

Phorbia phrenione (Seguy) (Diptera: Anthomyiidae) in Finland

Henry Väre & Juhani Itämies

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Phorbia phrenione (Seguy) is a poorly known fly in Finland; it is not included in the list of Finnish Diptera. *P. phrenione* feeds on an Ascomycete (*Epichloe typhina*: Clavicipitaceae), which infects the culms and leaves of various grass species. Based on the occurrence of eggs and larval covers in the stroma of its mutualistic counterpart *E. typhina* in herbarium specimens, the distribution of the fly in Finland was mapped. Eggs and larval covers occurred in over 90 % of herbarium specimens. *E. typhina* and *P. phrenione* are scattered but widely distributed in Finland, its northernmost positions being in the parishes of Enontekiö and Utsjoki. Only the fjeld region seems to be completely outside its range. *E. typhina* prefers *Dactylis glomerata* and *Phleum pratense* in southern Finland, but *Calamagrostis lapponica* and *C. purpurea* subsp. *phragmitoides* in northern Finland. It seems appropriate to assume that *E. typhina* and have reached Finland from two directions, as evidenced by the lack of both *E. typhina* and *P. phrenione* in Central Finland. Populations in SW Finland apparently originate from Central Europe, and those in northern Finland from the east. These assumptions are further supported by the fact that grass species infected by *E. typhina* in SW Finland are the same as those in Central Europe, but in northern Finland only *Calamagrostis* species are infected. This is a rare host genus in Central Europe; the species which host *E. typhina* and *Phorbia phrenione* there are not the same as in northern Finland. The nesting habitats are usually dry meadows in southern Finland, whereas in northern Finland the nesting habitats are moist forests, often situated near lakes or small rivers. In southern Finland *P. phrenione* often occurs in urban areas too.

Väre, H. Department of Botany, University of Oulu, P.O. Box 400, FIN-90570. Oulu, Finland

Itämies, J. Department of Zoology, University of Oulu, P.O. Box 333, FIN-90570 Oulu, Finland

Introduction

Phorbia phrenione (Seguy) is a fly feeding on an ascomycete, *Epichloe typhina* (Pyrenomycetes: Clavicipitaceae) (Kohlmeyer & Kohlmeyer 1960, Eckblad & Torkelson 1989). Only a few other ascomycetes are consumed by Diptera, e.g. *Daldinia concentrica*, *Gyromitra* spp., *Morchella esculenta* and *Verpa bohemica*, although basidiomycetes are commonly devoured by Diptera (Hackman & Meinander 1979, Hingley 1971, Yakovlev 1988). Most *Epichloe* species are tropical; only *E. typhina* reaches Fennoscandia. Seven species of the genus *Phorbia* have so far been recorded in Finland (Hackman 1980). Relatively little is known about the larval habits of *Phorbia*; *P. haberlandta* (Schmér) and *P. securis* Tiensuu mine in stems and shoots of various grasses (Ferrar 1987).

The global distribution of *E. typhina* and *P. phrenione* was mapped by Kohlmeyer &

Kohlmeyer (1974) and the Finnish distribution of *E. typhina* by Koponen & Mäkelä (1976). Kohlmeyer & Kohlmeyer (1974) examined two *E. typhina* samples collected in SW Finland, and were the first to report that *P. phrenione* occurs in Finland. However, this article has not been recognized by Finnish entomologists, and thus *P. phrenione* is not included in the list of Finnish Diptera (Hackman 1980). In this article we present the distribution of *P. phrenione* in Finland by checking the occurrence of eggs and larval covers in the herbarium specimens of *E. typhina*.

Recognition of the fly

Both the key to the species and a more specific description of the genus *Phorbia* are found in Hennig (1970), but below are given some features important in identification of the fly. Its length varies from four mm (male) to four and half mm (female). The thorax of the male is dull

gray-brownish, with three dark longitudinal stripes. The bristles on the shoulders are long. The wings are light, with gray hairs and yellowish veins, and have very small hairs on the edges. The halteres are yellow and the legs are black. The abdomen looks similar to the thorax from the front but without visible dark stripes. From behind the colouration seems much lighter, and in the middle of each tergite there is a narrow longitudinal triangle the fore edge of which is connected to a dark cross stripe. The female has a more grayish thorax, and it is less hairy. The male genitalia have a mesolobus with short (knapplike) projections which are separated by a wide roundish cap and simple surstylii which are not forked. A photograph of an adult is presented in Kohlmeyer and Kohlmeyer (1974).

Ecology of *E. typhina* and *P. phrenione*

The infection by *E. typhina* is systemic, meaning that once it is established, the fungi spreads vegetationally alongside with the grass clone. Thus the complete clone is usually infected, the size of the patch often reaching a few square metres. Occurrence of the stroma on the grass prevents usually the emergence of the inflorescence and is commonly known as "choke disease". However, sometimes seeds ripen and then the fungi spreads in these (Kohlmeyer & Kohlmeyer 1974). As larvae, *P. phrenione* feeds only on stroma of *E. typhina* and on culms and leaves of infected grass tissue. Adults are also known to feed on *E. typhina* in its conidial state. These asexual spores remain viable after passing through the fly's digestive tract and are able to germinate. Since *E. typhina* is heterothallic (White & Bultman 1987), an out-crossing ascomycete, copulation of hyphae of different genetic origin must proceed before sexual reproduction can take place, and *P. phrenione* is the only known vector for *E. typhina* conidial spores (Kohlmeyer & Kohlmeyer 1974). Because the occurrence of *E. typhina* is patchy, the wind is obviously an ineffective means of spore dispersion.

The formation of perithecia begins only after a visit by the fly, during which the fly deposits its white eggs (Kohlmeyer & Kohlmeyer 1974). Then the stroma turns yellow-orange, as a result of the growth of mycelium that contain carotenoids over the surface of the white primary anamorph stroma (White & Bultman 1987).

The eggs as well as the cover of larval burrows (probably composed of faecal material) remain in herbarium specimens of *E. typhina*. This conspicuous feature facilitates recognition

of the visit by *P. phrenione*, especially since other insects are not known to feed on *E. typhina*. *E. typhina* and related species in section *Balanisae* (Clavicipitaceae) produce a range of ergot alkaloids, which act as defence against herbivory and most insects or mammals do not feed on infected grasses (Clay 1988). *P. phrenione* must have evolved a mechanism for detoxification of these defensive substances. Thus this relationship is a highly specialized form of mutualism, as was already noted by Bradshaw (1959), and is comparable to pollination of flowering plants by insects or other animals. The life cycles of *E. typhina* and *P. phrenione* are described in more details by Kohlmeyer & Kohlmeyer (1960, 1974) and by Eckblad & Torkelson (1989). The flies appear in early summer, at the time when conidial stromata develop on diseased culms of grasses. The white elongate egg is attached to the surface, and a larva hatches four days later. The larva goes through three instars under an oblong cover, all the time feeding on the stroma and also penetrating the interior of the culm. In late summer the larvae leave their covers to pupate in the soil under the host plant. There seems to be one generation per summer. Kohlmeyer & Kohlmeyer (1960) found it especially difficult to get the pupae to hatch - this succeeded in conditions most closely resembling natural ones.

Material and methods

Phorbia phrenione (Seguy) eggs and larval covers (Fig. 1) and devoured culms and stroma (Fig. 2), were checked in the herbarium (H, KUO, OULU, TUR, TURA, collections in Department of Plant Pathology, University of Helsinki) specimens of *Epicloe typhina* (Fr.) Tulasne. About 300 specimens were investigated (240 collections, when duplicate specimens were excluded), many of which were listed by Koponen & Mäkelä (1976) and thus are not listed again here. The Finnish samples examined by Kohlmeyer & Kohlmeyer (1974) were re-examined (deposited in B and NFC) in order to get verify on the identity of eggs and larval covers.

Results and discussion

The distribution of *P. phrenione* and *E. typhina* in Finland is presented in Fig. 3. Being large and conspicuous, *E. typhina* has been collected very often, although it is of course possible that there are gaps as to the intensity of collection in various parts of Finland. The range of distribution extends northwards over 1000 km in Finland when compared against the distribution map

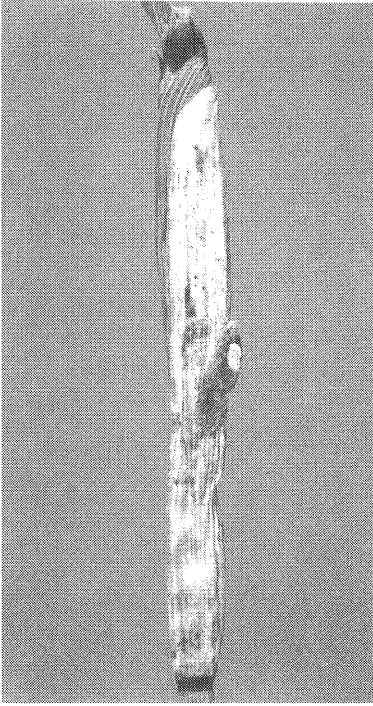


Fig. 1. Egg and larval cover of *P. phrenione* on *E. typhina* growing over a grass culm.

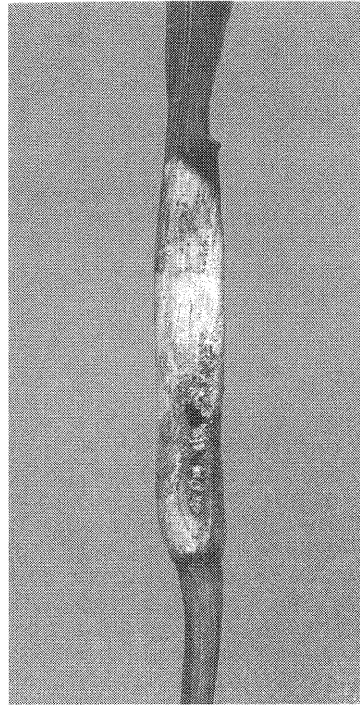


Fig. 2. Grass culm and *E. typhina* stroma devoured by *P. phrenione*.

presented by Kohlmeyer & Kohlmeyer (1974), and agrees largely with the distribution reported in Norway, where the fly was found up to 69°27'N (Eckblad & Torkelson 1989); thus the fly now covers the western part of the European boreal zone. *E. typhina* is very common in southern Norway and Sweden, but rare in the north (Eriksson 1967, Eckblad & Torkelson 1989). This seems to be the case in Finland too.

It seems that *P. phrenione* is as common in southern Finland as it is in Central Europe, which was reported to be the centre of distribution (Kohlmeyer & Kohlmeyer 1974). However, Kohlmeyer & Kohlmeyer (1974) assumed that the distribution of the fly is more extensive than indicated on their map. Outside of Europe, the fly is widely distributed in North America; in addition, isolated stations have been found in Mexico and East Asia (Kohlmeyer & Kohlmeyer 1974).

Most Finnish specimens of *E. typhina* were found to include eggs and larval covers of *P. phrenione*. Only young stroma collected early in spring were unattacked, and certain graminoids contained stromata only rarely (Table 1). Grass

samples identified only to genus level are not included in Table 1. Usually there were only a few eggs in each stroma, but sometimes as many as 20 eggs were found. Perithecia were never found in samples collected in Finland in L, and they were also very rare in samples collected in Central and Southern Lapland. In addition, perithecia were rare in the genera *Agrostis* and *Festuca*. Perithecial stromata have also been reported to be rare in *Agrostis hiemalis* and *Festuca rubra* (Sampson 1933, White et al. 1991). These species are relatively small when compared with other graminoids infected by *E. typhina*, but it is not known whether the size of the host plant is important. Worldwide, about 80 grass species have been reported to be infected by *E. typhina* and its mutualistic fly (Kohlmeyer & Kohlmeyer 1974). Eriksson (1967) listed 18 grass species infected by *E. typhina* in Fennoscandia, 17 of which grow in Finland, though seven were found to be uninfected. Koponen & Mäkelä (1976) added 3 species to the Fennoscandian list of infected grass species. Today in total 21 grass species have been found to be infected by *E.*

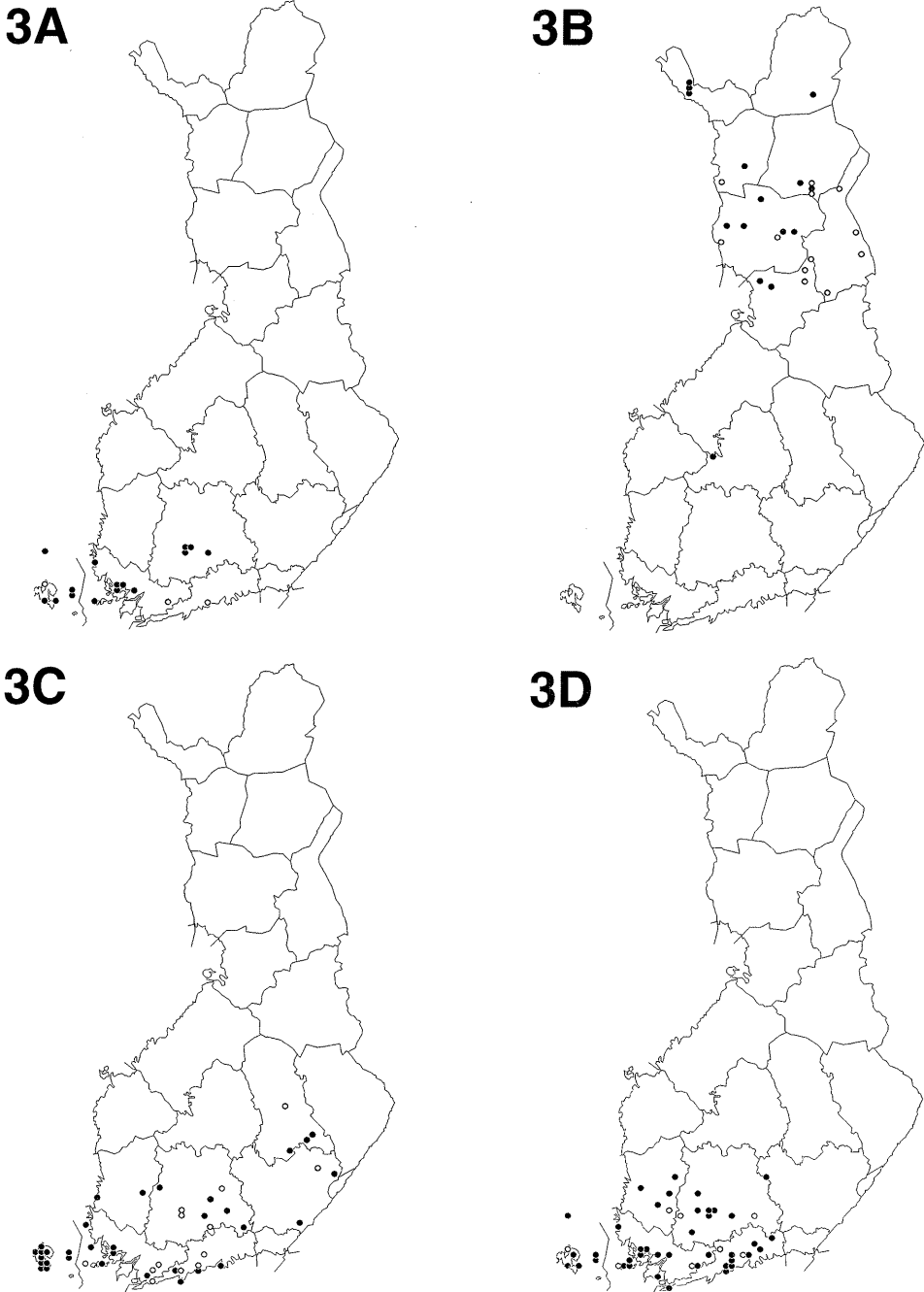


Fig. 3A-D. Occurrence (black dots) of *P. phrenione* eggs or larval covers on stroma of *E. typhina* growing over various grass species. A. *Agrostis capillaris*. B. *Calamagrostis lapponica* and *C. purpurea* subsp. *phragmitoides*. C. *Dactylis glomerata*. D. *Phleum pratense*. Open marks indicates samples which were not attached by *P. phrenione*.

Table 1. Plant species infected by *E. typhina*, their number of collections + = eggs or larval covers of *P. phrenione* found, - = not found.

Species	number of collections	infected/ not infected
<i>Agrostis capillaris</i>	24	+
<i>A. stolonifera</i>	1	-
<i>Alopecurus pratensis</i>	2	+
<i>Anthoxanthum odoratum</i>	4	+
<i>Avena pratensis</i>	2	+
<i>Brachypodium sylvaticum</i>	1	+
<i>Calamagrostis arundinacea</i>	4	+
<i>C. canescens</i>	1	-
<i>C. epigejos</i>	1	+
<i>C. lapponica</i>	6	+
<i>C. purpurea</i>		
subsp. <i>phragmitoides</i>	21	+
<i>C. stricta</i>	1	-
<i>Dactylis glomerata</i>	97	+
<i>Festuca rubra</i>	3	+
<i>Milium effusum</i>	1	+
<i>Phleum phleoides</i>	2	+
<i>P. pratense</i>	37	+
<i>Poa annua</i>	1	-
<i>P. nemoralis</i>	1	-
<i>P. pratensis</i>	4	-
<i>P. trivialis</i>	1	+

typhina in Finland (Table 1), 15 of which contained either *P. phrenione* eggs or larval covers or both.

E. typhina prefers *Dactylis glomerata* and *Phleum pratense* in southern Finland, but *Calamagrostis lapponica* and *C. purpurea* subsp. *phragmitoides* in northern Finland (Fig. 3). Rare grass hosts (Table 1) are not mapped. Most of these were found in southern Finland. Similar pattern in host plant selection was found also in Norway by Eckblad & Torkelson (1989). Even if collection intensity is taken into the consideration, it seems appropriate to suggest that *E. typhina* and *P. phrenione* have reached Finland and Norway from two directions, as evidenced by the lack of *E. typhina* in Central Finland (Fig. 3). Most obviously populations in SW Finland origin from Central Europe and those in northern Finland from the east, northern Russia. This is further evidenced by the fact, that grass species infected by *E. typhina* in SW Finland are the same than in Central Europe (Kohlmayer & Kohlmayer 1974), but *Calamagrostis* is rare host genus in Central Europe and the species which host *E. typhina* and *Phorbia phrenione* there are not the same than in Finland (Kohlmayer &

Kohlmayer 1974).

E. typhina strains are generally host specific (Leuchtmann & Clay 1990), which should provide a barrier to genetic exchange also between anamorph and teleomorph infecting different grass species (Schardl & al. 1991). Based on rRNA gene internal transcribed spacer sequences of *E. typhina* and its anamorphs in genus *Acremonium*, this fungus complex has obviously not coevolved with their host grasses. The sequence of teleomorph varied between strains infecting different host species, and it seems likely that the strains have arisen on multiple occasions (Schardl et al. 1991). The anamorph, *Acremonium*, is seed transmitted (White et al. 1991). Thus it is possible that the distribution of *E. typhina* strain infecting certain grass species is dependent on the spreading capability of *P. phrenione*. This could especially be true for *Calamagrostis*, which is the only known host genus in northern Finland and for *Dactylis glomerata* and *Phleum pratense* in southern Finland, since the distribution of these grasses are much broader than that of *E. typhina*. Also several other grass genera being infected (although rarely) by *E. typhina* in southern Finland are widely distributed in Finland. Many of these were not attached by *P. phrenione*, however, and in most cases perithecial formation was reduced in the other species.

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