, Switzerland, and Italy, on the Balkan Peninsula and in Asia Minor. *B. aptera* then occurs in Austria-Hungary, Germany, and Denmark, in the Netherlands, England, France and Italy. The species was reported also from Spain (Pujade-Villar, 1992; Rokas *et al.*, 2001; Rodriguez, Gomez and Nieves-Aldrey, 2015), Romania (Mustata and Rascanu, 1983), Ukraine (Dmitriev, 1975), Moldavia (Plugar, 1963) and Poland (Kierych, 1971; Banach and Lenowiecki, 2011). Many reports on the occurrence of *B. pallida* come from the British Islands (particularly from England). According to Forshage *et al.* (2017), it is abundant in England, Scotland, Wales, Ireland and on the Man Island. In the territory of the former Czechoslovakia (Bayer, 1912; Baudyš, 1921, 1954) and in Slovakia (Skuhravý *et al.*, 1998; Zúbrik and Kunca, 2011), it belongs to abundant and occasionally harmful species.

Host plants

Host plants of *B. pallida* are *Quercus robur* L., *Q. petraea* (Matt.) Liebl. and *Q. pubescens* Willd. (Dalla Tore, 1893; Kieffer, 1914). Apart from these most frequently mentioned hosts, galls were found also on *Q. cerris* L., *Q. robur "Fastigiata"* Lamk., *Q. ilex* L., *Q. lusitanica* Lamk., *Q. suber* L., *Q. pyrenaica* Willd. and *Q. canariensis* Willd. (Darboux and Houard, 1901). The species spectrum of hosts for unisexual and bisexual generations is to a certain extent identical. According to Gauss (1982), the unisexual generation develops on the roots of *Q. robur*, *Q. petraea*, *Q. pubescens*, *Q. pyrenaica*, *Q. frainetto* Ten. and *Q. ilex*, and the bisexual generation develops in bud galls on the same tree species and in addition on *Q. cerris* and *Q. suber*. Marković (2014) in Serbia found the bud galls on *Q. petraea* and *Q. frainetto*. According to Schimitschek (1944), in Turkey the species infests *Q. frainetto* and *Q. ilex*, according to Azmaz and Katılmış (2017), the infested tree species are *Q. petraea*, *Q. pubescens* and *Q. infectoria* Oliv. In the Mlynany Arboretum (southern Slovakia), galls were detected on *Q. petraea*, *Q. hispanica* Lamk. "*Ambrozyana*", *Q. lusitanica* and *Q.* × turneri Willd. "*Pseudoturneri*" (Barta, 2008).

The hitherto knowledge of species biology

Kieffer (1914) brought essential findings about the biology of *B. pallida*. A greater part of his data was taken over by for example Escherich (1942), Živojinović (1948), Sedlag (1959), Brauns (1964), Gauss (1982), Sedlag *et al.* (1986) and Hellrigl (2010). Vyržikovskaja (1962) reported the occurrence of two morphologico-biological forms of *B. pallida* (f. *pallida* Ol. and f. *aptera* Bosc.) in the former Leningrad region of Russia, including the characterization of galls and their development. Harper *et al.* (2004) studied the cytology of gall tissues, Bronner (1977) dealt with the histology, cytology and chemical composition of galls. Koncz *et al.* (2011) compared the histology of galls with the little known histology of the galls of *Neuroterus quercusbaccarum*. Leach (1995) demonstrated that the females of Cynipidae produce species-specific pheromones whose active substance in *B. pallida* is n-hexane. Atkinson (2001) revealed through the genetic analyses of adults emerged from galls that the percentage of buds with the future galls into which more than one female deposited eggs was ca. 70%. Folliot (1964), Stone *et al.* (2002) and Atkinson, Brown and Stone (2003) reported the occurrence of three reproduction types of unisexual generation (androphore, gynophore and gynandrophore). This is why a majority of bud galls exhibits development of either only males or only females, and only in a small part of galls the development of individuals of both sexes. Galls with individuals of both sexes originate from eggs deposited by gynandrophores or from eggs deposited by androphores and

gynophores (multiple oviposition) (Atkinson, Brown and Stone, 2003).

More than 75 insect species develop in galls of the bisexual *B. pallida* generation (Kieffer, 1914; Storch and Alberti, 1976; Hellrigl, 2010). Parasitoids are mentioned for example by Nikoľskaja (1952), Nikoľskaja and Zerova (1978), Zerova (1978), Džanokmen (1978), Trjapicyn (1978), Pujade-Villar (1992), O'Connor (2001, 2002), Williams (2010) and Ferracini *et al.* (2015). Gorny (1980) raised eight parasitoid species from galls on *Q. petraea* in Poland. Thúróczy, Melika and Csóka (1998) studied parasitoids in cynipid galls on *Quercus* spp. in the Czech Republic, Slovakia, Hungary and western Ukraine. Parasitoids (namely representatives of the superfamily of Chalcidoidea) often kill also a majority of host gall wasps in multi-cell galls.

Larvae of inquiline species commonly developing in the galls of *B. pallida* are those of *Synergus gallaepomiformis* and *S. umbraculus* (Cynipidae) (Melika and Bechtold, 1999; Kwast, 2012). Occurrence and development of *S. gallaepomiformis* a.o. was studied for example by Wiebes-Rijks (1979). There are also some other species from the *Synergus* Htg. genus, which is represented in the Czech Republic by 19 species (Mikula, 1989) that can develop as inquilines or facultative parasitoids of *B. pallida*.

Galls show the presence of the larvae of *Curculio villosus* (Curculionnidae) (Kieffer, 1914; Hellrigl, 2010) and occasionally also the presence of *Pammene argyrana* (Jong and Frankenhuyzen, 1976) and *P. gallicollana* (Tortricidae) (Mustata and Rascanu, 1983) caterpillars. Other species that can deposit eggs into the galls are among others *Meconema thalassinum* (Tettigoniidae) (Mustata and Rascanu, 1983) or *Clinodiplosis cilicrus* (Cecidomyiidae) (Kieffer, 1914; Escherich, 1942).

MATERIALS AND METHODS

Field research was conducted in oak stands nearby Brno in the period from 2014–2016. The surveyed forests north of Brno are managed by the Forest District in Bílovice nad Svitavou and by the Forest District in Vranov (ŠLP Masarykův les Křtiny/Masaryk Forest Training Forest Enterprise). Forests west of Brno are under management of Lesy města Brna, a.s. (Forests of the City of Brno) with the headquarters in Kuřim. Less frequent visits were paid to forest stands situated east of Brno managed by LČR, s. p. (Forests of the Czech Republic, State Enterprise–Forest District Pozořice), to a lesser extent by private forest owners. The area is orographically rather articulated with altitudes from 230 to 400 m a.s.l., mean annual temperature of 7.5 °C and mean annual precipitation amount of 610 mm.

In the growing season of 2014, the stands were visited at 2–10 day intervals. In 2015 and 2016, they were visited at 7–21 day intervals. Some partial observations were made in 2017 and 2018. The collected galls were subsequently examined in the laboratory. Recorded parameters included the diameter of shoots below the galls, gall dimensions, number of cells in the galls, size (length and width) of cells and their inner contents. Larvae, pupae and adults of *B. pallida* were micrometrically measured for cranium width and body length and width. In 2014, the course of eclosion of host cynipid males and females was monitored along with those of cynipid *Synergus* sp. Biopsy of ovaries served to determine the physiological natality rate of freshly emerged females.

RESULTS AND DISCUSSION

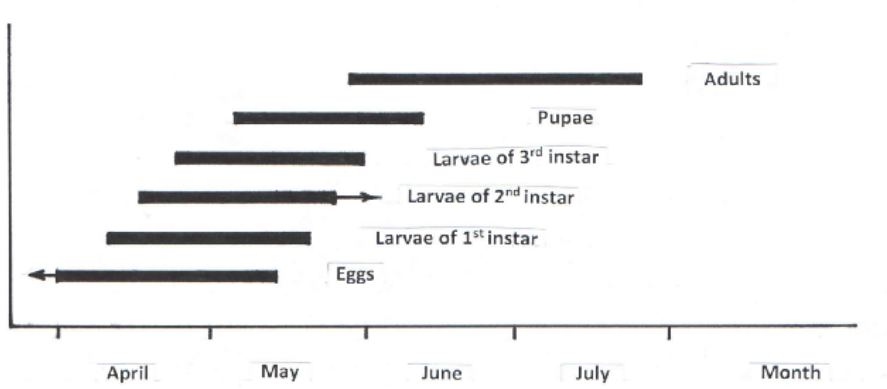
Host woody plants

Galls of the bisexual generation of *B. pallida* occur in the Brno region on *Quercus petraea*, *Q. robur* L. and rather frequently also on *Q. dalechampii* Ten., rarely on *Q. polycarpa*. Interesting finding was that the relatively little represented *Q. robur* was infested by the gall wasp more often and more intensively than the most abundant *Q. petraea*. No other autochthonous and allochthonous oak species exhibited the occurrence of galls. A more precise assessment of gall wasp trophic affinity would call for a longer-term and more extensive survey.

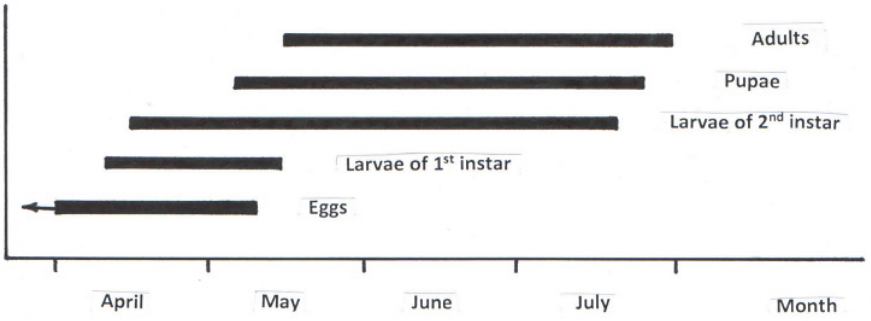
Basic scheme of development

The developmental cycle of *B. pallida* lasts two years. Adults of both sexes develop in bud galls and leave the places of their development after several days of maturation; then they appear in the open. In the Brno region, adult individuals were leaving the galls from 28 May to 25 July in 2014 and from 15 May to 30 July in 2015 (Figs. 1 and 2). Fertile females burry themselves into the ground to the roots of oak trees in July and deposit eggs into their bark, looking primarily for low-diameter roots.

Eggs are deposited individually and often close together. From the eggs, larvae of unisexual generation emerge, which develop in tiny single-cell galls growing up to the size of pea to cherry. The galls are pale at the beginning, soft and juicy, later reddish and in the end dark brown,



1: *Scheme of the development of Biorhiza pallida in bud galls on Quercus spp. Brno region, 2014*



2: *Scheme of the development of B. pallida in bud galls on Quercus spp. Brno region, 2015*

hard and lignified. They often form racemiform clusters around the roots, in which individual galls are in mutual contact, deformed and sometimes connate at the base. Larvae develop slowly and come to age as late as at the end of the following year when most of them pupate in the galls.

Parthenogenetic females are leaving the galls from September to December of the second year and in March of the third year (Williams, 2010). Using mandibles and legs, they get out from the ground and appear in the open. They survive stronger frosts hidden under the leaves or in other ground hiding places and become active already at temperatures around 0 °C, when they start climbing oak stems. Under cold weather, they would stay at the same place for a day or longer and they are often covered with numerous eggs (Kieffer, 1914). When the period of frost is over, they look for suitable terminal or sub-terminal buds into which they deposit infertile eggs. During oviposition, females inject a pungent secretion into the buds, which stimulates the growth of galls. Nevertheless, the essential influence on cecidogenesis is that of the secretions of eggs and young larvae. According to Kieffer (1914), larvae start occurring in eggs already at the beginning of March and galls develop shortly thereafter. With the onset of warmer spring weather and with the beginning of flushing time, the galls develop rapidly and reach their final size towards the end of April and at beginning of May (Tabs I and II). However, on the still little infoliated trees, the galls are noticeable already in the first half of April. Adults of bisexual generation emerge in the Brno region from mid- (or end of) May to the end of July when the cycle of development is closed. In contrast to the very long development of unisexual generation lasting 1.5 year at minimum, the bisexual generation develops only less than a half year.

Oviposition

In the Brno region, females of unisexual generation deposit eggs into winter buds of average up to above-average size on last year's shoots (scarcely on shoots from the year before last), usually towards the end of the winter period. For oviposition, they look for terminal (i.e. as a rule usually leaf) buds, less frequently lateral (i.e. as a rule flower or combined) buds. According to Kieffer (1914), females often deposit more than 300 eggs into a single bud. In the Brno region, they deposited 2–210 (on average 84.9) eggs in 2014. In 2015, they deposited 2–126 (on average 81.3)

I: *Basic data on field checks and galls of Biorhiza pallida. Brno region, 2014*

Month	Dates of checks	*Sites of controls	Total number of galls	Mean diameter of shoots (mm)	Average		Average number of cells
					height/width of galls (mm)	height/width of inner zone (mm)	
April	16/21/23/27/ /30	3/1/1/3/3	58	3.2	14.8/18.8	7.2/10.3	78.1
May	3/7/10/14/17/ /21/24/28/31	3/2/3/2/3/ /2/3/2/3	67	3.4	14.8/20.4	9.7/14.7	78.3
June	4/7/11/14/18/ /22/25/29	2/3/2/3/2/ /3/2/3	53	3.8	16.4/22.7	11.4/16.8	94.7
July	2/5/15/19	2/1/3/3	15	3.3	17.0/24.7	12.6/18.1	105.7
Total	–	–	193	(3.4)	(15.4/20.9)	(10.2/15.0)	(84.9)

*Legend: 1 – Forest district Bílovice nad Svitavou, 2 – Forest district Vranov, 3 – Forest administration Brno. The column before the last brings the average height/width of the cluster of inner galls after the removal of so-called outer galls.

II: *Basic data on field checks and galls of B. pallida. Brno region, 2015*

Month	Dates of checks	*Sites of controls	Total number of galls	Mean diameter of shoots (mm)	Average height/width of galls (mm)	Average number of cells
May	4/11/18/25	1/2/2/2	8	3.3	15.5/20.5	102.7
June	1/15/29	4/1/3	6	3.2	14.7/18.5	79.3
July	13/27	4/1	3	2.8	13.0/17.0	55.7
August	10/31	1/2	4	2.6	14.0/18.0	71.5
September	7/14/21	3/1/3	4	3.3	16.2/21.5	70.3
October	5/26	3/3	7	2.8	13.6/19.7	?
Total	–	–	32	(3.0)	(14.6/19.4)	(81.3)

*Legend: 1 – Forest district Bílovice nad Svitavou, 2 – Forest district Vranov, 3 – Forest administration Brno, 4 – Forest district Pozořice

eggs (Tabs. I and II) and in 2016, the number of deposited eggs ranged from 7–290 (on average 84.5). There are however two or more females that can deposit eggs into the same bud (Atkinson, 2001; Atkinson *et al*., 2003).

Prior to depositing eggs, females cut-off leaf or flower foundations from the meristem by using their ovipositor, thus creating a small but spatial transversal cavity inside the bud. Then they would deposit a group of eggs into the cavity on the apical growing point. The cut-off part of the bud would gradually turn brown and die. The eggs are round to oval, colourless, glossy, provided with long filiform pedicels, clearly distinguishable from egg bodies. Chorion is soft, extremely elastic so that the pedicels can be extended to at least twice a length without any harm to the egg. During embryogenesis, the eggs would become somewhat larger to an average length of 0.2 mm and width of 0.18 mm. The pedicel is 0.7–1.8 mm long and 0.01 mm wide at half the length. From the widened base, the pedicel gradually becomes narrower towards the end.

Embryogenesis (including a possible winter diapause) lasts for 1.5–6 months. Larvae emerge from eggs from April to the beginning of May. Non-hatched out eggs were detected in the Brno region still at the end of April when most of buds on oak trees had been broken already. For example, on 24 April 2016, we found 89.1% of non-hatched out eggs and 10.9% hatched eggs in Brno-Komín. Closely before eclosion, the buds were slightly enlarged and gall tissues filled approximately a half of the buds. At the time of larvae emergence, cover scales of buds were opening and the galls became visible. According to Kieffer (1914), larvae occur in the eggs at the beginning of March and galls are created soon thereafter.

Galls and their characteristics

Gall wasp *B. pallida* injures mainly terminal buds or buds in their close vicinity (Baudyš, 1954). Cecidogenesis is induced primarily by secretions exuded by vital eggs and young larvae (Stone *et al.*, 2002). The secretion injected into the buds by females during oviposition apparently participates in the creation of galls, too. Galls with dead eggs however reach a smaller size. In the Brno region, galls started to be formed in the first half of April, i.e. at the beginning of bud break on the host trees.

During the initial phases of cecidogenesis, gall tissue develops around the eggs, which is rugged, bulging or mildly recessed on the surface. The tissue would gradually surround the eggs so that only pedicels would protrude from it for a certain time. Concurrently (or somewhat later), larvae would emerge, which accelerate the differentiation of tissues including vascular bundles. Cover scales in the apical and central part of the bud would swell due to the gall growth and often stick to its apex until the gall fall. Basal scales, which form a shape of five-pointed rosette at the gall base, in which each points usually consists of 5 scales, persist on the gall even longer. The galls rapidly gain size, and groups of inner galls with the cells differentiate under collective epidermis and spongy parenchyma. The galls reach their final size in the second half of April (or at the beginning of May). According to Kieffer (1914), galls would reach their normal size as late as in May and June.

The galls are transversally oval, with uneven but smooth surface. Initially they are juicy, later porously spongy, shrivelled after maturation and drying out. Young galls are yellow-green to yellow, often reddish on sides or from above. Sometimes even the youngest galls, still covered by the bud scales, are carmine red, not only the sunlit sides of growing and grown-up galls. On the cut, the tissues are light, acquiring a brown, auburn or up to purple-reddish colour within several minutes after oxidation. Towards the end of April, the galls begin to turn brown and already in mid-May, they are usually light brown.

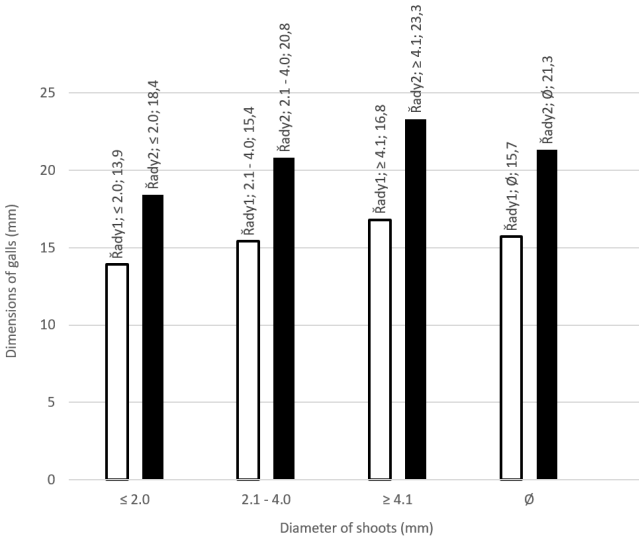
The inner galls reach their final size at the end of May and beginning of July. Upon finalizing their growth, they are on average 2.4 mm long and 1.6 mm wide with cavities, the average length and width of which is 2.3 mm and 1.5 mm (Tab. III), respectively. They are located closely to each other, rather at the base of the outer gall. Their longitudinal axis is as a rule oriented towards the base of outer galls (i.e. to points where galls are set to shoots). The trophic layer of tissues in the cells diminishes with the growth of larvae, the cells become larger, their walls becoming thinner and lignified.

Due to their size, shape and colour, the galls are very conspicuous. According to Kieffer (1914), their final size may be that of hazel nut up to apple; according to Gauss (1982), it is the size of child's fist. According to Escherich (1942), the galls are oval, with a larger transversal of 2–4 cm. Vyržikovskaja (1962) mentions irregularly oval galls of 1–4 cm in diameter, located at the ends of shoots. Sedlag (1959) reported a size of galls, which is little probable (up to 8 cm). In the Brno region, the grown up galls were from 3–30 (on average 15.7) mm high and from 3–45 (on average 20.9) mm wide in 2014. Average height of the galls was by 5.2 mm (i.e. by 33.1%) smaller than their width. In 2015, the galls were from 10–22 (on average 14.6) mm high and from 9–28 (on average 19.4) mm wide. Average height of the galls was by 4.8 mm (i.e. by 32.9%) smaller than their width (Tabs. I and II).

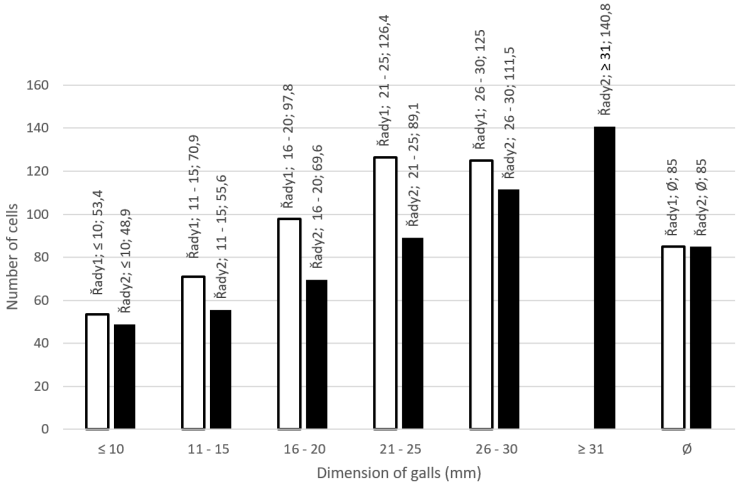
Average size of the galls increases with the increasing diameter of shoots (measured just below the galls). Average size of the buds, average number of deposited eggs and average size of the galls increase with the increasing growth activity of trees (Figs. 3–5). In 2014, galls on low-diameter shoots (diameters below 2 mm) contained on average 67.4 cells and galls on large-diameter shoots (diameters above 3.1 mm) contained on average 94.3 cells (i.e. by 39.9% more) (Fig. 5). More scarcely, females would deposit eggs into below-average sized buds, which then change into galls of below-average size. In Brno-Soběšice, tiny acrocecidia sized about 10 mm were found on 5–10 cm long last year's epicormic shoots in lower parts of *Q. petraea* stems with a diameter at breast height of about 35 cm on 8 May 2018.

Development of bisexual generation

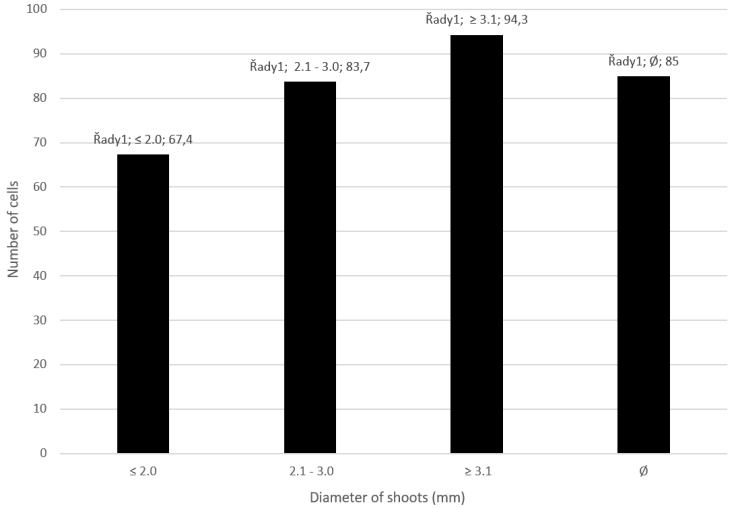
Development of *B. pallida* in bud galls in the Brno region in 2014 is shown in Fig. 1. First larvae from eggs deposited by unisexual females during the period of dormancy emerged on 10 April. Larvae of the 1st instar were detected in the galls until 20 May and moulted after a week of development. A majority of the 2nd instar larvae moulted again after several days of food intake; however, a smaller part of the larvae diapaused in the galls. Larvae of the 3rd instar pupated and adult individuals were detected in the galls from 28 May to 25 July. Adults were emerging from galls



3: *Relationship between the diameter of Quercus spp. shoots and the average height (light columns) and width (dark columns) of B. pallida galls. Brno region, 16 April–19 July 2014*



4: *Relationship between the average size of galls (height-light columns/width-dark columns) and the average number of cells in the galls of B. pallida. Brno region, 16 April – 19 July 2014*



5: *Relationship between the diameter of Quercus spp. shoots and the average number of cells in the galls of B. pallida. Brno region, 16 April – 17 July 2014*

brought to the laboratory on 12 May 2014 from 15 May to 15 July (Tab. VII). Males were emerging on average by less than a week earlier than females (at a ratio of 1♂ : 3 ♀♀). Flight holes of adults are circularly oval, with diameters ranging from 0.8–1.3 (on average 1.1) mm. Deserted cells are usually filled with the fine light-coloured amorphous bore dust.

In the extremely warm and dry growing season of 2015, larvae were developing through two instars (Fig. 2). Larvae of the 2nd instar were pupating and adult individuals were found in the galls from 15 May to 30 July, most often in the 2nd half of June and at the beginning of July. The adults left the galls after several days of maturation. Males die soon after copulation; females die only after having deposited eggs into roots. After the emergence of adults, the internal walls of cells turn soon brown while the walls of cells with deserted parasitoids remain velvety yellow for a long time. Darboux and Houard (1901) inform that adults occur in June and July. According to Kieffer (1914) and Gauss (1982), adults leave the galls in June, according to Escherich (1942) at the end of June and in the first half of July, and according to Williams (2010) from May up to August. Marković (2014) found a male of *B. pallida* even as early as on 2 May 2013.

In the Brno region, females markedly outnumbered males. Analyses of galls and laboratory stock yielded 17.9% of males and 82.1% of females. Only females and males emerged from 64.3% and 21.4% of galls, respectively; 14.3% of galls gave individuals of both sexes. According to Atkinson *et al.* (2003), 75% of galls yield only individuals of one sex. Males are 1.8–3.4 (on average 2.5) mm long and 0.5–1.1 (on average 0.8) mm wide. The length of females is 1.6–3.6 (on average 2.6) mm and their width is 0.6–1.8 (on average 1.1) mm. Males have the cranium 0.68–0.90 (on average 0.80) mm wide, and the width of cranium in females is 0.54–0.90 (on average 0.78) mm. By their colouration and body shape (namely narrowed thorax), females strikingly resemble tiny ants. Individuals of both sexes are considerably smaller than in the unisexual generation. Dimensions of larvae, pupae and adults are presented in Tabs. IV–IX. Literary data on body proportions of *B. pallida* are scarce and inaccurate, and therefore not mentioned in this study.

Adults of bisexual generation feature wing polymorphism. Males are always macropterous with wings reaching far beyond their abdomen. Females are mostly apterous and, unlike flyable males, move only by crawling. In the Brno region, 88.5% of females were apterous, 10% were micro- to brachypterous and 1.5% of females were macropterous. The tendency to apteria is apparently associated with the place of oviposition into the bark of oak roots. According to Gauss (1982), the formation of wings in females may greatly differ regionally.

Parasitoids

Bud galls of *B. pallida* host numerous insect species (mainly from the superfamily of Chalcidoidea), which find food and hiding place in them. The most abundant of them are representatives of Torymidae and Megastigidae families (Zerova and Djakončuk, 1978). Nikoľskaja (1952), Gorny (1980) and Williams (2010) consider as parasitoids of *B. pallida* the following species: *Torymus affinis*, *T. angelicae*, *T. arundinis*, *T. auratus*, *T. cingulatus*, *T. cyaneus*, *T. flavipes*, *T. geranii*, *T. glechomae*, *T. microcerus*, *T. notatus*, *T. phillyreae*, *T. roboris* (all Torymidae) and *Bootanomyia dorsalis* (Megastigmidae). According to literary data, other parasitoids are *Cecidostiba fungosa*, *C. semifascia*, *Mesopolobus amaenus*, *M. dubius*, *M. sericeus*, *M. tibialis* and *Hobbya stenonota* (Pteromalidae), *Eurytoma brunniventris*, *E. strigifrons*, *Sycophila biguttata*, *S. flavicollis* and *S. variegata* (Eurytomidae), *Baryscapus diaphantus*, *Aprostocetus aethiops*, *Aulogymnus skianeuros* (Eulophidae), *Ormyrus nitidulus* and *O. pomaceus* (Ormyridae), *Aphelinus subflavescens* (Aphelinidae) and *Eupelmus urozonus* (Eupelmidae). Kalina (1989) mentions a majority of these species from the territory of the former Czechoslovakia.

In the Brno region, eggs of parasitoids were detected in the galls from mid-April to mid-May, larvae from 20 April to the end of July. A greater part of the larvae pupated from the beginning of June to the end of July when adults were leaving the galls. Unlike gall wasps, which leave the galls through flight holes of 0.9–1.3 mm in diameter, parasitoids would bite their way out through holes whose diameter ranges from 0.3–0.7 mm. Success of *B. pallida* development can be thus estimated by the size of flight holes. Such estimation is however distorted by the fact that a small part of the larvae or pupae of parasitoids hibernates in the galls. In the Brno region, parasitoids (including inquilines) killed 30–100 (on average 65) percent of *B. pallida* population. Percentage of parasitisation greatly fluctuated in the respective localities (even in individual galls). The species spectrum of parasitoids was not identified.

III: *Dimensions of inner galls of B. pallida, their inner cavities and wall thickness. Brno region, 2014*

Month	Average length/width of inner galls (mm)	Average length/width of cavities (mm)	Wall thickness (mm)	
			from–to	average
April	1.8/1.2	0.9/0.7	0.5–0.9	0.70
May	2.2/1.5	1.8/1.2	0.3–0.4	0.35
June	2.4/1.6	2.3/1.5	0.08–0.12	0.10
July	?	?	?	?
Total	(2.1/1.4)	(1.6/1.1)	–	–

IV: *Cranium width, body length and width of larvae of individual instars of B. pallida (1 division = 0.0357 mm). Larvae of 1st, 2nd and 3rd instar had the cranium on average 0.29 mm, 0.45 mm and 0.56 mm wide, respectively. Brno region, 23 April–31 May 2014*

Cranium width (divisions)	Number of larvae			Mean body length (mm)			Mean body width (mm)		
	1st instar	2nd instar	3rd instar	1st instar	2nd instar	3rd instar	1st instar	2nd instar	3rd instar
7	30	–	–	0.4	–	–	0.3	–	–
8	37	–	–	0.4	–	–	0.4	–	–
9	25	–	–	0.6	–	–	0.5	–	–
10	10	11	–	0.6	0.9	–	0.5	0.6	–
11	–	31	–	–	1.2	–	–	0.6	–
12	–	58	–	–	1.3	–	–	0.7	–
13	–	83	5	–	1.3	1.4	–	0.8	0.9
14	–	30	49	–	1.4	1.4	–	0.8	0.9
15	–	4	86	–	1.3	1.4	–	0.8	1.0
16	–	–	112	–	–	1.5	–	–	1.0
17	–	–	45	–	–	1.7	–	–	1.1
18	–	–	12	–	–	1.9	–	–	1.3
19	–	–	3	–	–	1.9	–	–	1.2
20	–	–	3	–	–	2.2	–	–	1.4
Total/Mean (mm)	102	217	315	0.5	1.3	1.5	0.4	0.7	1.0
from–to	–	–	–	0.3–0.7	0.7–2.1	1.3–2.5	0.3–0.6	0.5–1.1	0.8–1.6

V: *Cranium width, body length and width in the grown-up 2nd instar larvae of B. pallida (1 division = 0.0357 mm). Larvae from 2014 had the head on average 0.42 mm wide and a small part of them diapaused. Larvae from 2015 had the head on average 0.45 mm wide and adults developed from them in the same year. Brno region, 31 May – 19 July 2014 and 4 May–13 July 2015*

Cranium width (divisions)	Number of larvae		Mean body length (mm)		Mean body width (mm)	
	2014	2015	2014	2015	2014	2015
9	5	2	1.3	1.4	0.6	0.7
10	12	9	1.3	1.1	0.7	0.6
11	44	31	1.5	1.4	0.8	0.7
12	70	36	1.7	1.7	0.9	0.8
13	42	31	1.9	1.7	1.0	0.9
14	5	23	1.8	1.7	1.0	0.9
15	3	16	2.0	1.7	1.1	1.0
16	–	5	–	2.0	–	1.2
Total/Mean (mm)	181	153	1.7	1.6	0.9	0.9
from–to	–	–	0.9–2.3	0.9–2.6	0.5–1.3	0.5–1.4

VI: *Length and width of B. pallida pupae in dependence on cranium width (1division = 0.0357 mm). Average cranium width was 0.79 mm. Brno region, 2014*

Cranium width (divisions)	Number	Body length (mm)	Body width (mm)
18	2	1.5	0.9
19	2	1.9	1.1
20	10	2.0	1.1
21	12	2.2	1.2
22	32	2.3	1.2
23	23	2.4	1.3
24	9	2.5	1.4
25	7	2.4	1.2
26	2	2.4	1.3
Total/Mean (mm)	99	2.3	1.2
from–to	–	1.4–2.9	0.8–1.5

VII: *Course of eclosion and size of adults of B. pallida from galls brought to the laboratory on 12 May 2014 (mm). Brno region, 2014*

Period of eclosion	Males				Females			
	Number	Average width		Average body length	Number	Average width		Average body length
		Head	Abdomen			Head	Abdomen	
15–31 May	13	0.81	0.7	2.7	15	0.85	1.4	3.0
1–15 June	18	0.80	0.8	2.5	29	0.75	0.9	2.4
16–30 June	16	0.81	0.8	2.4	103	0.78	1.1	2.6
1–15 July	6	0.80	0.7	2.3	10	0.83	1.0	2.5
Total/ Mean	53	0.80	0.8	2.5	157	0.78	1.1	2.6

VIII: *Size of B. pallida adults according to cranium width (1 division = 0.0357 mm). Average cranium width of males and females was 0.80 mm and 0.78 mm, respectively. Brno region, 2014*

Cranium width (divisions)	Number		Body length (mm)		Abdomen width (mm)		Thorax width (mm)	
	Males	Females	Males	Females	Males	Females	Males	Females
15	–	3	–	1.7	–	0.7	–	0.4
16	–	4	–	2.0	–	0.9	–	0.4
17	–	2	–	2.0	–	0.9	–	0.5
18	–	4	–	2.1	–	0.8	–	0.5
19	1	4	2.0	2.1	0.7	0.8	0.6	0.5
20	4	21	2.1	2.4	0.7	1.0	0.7	0.5
21	4	17	2.4	2.4	0.7	1.0	0.7	0.6
22	17	33	2.4	2.6	0. 8	1.0	0.8	0.6
23	15	25	2.5	2.8	0.7	1.2	0.8	0.6
24	9	28	2.7	2.9	0.9	1.2	0.8	0.6
25	3	16	3.0	3.0	1.0	1.3	0.8	0.7
Total/Mean (mm)	53	157	2.5	2.6	0.8	1.1	0.8	0.6
from–to	–	–	2.0–3.2	1.6–3.6	0.4–1.1	0.6–1.8	0.6–0.9	0.4–0.7

IX: *Size of individual developmental stages (incl. instars) of B. pallida (mm). Brno region, 2014*

Stage/instar		Number	Size from–to (average)		
			Cranium width	Body length	Body width
Eggs (prior to eclosion)		252	–	0.3–0.5 (0.4)	0.3–0.4 (0.4)
Larvae of 1st instar (prior to moulting)		25	0.28–0.36 (0.31)	0.5–0.9 (0.6)	0.4–0.6 (0.5)
Grown-up larvae of 2nd instar (prior to diapause)		181	0.32–0.57 (0.42)	1.1–2.3 (1. 7)	0.5–1.3 (0.9)
Grown-up larvae of 3rd instar (prior to pupation)		407	0.43–0.71 (0.56)	1.2–2.0 (1.5)	0. 9–1.3 (1.0)
Pupae (males + females)		104	0.64–0.93 (0.79)	1.4–2.9 (2.3)	0.8–1.4 (1.2)
Adults	**Males**	53	0.64–1.00 (0.80)	1.8–3.4 (2.5)	0.5–1.1 (0.8)
	Females	157	0.60–0.90 (0.78)	1.6–3.6 (2.6)	0.6–1.6 (1.1)

Inquilines

Galls of *B. pallida* in the Brno region often exhibit development of the larvae of *Curculio villosus* F. (Curculionidae). In April and at the beginning of May, the weevil deposits eggs into the growing and freshly grown-up galls. The eggs are semi-glossy, whitish to yellowish, oval-shaped, 0.6–0.7 mm long and 0.5–0.6 mm wide. Females push them with their rostrum into 2–5 mm long hyponomes bitten in the parenchymatic tissues of the galls. Larvae emerge from the eggs in about 10 days, moult three times (i.e. they have four instars) and reach maturity in the second half of May and first half of June. Their head is 0.85–1.25 (on average 1.07) mm wide, body is 3.2–5.7 (on average 3.7) mm long and 1.6–2.1 (on average 1.8) mm wide. Grown-up larvae leave the galls from the end of May to mid-June and crawl into the ground. Their leaving holes are circularly oval, 1.2–2.0 mm in diameter.

On the surveyed sites, the weevil infested 0–100 (on average 40)% of galls. The galls contained max. 10 (on average 3.3) larvae. About 20% of weevil larvae died due to parasitisation or premature drying out of galls. The larvae mine in gall tissues, transforming them into cylindriform frass pellets and fine amorphous bore dust. If they would run up with a gall wasp or another inhabitant of the gall, they would kill it. Occurring at higher numbers, they can kill up to a third of gall inhabitants.

Common inquilines in the galls of *B. pallida* are *Synergus* spp. (Cynipidae). Females of *Synergus* deposit eggs in April and at the beginning of May into young galls. Larvae develop in cells localized in middle parts of the galls and pupate in the galls from mid-May. Adults emerge from the end of May to the beginning of July. Adults were emerging from galls brought to the laboratory from various localities in the Brno region on 12 May 2014 from 20 May to 2 July, i.e. by 1–2 weeks earlier than *B. pallida*. Individuals of both sexes emerged at the same time in the ratio 1 ♂ : 2.2 ♀♀. Adults were emerging from galls found in Bílovice nad Svitavou on 11 May 2018 from 20 May to 4 June in the ratio 1.3 ♂♂ : 1 ♀. Galls collected in Brno-Komín yielded only females, which emerged in the first half of June. Unlike *B. pallida*, both sexes of *Synergus* spp. are winged. The genus of *Synergus* spp. was represented only by 8.4% in the total number of emerged adults of Cynipidae. The regulatory influence of *Synergus* spp. cynipids is apparently low in the Brno region.

Literary sources indicate that the galls of *B. pallida* may host also the caterpillars from the genus of *Pammene*, namely *P. argyrana*, *P. gallicollana* and *P. albuginana* (Tortricidae). In the Brno region, the caterpillars were found only in 2% of galls, at all times individually from mid-April to the beginning of July. As a rule, they caused damage only to the outer parenchyma and had hardly any significant impact on the mortality of the gall wasp. Rare inhabitants of buds injured by *B. pallida* in the Brno region are individuals of *Clinodiplosis* prope *biorrhizae* (Cecidomyiidae). In Brno-Komín, there were up to 23 (on average 5.0) of gall midge larvae found on 24 April 2016 in the buds of *Q. robur* (average length 6.5 mm and width 3.2 mm) together with the eggs and larvae of *B. pallida*, whose average length and width was 2.14 mm and 0.64 mm, respectively. Towards the end of April, gall midge larvae often occurred also in buds injured by late frost.

In the Brno region, birds injured on average 3.1% of galls and sporadic injuries by insects were observed at the end of April and in May. In galls harmed by birds, *B. pallida* was killed at 10–100%, in the galls injured by insects (probably by polyphagous species of Carabidae) only at 0–10%.

Nevertheless, the two agents participated only minimally in regulating the pest abundance. Gall tissues contain tannins and phenolic substances, which apparently repel wildlife (Stone *et al.*, 2002).

Late frosts can have a very negative impact on the eggs and larvae of *B. pallida*. A severe frost damage to the flushing *Q. robur* occurred on 28 and 29 April 2016 in Brno-Komín, which was survived only by individuals (eggs and young larvae) surrounded by the tissue of developing galls. Freshly deposited eggs and larvae hitherto localized freely in the cavity near the bud meristem were killed. Since the impact of frost on the *B. pallida* population was devastating, galls occurred only sporadically on this site in 2016.

Economic importance

According to Escherich (1942), galls of *B. pallida* occur primarily on shrubs and mid-aged trees of 5–10 m in height. Gauss (1982), for example, mentions plentiful to mass infestation of mainly older woody plants. In the Brno region, the galls were found mostly on grown-up trees, rarely on the woody plants of the youngest age classes. In the Vranov Forest District, sporadic damage to 2–5 years old oak trees in the understorey was recorded in 2018. Galls were also found not abundant on 10–25 cm long epicormic branches on the stems of older oak trees with the diameter at breast height ranging around 40 cm.

An unprecedented outbreak of *B. pallida* occurred in 2014 on a 7 m high solitary *Q. robur* in Brno-Komín. Galls were coming to age there towards the end of April and at the beginning of May, and often enveloped last year's shoots in large clusters. Shoots and branches were bending under the weight of huge numbers of galls and even sporadically breaking due to gusty wind. At the first sight, the oak resembled a wide-spreading apple tree with thousands of green, yellow and reddish apples. Due to their striking resemblance to apples, cecidia are aptly denoted in English as oak apple galls, in German Eichäpfel, in Russian dubovye jabloka etc. Broken shoots with galls were found on the ground in other localities, too (e.g. in the Pozořice Forest District in 2016). The galls dry out after the emergence of adult individuals by which their weight would considerably decrease and the danger of shoot breakage would cease to exist.

Gall wasp *B. pallida* damages buds on the last year's shoots of oaks and weakens them physiologically, negatively affecting not only increment but also aesthetic appearance of trees especially in botanical gardens and parks. Since the pest as a rule does not represent a serious risk to the health condition of oak trees, it is usually not necessary to fight against it. In young trees, timely removal of galls and their burning is advised.

CONCLUSION

This paper is a result of several years of studying occurrence, biology and galls of the bisexual generation of *Biorhiza pallida* in the Brno region. Our findings include among other things the following facts:

1) Galls of *B. pallida* were most frequently found on *Quercus petraea* and on *Q. robur*, less often on *Q. dalechampii* and scarcely on *Q. polycarpa*. *Q. robur* was infested more often and more intensively than the most abundant *Q. petraea*.
2) Females of unisexual generation deposited eggs at the end of winter period into average- to above-average sized terminal and sub-terminal buds on the last year's (rarely of year before the last) shoots. They deposited 2–290 (on average 83.6) eggs into one bud. Larvae of bisexual generation emerged from eggs as late as at the time of oak trees flushing. In 2014, larvae came to age in May (3rd instar). In the extremely hot and dry growing season of 2015, they came to age in the 2nd instar.
3) Adults of bisexual generation were leaving the galls from the end of May to the end of July, and their occurrence showed a slight (one-week) protandry. Females outnumbered males by 3–4.5 times. Only females and only males emerged from 64.3% and 21.4% of galls, respectively, and 14.3% of galls yielded individuals of both sexes. Males were at all times macropterous, females were apterous in 88.5%, micro- to brachypterous in 10% and macropterous in 1.5%.
4) Galls started to develop in the first half of April and reached their final size in the second half of April (or at the beginning of May). Grown-up galls were 3–35 (on average 15.2) mm high and 3–45 (on average 20.2) mm wide. Mean height of galls was by 33% lesser than their mean width.

The mean size of buds and their percentage of damage as well as the average number of eggs in the galls and the mean size of galls increased with the increasing size of shoots.

5) Parasitoids (mainly from the superfamily of Chalcidoidea) incl. parasitoid inquilines killed 30–100 (on average 65) percent of *B. pallida* population. A greater part of parasitoid larvae pupated in June and July and imagos were leaving the galls. A smaller part of the parasitoids hibernated in the galls at the stage of larva or pupa.
6) On average 40% of *B. pallida* galls were found with the eggs and larvae of Curculio villosus (Curculionidae). Females deposited eggs from April to the beginning of May. Larvae were coming up to age in the 4th instar in the second half of May and first half of June, and they were crawling into the ground from the end of May to mid-June. Occupied galls contained up to 10 (on average 3.3) larvae, which killed as much as up to a third of *B. pallida* larvae.
7) On average 10% of *B. pallida* galls were infested by the gall wasp *Synergus* spp. (Cynipidae). Females deposited eggs into young galls in April until the beginning of May. Larvae pupated from mid-May and adults were emerging from the end of May to the beginning of July. Regulatory importance of the species was low.
8) In April 2016, nearly all eggs and freshly emerged larvae of *B. pallida* in Brno-Komín were killed by late frosts.
9) Galls occurred most frequently on mid-aged trees, sporadically also on young growths and last year's epicormic shoots of old oak trees. A mass gall wasp outbreak weakens the trees physiologically and furthermore impairs their aesthetic value in parks and botanical gardens. Protective measures are usually not necessary.

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