



## Extremely low infection levels of pathogens and nematodes in *Trypodendron* spp. (Coleoptera: Curculionidae)

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### Abstract

The striped ambrosia beetles *Trypodendron lineatum* and *T. domesticum* are timber forest pests in the Palearctic region and North America. Because only a few pathogens are known for *Trypodendron* species, the aim of this work was to determine the spectrum of pathogen species of *T. lineatum*, *T. laeve*, and *T. domesticum*. *Trypodendron* species were collected in pheromone traps at nine localities in the Czech Republic, five localities in Poland, and one locality in Austria. In total, 2,439 *T. lineatum*, 171 *T. domesticum*, and 17 *T. laeve* beetles were dissected and examined. Infection was found in only two of the 17 specimens of *T. laeve* and in only two of the 171 specimens of *T. domesticum*; in all four cases, the parasites were nematodes. Parasitisation of *T. lineatum* by nematodes was found in *T. lineatum* at eight localities with a mean ( $\pm$  SE) parasitisation level of  $8.1 \pm 4.7\%$ . A *Chytridiopsis* sp. was detected in cells of the midgut epithelium of one *T. lineatum* specimen, and *Gregarina* sp. was detected in the midgut lumen of two *T. lineatum* specimens; no other pathogens were found in *T. lineatum*. The low infection rates and the tendency for infection by nematodes can be explained by the monogamy of *Trypodendron* spp. and their feeding on fungi in short galleries that are not connected to the galleries of conspecifics.

**Keywords:** *Trypodendron* spp.; nematodes; *Chytridiopsis* cf. *typographi*; *Gregarina* cf. *typographi*; monogamy

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### 1. Introduction

Ambrosia beetles (including *Trypodendron* spp.) are persistent forest pests that significantly reduce the quality of cut wood by producing dark-stained pin holes in lumber or in veneer processed from infested logs. Wood degradation and dark staining arise from the growth of associated fungi (“ambrosia fungi”) that are carried into the sapwood by parental adult beetles and that serve as food for their larvae (Massoumi Alamouti et al. 2009; De Fine Licht & Biedermann 2012).

The various species of ambrosia beetles attack both conifers and deciduous trees. The beetles typically attack trees that have been cut or weakened by disease, but some taxa attack apparently healthy trees (Kühnholz et al. 2001). In addition to reducing value of wood products by generating pinholes and staining, the beetles can also vector fungi that are highly pathogenic to living trees (Hulcr & Dunn 2011; Suh et al. 2011; Evans et al. 2013; Freeman et al. 2013; Carrillo et al. 2014).

While the striped ambrosia beetle *Trypodendron lineatum* (Olivier, 1795) and *T. domesticum* (Linnaeus, 1758) are recognized as timber forest pests in the Palearctic region and North America (Wood 1982), the importance of the ambrosia beetle *T. laeve* (Eggers, 1939) is unclear. *T. laeve* is apparently rare but has been occasionally detected in many

parts of Europe (Muona 1994; Martikainen et al. 1996, 1999; Martikainen 2000; Daisie 2009; Kirkendall & Faccoli 2010; Knížek 2011; Lukášová et al. 2012).

The species of pathogens that attack bark beetles in the genus *Ips* have been well described for the most important species in this genus (Wegensteiner 2004; Takov et al. 2010; Lukášová & Holuša 2012; Holuša et al. 2013; Lukášová et al. 2013), including the European spruce bark beetle (*Ips typographus*) (Linnaeus, 1758) and the economically important species associated with spruce in Central Europe (Christiansen & Bakke 1988; Wermelinger 2004). In contrast, only a small number of pathogens of *Trypodendron* species have been described.

The microsporidium *Pleistophora xyloteri* (Purrini & Ormières 1981) was described in *T. domesticus* (syn. *Xyloterus domesticus*) in Lower Saxony. According to this one report, *P. xyloteri* spreads in the cells of the posterior part of the beetle midgut. The pathogen also invades oenocytes on the surface of the gut, and the infected elements form spherical pseudocysts with masses of spores. In the specimens examined by Purrini & Ormières, only spores were present. They were broad and oval and ranged from  $2.5 \times 2.0 \mu\text{m}$  to  $4.0 \times 2.3 \mu\text{m}$ ; the most common size was  $3.0 \times 2.0 \mu\text{m}$ . Such variability in the size of spores is common among microsporidian parasites of bark beetles. Purrini & Ormières (1981) also observed the presence of one spheri-

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cal nucleus in the middle of the spore. Although the authors examined almost 500 beetles from 11 localities, the rate of infection was only 2%, and infection was detected in only two localities.

In *T. lineatum*, the bacteria *Pseudomonas caviae*, *Pseudomonas septica*, *Cloaca cloacae*, and *Bacillus coagulans* have been reported (Novák 1960; Lysenko 1959). Fungi detected in *T. lineatum* include *Beauveria bassiana* (Magama et al. 1981), *Paecilomyces farinosus* (Kirschner 2001), and *Mucor hiemalis* (Magama et al. 1981). In laboratory tests, Novák & Samsinakova (1962) found that *B. bassiana* caused 100% mortality of *T. lineatum* larvae in 6 to 8 days and 100% mortality of adults in 12 days. The latter authors also found that the effects of temperature, humidity, spore formulation, and spore dose on the infection of *T. lineatum* by *B. bassiana* were similar to those reported by Pražák (1988, 1991, 1997) for other bark beetle species, but different test conditions caused 36% to 55% mortality in most cases, while only a few experiments lead to mortality rates higher than 80% (Pražák 1988, 1991, 1997). Novák & Samsinakova (1962) reported that male beetles inoculated with *B. bassiana* transmitted the fungus to healthy female beetles and that the transmission reduced the number of eggs laid by 20%. Application of *B. bassiana* spores to the bark surface reduced the number of

egg niches by up to 44% depending on the spore concentration, and treatment of soil caused 88 to 100% mortality of hibernating offspring beetles (Pražák 1988).

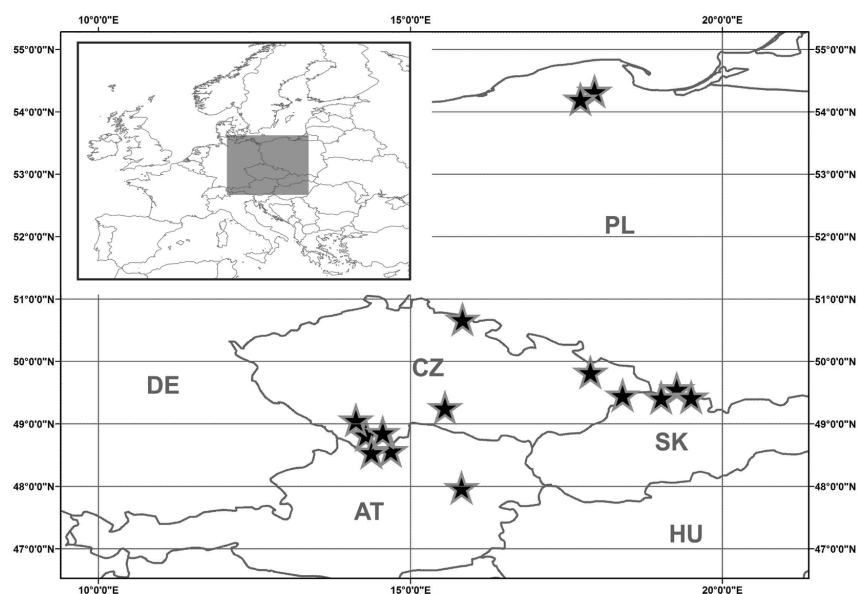
The aim of the current research was to determine the spectrum of species pathogenic to *T. lineatum*, *T. laeve*, and *T. domesticum* in Central Europe.

## 2. Methods

*Trypodendron* species were studied at nine localities in the Czech Republic, five localities in Poland, and one locality in Austria. Beetles were collected with Theysohn pheromone traps containing the lure Linoprax®, Trypodor®, or XL Ecolure® (Table 1, Fig. 1). Traps were placed in forests or, as in the Austrian location, near the forest in early March and were checked at 1-week intervals until the end of June in 1998, 2010, and 2011. The trapped beetles were individually placed in 2-cm<sup>3</sup> Eppendorf micro-test tubes with a piece of wet gauze to maintain 100% relative humidity. The beetles from all localities except Austria were immediately frozen and stored at –10 °C until they were dissected. The beetles collected in Austria were immediately dissected or were stored for < 8 days at 4 °C before they were dissected.

**Table 1.** Background information on *Trypodendron* beetles trapped and dissected in this study. A = Austria; CZ = Czech Republic; PL = Poland; Lae, Lin, and Dom = number of *T. laeve*, *T. lineatum*, and *T. domesticum*, respectively.

Locality	GPS coordinates	Altitude [m a.s.l.]	Year	Lae	Lin	Dom	Pheromone lure
Dubová (CZ)	48°45'N, 14°23'E	790	2011	5	20	—	XL Ecolure
Hainfeld/Ramsau (A)	47°59'N, 15°49'E	500	1998	—	31	—	Linoprax
Hněvanov (CZ)	48°41'N, 14°25'E	700	2011	12	17	3	XL Ecolure
Horní Maršov (CZ)	50°41'N, 15°50'E	850	2011	—	208	4	XL Ecolure
Hradec nad Moravicí (CZ)	49°50'N, 17°53'E	500	2011	—	1,220	114	XL Ecolure
Jaronín (CZ)	48°58'N, 14°13'E	735	2011	—	2	—	XL Ecolure
Jeleśnia (PL)	49°34'N, 19°16'E	850	2011	—	161	12	Trypodor
Kartuzy (PL)	54°20'N, 17°57'E	260	2011	—	270	15	Trypodor
Lazec (CZ)	48°50'N, 14°17'E	800	2011	—	21	—	XL Ecolure
Lipusz (PL)	54°14'N, 17°47'E	170	2011	—	28	—	Trypodor
Otín (CZ)	49°16'N, 15°33'E	590	2011	—	16	—	XL Ecolure
Staré Hamry (CZ)	49°28'N, 18°24'E	525	2011	—	42	—	XL Ecolure
Tichá (CZ)	48°38'N, 14°33'E	750	2010	—	12	—	XL Ecolure
Węgierska Górka I. (PL)	49°32'N, 19°11'E	860	2011	—	66	13	Trypodor
Węgierska Górka II. (PL)	49°32'N, 19°14'E	1100	2011	—	325	10	Trypodor



**Fig. 1.** Map of study localities in 1998, 2010, and 2011.

Each beetle was dissected by removing the whole gut together with parts of the muscles, the fat body, Malpighian tubules, and ovaries or testes (Wegensteiner et al. 1996). The dissected tissue was then inspected with a light microscope at 40 to 400× magnification.

### 3. Results

In total, 2,439 *T. lineatum*, 171 *T. domesticum*, and 17 *T. laeve* beetles were trapped and examined (Table 1).

In *T. laeve*, parasites were found in only two of the 17 specimens. Again, nematodes in both cases, were located in the intestines of specimens from Hněvanov.

In *T. domesticum*, parasites were found in only two of the 117 specimens. Once again, nematodes were the only parasites detected; nematodes were found in one male from Jelešnia and in one female from Węgierska Górka I.

In *T. lineatum*, nematodes were the main parasites detected. They were detected in *T. lineatum* from eight of the 15 localities, and the average ( $\pm$  SE) parasitisation level was  $8.1 \pm 4.7\%$ . One *T. lineatum* beetle had *Chytridiopsis* sp. in the cells of its midgut epithelium, and two beetles had *Gregarina* sp. in their midgut lumina (Table 2). No other parasites were found in *T. lineatum* specimens.

**Table 2.** The percentage of *Trypodendron lineatum* specimens at the 15 localities with parasites.

Localities	Nematodes	<i>Chytridiopsis</i> sp. [%]	<i>Gregarina</i> sp.	Number of specimens examined
Dubová (CZ)	—	—	—	20
Hainfeld/Ramsau (A)	—	3.4	6.9	31
Hněvanov (CZ)	12.0	—	—	17
Horní Maršov (CZ)	—	—	—	208
Hradec nad Moravici (CZ)	—	—	—	1,220
Jaronín (CZ)	—	—	—	2
Jelešnia (PL)	3.1	—	—	161
Kartuzy (PL)	—	—	—	270
Lazec (CZ)	4.8	—	—	21
Lipusz (PL)	7.1	—	—	28
Otín (CZ)	11.1	—	—	16
Staré Hamry (CZ)	—	—	—	42
Tichá (CZ)	16.7	—	—	12
Węgierska Górka I. (PL)	1.5	—	—	66
Węgierska Górka II. (PL)	8.3	—	—	325

### 4. Discussion

Bark beetles include highly aggressive tree-killers, facultative colonizers of weak or recently killed trees, less-aggressive consumers of living trees, and saprophagous exploiters of dead trees (Paine et al. 1997). As is true for many insects with microbial symbionts (Martin 1987), bark beetles feed in nutritionally poor substrates including woody tissues, bark, and phloem, fruits, and the pith of twigs. Associations with fungi are apparently universal within this group, and many species have specialized structures, termed mycangia, for the transport of fungi (Wood 1982).

Ambrosia beetles represent the most advanced of such associations, and this specialization has allowed them to exploit the three-dimensional niche of xylem and not to be limited to the essentially two-dimensional niche of inner bark, where competition with other phloeophagous organ-

isms may be fierce (Lindgren & Raffa 2013). *Trypodendron* spp. are included among ambrosia beetles because the brood in the chambers along the galleries feed on a cultivated ambrosia fungus. Adults bore into dead trees and winter-felled logs and introduce “ambrosia” fungi upon which they and their larvae feed (Borden 1988). Infestation density is indicated by the number of penetration holes in the host, and *T. lineatum* can produce almost 400 entrance holes/m<sup>2</sup> (Borkowski & Skrzecz 2016).

The genus *Trypodendron* includes 14 species (Robideau et al. 2015) that differ in the amount of damage they cause to host trees, as well as in geographic distribution and host range. The most economically important species *T. lineatum* commonly attacks coniferous trees. On the contrary, *T. domesticum* is usually found in deciduous forest (Salom & McLean 1990; Petercord 2006; Humble 2009). It was therefore not surprising that, in the current study, *T. lineatum* was the most abundant and most common of these beetles, followed by *T. domesticum* and *T. laeve*.

In bark beetle genera other than *Trypodendron*, larvae and offspring beetles can feed in the gallery formed by the parent and also in the galleries formed by neighbouring beetles because the galleries could interconnect. This facilitates the horizontal transfer of pathogens that are spread perorally via pathogen-loaded faeces (for pathogens localized in the intestine, including *C. typographi* and *G. typographi*) and of those that are transmitted after the death of the host [for pathogens localized in the fat body, such as *Mattesia schwenkei* (Purrini, 1977)]. Infection levels by these pathogen species are influenced by beetle population density (Wegensteiner & Weiser 1996). In contrast, the gallery systems of *Trypodendron* species don't interconnect, and offspring larvae only feed on fungi in their own galleries. This may explain why nematodes were the dominant parasite at some localities and why levels of infection were very low in the current study relative to those reported for *Ips* spp. (Grucmanová & Holuša 2013; Grucmanová et al. 2014, 2016).

The low rate of parasitism documented in the current study may also be explained by monogamy of *Trypodendron* spp. Females initiate the attack and are joined by a single male. Although the *Trypodendron* male remains with the female in the gallery and helps the female clean the gallery (McIntosh 1994), only one pair of beetles is in close contact per gallery. In polygamous species, like *Ips* spp., the male initiates the attack, generally by excavating a nuptial chamber, and mates with several females (Raffa et al. 2015). This increases parasite transmission and infection levels in the population (Lukášová & Holuša 2011).

Other than nematodes, only two pathogens were found in the current study: a *Chytridiopsis* sp. and a gregarine *Gregarina* cf. *typographi* commonly occur in the midgut of a number of representatives of the Scolytinae subfamily, and their infection level varies greatly among sites (Takov et al. 2007; Holuša et al. 2009; Takov et al. 2010). *Chytridiopsis typographi* [(Weiser, 1954) Weiser, 1970] also occurs in many species of bark beetles (Haidler 1998; Händel et al. 2001) and is apparently a non-specific pathogen in the intestine of a number of pests in coniferous stands (Wegensteiner 2004). The *G. cf. typographi* infection level varies greatly



(Holuša et al. 2009; Wegensteiner et al. 2010). Because molecular and morphological data were lacking or limited in the current study, we presented both pathogens only as *Chytridiopsis* sp. and *Gregarina* sp.

## 5. Conclusion

The current study documents very low infection levels by pathogens and nematodes of the ambrosia beetles *T. lineatum*, *T. laeve*, and *T. domesticum*. We suspect that the low infection levels result from the monogamy and feeding behaviour of *Trypodendron* species. These ambrosia beetles feed on fungi in galleries that do not connect with the galleries of conspecifics; this reduces contact and therefore the probability of horizontal transmission.

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