



## **Cameraria ohridella Deschka & Dimic 1986**

David Lees, Carlos Lopez-Vaamonde, Sylvie Augustin, . Biodiversity Heritage Library, . Field Museum, . Museum of Comparative Zoology, . Macarthur Foundation, . Marine Biological Laboratory, . Missouri Botanical Garden, . Alfred P. Sloan Foundation, et al.

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# *Cameraria ohridella* Deschka & Dimic 1986

Animalia

Arthropoda

Insects

Lepidoptera

family Gracillariidae

genus *Cameraria*

## Overview

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### General Description

Small moth, adults around 3.5 mm in forewing length, orange-brown with basal white longitudinal streak and four whitish bent or interrupted fasciae edged in black, fringed towards dorsum (Figs 3, 4). Hindwings greyish brown, long-fringed on both sides. Head orange-tufted. Antennae over 4/5 forewing length. Legs equally banded white and black. Mines easily recognised as multiple conspicuous whitish yellow and brown blotches on surface of horse-chestnut leaves that cause significant browning towards the end of the summer (Fig. 1).

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

### Introduction

The horse-chestnut leafminer *Cameraria ohridella* Deschka and Dimi?, 1986 is a small species of leaf-mining moth in the family Gracillariidae. This species would probably have remained obscure but for its recent dramatic rise into public prominence as a result of a spectacular process of biological invasion in the past 25 years. The basic information given on this page marks the first quarter century of biological invasion of this species, since the first records reported within the type series information (i.e. 8-14 July, 1984). The moth's type locality is 6 km. south of Ohrid (Lake Ohrid) in Macedonia at 705 m. elevation, as reported in the original description (<https://www.orleans.inra.fr/content/download/2649/47277/version/1/file/D...>). The species was certainly present in the Balkans of Europe at least a few years previously, possibly longer. The species has come to wide public recognition in many countries only in the last decade owing to the extreme browning it causes to the white flowered, Common Horse-chestnut tree *Aesculus hippocastanum* L. (hereafter ?horse-chestnut?).

It is relevant to understand the history of this tree species in Europe. This tree derives its latin and common names in several languages from the use of its seeds or their extracts for prevention of equine pulmonary heart disease, coughs or parasites, a practice that dates back to such use in the Ottoman empire centered in Istanbul, which included the Balkans (Lack, 2000; 2002). This tree has been widely planted in European parks and cities since the 1570-80s (it was introduced to Paris around 1615: Augustin, 2005). By 1581, the "Castanea equina" had been introduced to Vienna from Istanbul by Karl Clusius, probably as a present from the Turkish Ambassador David Ungnad Graf von Weissenfels, and likely as a living tree (Lack, 2000). Leaf samples were earlier (1563) sent to Ulysse Aldrovandi in Bologna. In 1795-1798, the tree was first discovered growing naturally in the Pindus Mountains of Greece by English botanist John Hawkins, although it had been widely supposed to be of north Indian origin, as reflected in the French common name "Marronnier d'Inde" (Lack, 2000).

The fact then that the appearance of *C. ohridella* (and indeed the genus *Cameraria*) in much of Western Europe has been so recent and dramatic, without earlier detection by entomologists, has made its origin a far greater mystery than that of its hostplant. Originally thought to be a relict species in the Balkans (Deschka and Dimi?, 1986; Pschorn-Walcher, 1994; Grabenweger and Grill, 2000), where the horse-chestnut is considered to be a relict from the Tertiary period (Xiang et al., 1998; Avtzis et al., 2007; Harris et al., 2009), a more recent hypothesis (Hellrigl, 1998; 2001) is that the moth is an example of a sudden host plant shift to horse-chestnut, probably from maple or sycamore (*Acer* spp.), maybe combined with long distance translocation (Kenis et al., 2006; but see also under Origin). Another hypothesis is that this species may have originated in North America (e.g. Kenis et al., 2005), but this is not considered likely, despite the high *Cameraria* diversity in this region (52 out of 74 described species: Grabenweger and Grill, 2000; de Prins and de Prins, 2005), because of the lack of close relatives of Old World species in the New World and the good knowledge of the North American fauna (Kumata, 1963; Pschorn-Walcher, 1997).

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# Conservation and Management

## Conservation Status

The species is invasive and not threatened.


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## Control Procedures

The most effective control measures are for trees to be completely removed, or, more cheaply, for the leaves to be carefully swept up and incinerated, but this may be difficult for plants in rough herbage or on private land, and must be done before adult emergence e.g. by the end of March (Kehrli and Bacher 2004). One chemical control measure is the injection of the insecticide imidacloprid ("Gaucho") in the trunk (Buszko, 2006) but however this is banned in some countries due to high toxicity to bees. Lufox 105 EC (Syngenta) which includes Fenoxycarb, an inhibitor of chitin synthesis, and also with a relatively low (WHO class III) level of environmental toxicity, has been successfully used combined with a surfactant Cide-Kick II in spraying, with 98-100% mortality to pupae and can be combined successfully with manual leaf removal measures (Syeryebryennikov, 2008). Whilst a synthetic pheromone is successful in catching males (<http://www.uochb.cas.cz/~natur/cameraria/chemec.htm>), until now pheromone traps have not been shown to provide effective control (Svato? et al. 2009). The spreading moths have been successful themselves in recruiting generalist members of the local parasitoid community.


Biocontrol measures using parasitoids have so far not proved successful, owing to the lack of specialist parasitoids so far being detected in natural horse-chestnut stands in the Balkans, a possible exception being the eulophid parasitoid wasp *Pediobius saulius*, whose attacks are much more prevalent in Balkan populations of *Cameraria ohridella* than elsewhere in Europe (Kenis et al., 2005).

For monitoring, a system of pheromone traps and Rothamsted traps are used in many places in Europe (Kindl et al., 2002, Augustin et al., 2004, 2009).

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## Legislation

Not legislated. However, the deliberate transport of any living stage needs to be strongly discouraged.

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## Management


The species is not generally considered to need conservation management except for its control. However, the discovery of unique, not yet invasive haplotypes in remote parts of the Balkans (Valade et al., 2009) might alter this viewpoint. In fact also the hostplant is red-listed in Albania (see under Threats).

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

## Threats


The moth is a major threat to the white-flowered horse-chestnut as an amenity tree and source of conkers for childrens' games (which are traditional in the UK), not because it kills the trees (the attacks have not caused tree mortality in the last 15 years and they can still usually produce conkers, although of lesser weight) (Thalman et al., 2003), but because councils are increasingly replacing the trees with other species whose aesthetic value is not affected. In some towns, it can be expected that local authorities will quickly remove all trees. There is evidence trees can adjust to heavy attack by increasing the hydraulic efficiency of the wood thus ameliorating the water and the nutrient supply to leaves (Salleo et al., 2003). Although oviposition can occur on other species of *Aesculus*, some species like red-flowered horse-chestnuts (*A. x carnea*) are not seriously affected and are not conducive to larval survival and development. The larva can however develop on the sister species of the white flowered horse-chestnut, *A. turbinata* (Xiang et al., 1998; Grabenweger and Grill, 2000) and various American species that are not widely planted in Europe such as *A. octandra*, *A. glabra*, *A. sylvatica* and *A. pavia* (Grabenweger and Grill, 2000; Freise et al., 2004). In some places, the species is observed to spill over on to and sometimes develop on sycamores *Acer pseudoplatanus* or other *Acer* species (Hellrigl, 2001; Kenis et al. 2005; Fig. 15). This appears especially true of one haplotype, (haplotype "B" of Valade et al., 2009).

In Albania, horse-chestnut has been classified as "Endangered" (Vangjeli et al., 1997). The tree also occurs at a single site in the eastern Predbalkan mountain range of Bulgaria (Fet and Popov, 2007: 584). Natural stands of the host plant in Greece are often isolated in mesic canyons in mountain ranges where they may be composed of isolated trees growing to smaller stature than ones planted in cities (Lack, 2000). The effect of outbreak populations or novel mutations, if they exist, of *Cameraria ohridella* on these natural stands therefore needs investigation.

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## Trends

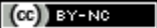
Dispersal trends are covered under Distribution. The moth shows no sign of having yet attained its full potential distribution in Europe or outside it (Fig. 11). The potential affect of climate change in accelerating the spread of this invasive species has not yet been quantified.

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

## Description


### Behaviour

The moths are diurnally active with peaks of activity in mid morning and mid afternoon, most active at moderate temperatures between 20-24 degrees centigrade (Syeryebryennikov, 2008).

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### Cytology

The haploid chromosome number is 30 (de Prins et al., 2002).

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### Life Cycle

Eggs are laid on upperside of leaf, usually the primary hostplant *Aesculus hippocastanum*, flattened, elliptic, around 0.25 mm. long, whitish-translucent when laid (Fig. 5). Larvae hypermetamorphic (with an initial greenish sap feeding stage shown in Figs 10 and 12), which evolves into tissue feeding stages) as typical for Gracillariidae, maximum size 5.5 mm. There are at least four feeding instars with an optional fifth instar (Figs. 6, 7) and then two spinning instars (Figs 13, 14). Pupa (Fig. 8) 3.25-3.7 mm. long and up to 0.7 mm. wide, orange before development of adult, with long wing cases and antennal sheath nearly reaching tip of abdomen, second to sixth abdominal segments bearing prominent stout white spines (Deschka and Dimi?, 1986; Pshorn-Walcher, 1994; de Prins et al., 2003; Syeryebryennikov, 2008). Head equipped with a pronounced beak for cutting open the disc-shaped cocoon (de Prins et al., 2002), which is around 5 mm. in diameter (Fig. 9), in which the pupa overwinters on the upper surface of the leaf.


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### Development

The female lays a range of 20-82 eggs (in captivity) (?efrová, 2001; Girardoz et al., 2006) on the leaf upper surface, which hatch in 4-21 days (?efrová, 2001; Pshorn-Walcher, 1994). The larva on hatching from the egg (Fig. 12), develops a gallery mine on the upper surface of the leaf, and sap-feeding early instars are flattened in shape for such a lifestyle and legless with forward oriented mandibles (Fig. 10). The larva has four feeding instars, occasionally a fifth, developing in 20-45 days depending on season and climate, and two non-feeding, spinning stages (Figs 13, 14), one outside the cocoon and one within, although a cocoon is optional for earlier generations (?efrová, 2001; Pshorn-Walcher, 1994; Freise, 2001). The cylindrical, normally 4th instar, larva enlarges the originally circular, reddish-brown mine along the main veins of the leaf during which time it is adapted to eat the palisade tissue of the parenchyma, damaging a surface of 4-7 square centimetres. The pupa stage lasts for 12-20 days during summer generations (?efrová, 2001). Pupation of late summer generations always occurs in a round cocoon, and the moth hibernates during the winter in the pupal stage. The adult lives for a few days, and although they have a developed proboscis, but there seem to be no published observations of their feed as an adult. Adults flight peaks are in May (20th April - early June), July (20th June - early August) and August/September (10th August - 15th September), with some adults appearing up to early October (?efrova and La?t?vká, 2001).The total life cycle lasts 6-11 weeks in summer generation. An increasing proportion (up to 90%) of each generation goes into to diapause, which can last up to two or three years (?efrová, 2001).


## Diagnostic Description

Small moth (Figs 3, 4), adults around 3.5 mm in forewing length, forewings background colour orange-brown with basal white longitudinal streak and white v-marks bent towards costa and running straight across dorsum at rest, edged posteriorly in black, two of these fasciae continuous medially, one post-medial fascia interrupted and a final convex fascia towards wing apex, bisected by a diffuse blackish subapical streak. Fringe forming a conspicuous orange tuft that is longest dorsally at rest (Fig. 1). Head tufted with orange hair-like scales intermixed with white, scape and base of antenna silvery white. Antennae about 4/5 forewing length. Fore and mid-legs equally banded white and black, hindleg with relatively more white.

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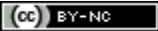
## Lookalikes

The mine (Fig. 2) is not easily confused with that for any other insect species as no other *Cameraria* recorded in Europe and no other leaf miners on horsechestnut. The fungal pathogen *Guignardia aesculus* also causes brown patches that could be confused with *Cameraria mines*, but more uniformly brown. Mines of *Cameraria aesculisella* in USA are of similar appearance to those of *C. ohridella*, but the species does not appear closely related. The adults resemble closely some species of *Phyllonorycter*, from which larvae may be distinguished by reduced legs and pupae by the absence of cremastral hooks, and the presence of strong spinoid setae in the 1st to 5th abdominal segments (de Prins et al., 2003).

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## Mitochondrial DNA Sequences and Barcodes

A recent analysis of cytochrome oxidase I sequences (the DNA barcode fragment) of 486 individuals from 88 localities identified 25 geographically structured haplotypes (Valade et al., 2009). NCBI: *Cameraria ohridella* cytochrome oxidase subunit I (COI) gene, partial cds; mitochondrial gene for mitochondrial product gi|31871807|gb|AY277401.1|[31871807] BOLD: 99 COI sequences (Mon Apr 27 04 2009) 508 COI sequences of > 500 bp (Mon Apr 27 04 2009)

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 


## Nuclear RNA and DNA Sequences

Genbank entries to date (NCBI): two *Cameraria ohridella* 28S ribosomal RNA gene, partial sequence gi|33319966|gb|AF477544.1|[33319966]

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## Microsatellites

A set of six polymorphic microsatellite markers has recently been developed (Mari Mena et al., 2008). Interestingly, all six loci were amplified for 20 other gracillariid species belonging to eight different genera, including another invasive species *Phyllonorycter platani*. These are the first microsatellite markers described for a species within the lepidopteran family Gracillariidae.

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## Size

Adults are small, 3-4 mm. forewing length and 7-9.5 mm. wingspan. Larvae are also small, up to 5.5 mm. in length.

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## Ecology

### Habitat

Parks and urban areas where horse-chestnut planted, generally avoiding trees planted close to the sea, and within natural stands in the

Balkans (Valade et al., 2009). The moth prefers the shadier lower to mid-stratum of trees within parks tending to avoid the canopy (Syeryebryennikov, 2008). Horse-chestnut itself prefers moist, well drained soils and is thus not widely planted in North America owing to the possibility of leaf scorch. Natural stands of *A. hippocastanum* in the Balkans (Greece, Macedonia, Albania) are found in shady, humid ravines between 380-1330 m. (Avtzis et al., 2007; Lack, 2000), and this is presumably the natural habitat of the moth.

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## Distribution

Palearctic (Fig. 11): Austria (1989, first detection outside Balkans, near Linz), Belgium, Bosnia (1994) and Herzegovina, Bulgaria, Croatia, Czech Republic (by 1993), France (by 2000 to Paris; must have been in Alsace from 1998, and, throughout the country by 2007), Germany (by 1993), Greece, Hungary, Italy, Liechtenstein, Luxembourg, Macedonia, Netherlands, Poland (by 1998), Romania, Serbia and Montenegro, Slovakia, Slovenia, Switzerland, (de Prins and de Prins, 2005). Lithuania, Ukraine, Spain, Denmark (by 2002) and Sweden (by 2003). Since 2002: United Kingdom (first detection Wimbledon, July 2002; front north to York by 2007), Finland (by 2006), Albania, Turkey, Moldova, Belarus, Central Russia (Forest Research, see link below). The most recent distribution map for Europe is that of Augustin (2009), and fine scale distribution maps are available for various countries such as UK (<http://www.forestry.gov.uk/website/forestresearch.nsf/ByUnique/INFD-6YUBY5>) and Poland (Buszko, 2006) and Lithuania (Ivinskis and Rimaitė, 2006)

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## Trophic Strategy

Leaf-miner.

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## Ecological Niche

The absence of many other organisms on the leaves of planted trees - except for the probably Asian horse-chestnut scale insect *Pulvinaria regalis* Canard, the dothidiomycete leaf blotch fungus *Guignardia aesculi* (Peck) V.B. Stewart of North American origin (Augustin, 2005) and in the last few years, a powdery mildew *Erysiphe flexuosa* (Peck) U. Braun et S. Takamatsu has that is either invasive from North America or may be of Balkan origin (Denchev, 2008) - has given this moth an almost free reign to colonise clean plants. It should be noted, in this respect, that the niche is a vacant one, as there are no other leaf-miners nor other regular lepidopteran herbivores on horse-chestnut, although up to 11 polyphagous species of tortricids, geometrids and noctuids have been reported to attack the tree outside its natural range in Turkey (Cebeci and Acer, 2007). 24 species, mainly noctuids, lymantriids, geometrids, saturniids and tortricids are also recorded on the NHM hosts database feeding on *A. hippocastanum* but most of these are polyphagous nearctic species and in Europe, only *Acronicta aceris* and *Saturnia pyri* and the internal feeder *Zeuzera pyri* were previously recorded to feed this tree (<http://www.nhm.ac.uk/jdsml/research-curation/research/projects/hostplant...>). Thus, the report by Cebeci and Acer (2007) that includes the Horse Chestnut moth *Pachynemima hippocastanaria* (Hübner, 1799) (which is normally ~~leaf~~ feeding) as a "pest" of the tree seems surprising, since there appears to be no other evidence that this species regularly feeds on horse-chestnut. The names of this last species and the March Moth *Alsophila aescularia* ([Denis & Schiffermüller], 1775) seem more likely to have been derived from observations of the adults sitting on the trunks.

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## Hostplants

The larva forms a blotch mine on upperside of leaf of *Aesculus hippocastanum* L. (primary host of this species, formerly Hippocastanaceae, but Sapindaceae according to the APG II classification). Other artificially planted species that are used are *A. glabra* Willd., *A. turbinata* Blume, *A. x bushi* Schneid, and the moth is capable of full development on American species such as *A. octandra*, *A. glabra*, *A. sylvatica* and *A. pavia* (Freise et al., 2004), although dies on *A. chinensis*, *A. californica* and the common red-flowered hybrid *A. x carnea* and *A. indica*. The females quite frequently oviposits on sycamore trees *Acer pseudoplatanus* L. (formerly Aceraceae, Sapindaceae following APGII classification) (de Prins and de Prins, 2005: 147), usually ones neighbouring horse-chestnuts. Alarming, the insect is capable of full development on both *A. pseudoplatanus* and *Acer platanoides* (Grabenweger and Grill, 2000; Freise et al., 2004), and this poses a new threat if mutations now exist that can adapt to this genus in Europe. Although oviposition certainly occurs on a range of plants that may abut horse-chestnuts, there is so far no evidence that *Cameraria ohridella* can develop successfully on any plant genera outside *Aesculus* and *Acer*



## Predators

Natural enemies are essentially parasitoids (see below), but various predators have been recorded including spiders and birds, especially the Blue Tit (*Parus caerulea*), ants such as *Crematogaster scutellaris*, earwigs *Forficula auricularia*, and grasshoppers such as *Phaneroptera paleata* and *Meconema meridionale* (Grabenweger, Kehrli et al., 2005). Death by predators provides little control and far greater mortality is caused by intraspecific competition on leaves, death by microorganisms at various stages and especially, in the adult stage, by rain (Augustin, 2005).

## Parasitoids

Most parasitoids are generalist and *Cameraria ohridella* has successfully recruited many species (see Girardoz et al., 2006). The invasive moth appears to have an ecosystem impact by depressing the abundance of leaf miner communities in the vicinity of infected trees, possibly via shared natural enemies (P  r   et al., 2009). Current research with the aim of finding a biocontrol agent focuses on parasitoids in the region of relict populations. There are many parasitoids so far recorded, but the chalcidoid eulophid genera *Chrysocharis*, *Closterocerus* (*C. trifasciatus* Westwood) *Minotetrastichus* (*M. frontalis*), *Pnigalio* (*P. agraulius*) and *Pediobius* are important and especially *P. saulius*, a pupal parasitoid, which seems to respond sensitively to *Cameraria* abundance following several years of presence (Grabenweger, Stolz et al., 2005). *Cirrospilus talitzkii* also seems to be actively tracking the colonisation of the moth (Augustin, 2005). Most chalcidoids and braconids attack larval stages but some ichneumonids parasitize the pupa. No parasitoids have been found on eggs although the eggs are very small. The parasitoid community has been investigated in detail in some places such as Serbia, where it has little effect on *Cameraria* abundance (Stojanovi   and Markovi  , 2004) and Slovenia (T  th and Luk    , 2005). Rate of parasitism is exceptionally low for a gracillariid species, usually below 10%, and does not generally exceed 25% with a normal range in the Balkans of 3.6-21%, a range not varying between natural and artificial stands (Grabenweger, Avtzis, et al., 2005). One reason for this low level may be that local generalist parasitoids are busy using different hosts and thus do not tend to adopt *Cameraria* rapidly in the season soon after emergence of adults (Girardoz et al. 2006).

Over 60 generalist parasitoids have been recorded. The list of de Prins and de Prins, 2005 (supplemented by Stojanovi   and Markovi  , 2004 and T  th and Luk    , 2005; Grabenweger et al., 2005) documents the following parasitoid generic and species records ***C. ohridella***:

**Chalcidoidea: Encyrtidae:** *Isodromus vinulus* (Dalman, 1820); **Eulophidae: Elachertinae:** *Cirrospilus elegantissimus* Westwood, 1832, *C. pictus* (Nees, 1834), *C. singa* Walker, 1838, *C. talitzkii* Bou  ek, 1961, *C. variegatus* (Masi, 1907), *C. viticola* (Rondani, 1877), *C. vittatus* Walker, 1838; **Elachertus inunctus** Nees; **Aprostocetus** sp.; **Elasminae: Melittobia acasta** (Walker, 1922); **Entedoninae: Chrysocharis nephereus** (Walker, 1839), *C. orchestis* (Ratzeburg), *C. pentheus* (Walker, 1839), *Chrysocharis phryne*, *C. purpurea* Bukowski, 1938, *Closterocerus delucchi* (Bou  ek, 1971), *Closterocerus lyonetae* (Ferriere), *C. trifasciatus* Westwood, 1833, *Neochrysocharis chlorogaster* (Erd    ), *Diglyphus isaea* (Walker, 1838), *Euplectrus bicolor* (Swederus, 1795), *Hemiptarsenus dropion* (Walker), *H. ornatus* (Nees, 1834), *Pediobius saulius* (Walker, 1839); *Pnigalio agraulis* (Walker, 1839), *P. longulus* (Zetterstedt, 1838), *P. pectinicornis* (Linnaeus, 1758), *Pnigalio populifoliellae* Erd    , *soemius* (Walker, 1839), *Sympiesis euspilapterygis* (Erd    ), *gordius* (Walker, 1839); *S. sericeicornis* (Nees, 1834); **Tetrastichinae: Baryscapus nigroviolaceus** (Nees, 1834); *Eutetrastichus amethystinus* (Ratzeburg), *Minotetrastichus frontalis* (Nees, 1834), *M. plataneus* (Mercet); **Eupelmidae: Eupelmus urozonus** (Kiss, 1924), *E. vesicularis* (Retzius, 1783); **Pteromalidae: Mesopolobus** sp., *Pteromalus semotus* (Walker, 1834); **Ichneumonoidea: Braconidae: Blacus maculipes** Wesm  el, *Colastes braconius* Haliday, 1833, *C. flavitarsis* Thomson, *Pholetesor circumscriptus* (Nees, 1834); **Ichneumonidae: Adelognathus** sp., *Gelis aerator* (Panzer, 1804), *G. agilis* (Fabricius), *Itopectis alternans* (Gravenhorst, 1829), *I. clavicornis* (Thompson), *I. maculator* (Fabricius), *Scambus annulatus* (Kiss, 1924), *S. brevicornis* (Gravenhorst), *Zatypota percontatoria* (M  ller).

## Cyclicality

One to four generations occur per year; the usual is three (June, August and October are common months for adult flight). In some places such as Lithuania up to 2006 (Ivinskis and Rim  ait  , 2006), there has only been initially an autumn generation.

## Dispersal

This species has provided an excellent experimental opportunity to determine patterns and mechanisms of invasion. Rates of spread of 40-58 km year have been recorded in Europe, up to 100 km a year in Poland (Buszko, 2006) and in the Ukraine, moving rapidly eastwards and southeastwards at 75-114 km. per year, and this has been corroborated on studies in particular countries and islands like the UK (<http://www.forestry.gov.uk/website/forestresearch.nsf/ByUnique/INFD-6YUBY5>; Gilbert et al., 2004; Augustin et al., 2004). Such rates may be relatively high, up to an order of magnitude greater than rates of spread observed in other invasive leaf miners (Agassiz, 1996: 20; Agassiz and Peters, 2002). The mechanism of spread has probably been natural (limited) aerial dispersion as adults aided by wind drift and accelerated by high late summer aerial densities owing to productive capacity of up to an order of magnitude per generation, possibly accelerated by climate change, but greatly by artificial transport as mines from cars parked under trees for a while as well as adults in cars and public transport, even ferries. Vehicular transport probably explains its punctuational dispersal pattern in Europe. A stratified model incorporating human population density has been found to explain the dispersion much better than a simple diffusion model (Gilbert et al., 2004.). This model has been found to have excellent predictive power (Gilbert et al., 2005). New records are generally found close to transport routes (Gilbert et al., 2004). Deliberate transport of leaves from parks to peripheral areas in the summer and autumn was also probably a major agent of its spread before burning policies have been adopted. Under suitable conditions significant wind drift can also occur, and with the high density of aerial plankton in the summer months generating arrivals that may be several km from the nearest tree, and a high density of trees in towns has undoubtedly been a significant factor in its spread, which would by normal flight only be of the order of 100 m. (Augustin, 2009).

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

## Bioclimatic Limits


Elevational limits are from sea level to 1500 m.; occurring to lower elevations at higher latitudes e.g. 900 m. in Poland (Buszko, 2006). In Spain, the species apparently avoids hot climates near sea level and may also avoid trees exposed to salinity. Horse-chestnut natural stands occur at 566-1485 m. in Albania, Greece and Macedonia with one lowland population at 228 m (Avtzis, 2007). Tolerance of pupae to mortality occurs at a low threshold of up to -21 oC (Lethmayer, unpublished). Nearly 90% of overwintering pupae may die in the leaves from various causes.

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

## Origin

There are three main hypotheses for the biogeographic origin of this species. The first proposed is that the species originated in the Balkans, where it forms a relict population as the only known European ***Cameraria***, along with its hostplant (Dimi? and Deschka, 1986; Grabenwager and Grill, 2000; Pschorn-Walcher, 1994; Valade et al., 2009), or in E. Asia, perhaps China, where ***Acer*** and ***Aesculus***-feeding relatives are known to exist (Grabenwager and Grill, 2000; Kenis et al., 2005). There are two other, apparently less probable hypotheses for its biogeographic origin. An origin in the US, where ***Cameraria*** is very diverse and at least one species is ***Aesculus***-feeding (Kenis et al., 2005, 2006), has been more or less ruled out due to intensive searches and entomological knowledge there, and lack of close relatives; however the genus occurs south to Mexico, where it is less well known. An origin in South-east Europe from another host such as ***Acer*** is another hypothesis (Hellrigl, 2001) that seems unlikely unless from an extremely localised site (Kenis et al., 2005). Finally, origin from another host entirely, perhaps also Sapindaceae (but not ***Aesculus*** or ***Acer***) seems very unlikely based on current knowledge of hostplant preferences (Kenis et al. 2005). The deeper phylogenetic aspects of the origin of this species have not yet been explored.

A recent analysis of mtDNA and microsatellites showed a reduction in genetic diversity of ***C. ohridella*** populations sampled from artificial habitats (e.g. planted trees in public parks, gardens, along roads in urban or sub-urban areas) across Europe, compared to ***C. ohridella*** sampled in natural stands of horse-chestnuts in the southern Balkans (Valade et al., 2009). These findings suggest that European populations of ***C. ohridella*** may indeed derive from relict horse-chestnut populations in the southern Balkans, where in that case they must have been biogeographically isolated until the advent of modern road infrastructure and transport mechanisms.

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

## Evolution and Systematics

### Systematics and Taxonomy

No paper has yet been focused on the phylogenetics of the genus ***Cameraria***.




## Sister Taxon

Lopez-Vaamonde et al (2003) presented DNA sequence data (28S rDNA) for the first time for the species. They showed *Cameraria* as the sister taxon to the genus *Phyllonorycter*. In a second paper, Lopez-Vaamonde et al (2006) included *C. ohridella* in their molecular phylogenetic analysis and, in the limited sample of species then used, this species fell as sister to the North American species *C. hamadryadella*. However, the sister species of *Cameraria ohridella* is not yet known for certain, but the male and female genitalia of the Eastern Asian *C. nipponica* Kumata, 1963 (Kumata, 1963: p. 35, figs a to c) are particularly similar to those of *C. ohridella* (compare Deschka and Dimi?, 1986, p. 12-15, figs 2, 4, and 5).

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

## Phylogeography

Valade et al. (2009) have identified 25 geographically structured haplotypes, based on analysis of the mitochondrial DNA of 486 individuals from 88 localities. In addition, they have showed that there is significantly higher mitochondrial haplotype diversity in the probable region of origin, the southern Balkans, than in central and western Europe (Valade et al., 2009).

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

## Relevance

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### Diseases

No diseases have been recorded as a direct result of damage and the attacks cause mortality to trees only indirectly through being cut down as the result of no longer having aesthetic value.

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

### Risk Statement

As an invasive species, the moth is a grave risk to planted horse chestnut trees and may also pose a risk to sycamores *Acer pseudoplatanus* and *A. platanoides*, due to increased attacks in some parts of Europe. This aspect has recently been investigated (P  r   et al., in press). If the insect arrives in North America or the Far East, it could also threaten some *Aesculus* or possibly *Acer* species there on which it can complete development, both of which genera have a community of native gracillariid-leaf miners and their parasitoids.

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

### Uses

The moth has no obvious positive benefit to humans except to be used as a dramatic example of the spread of an invasive species in Europe and the risks associated with increases in human transport and activity including the use of amenity trees.

Author(s): Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S. 

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**Fig. 1. Mines on horse chestnut leaf**

**Photographer:** Lees, David C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



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**Fig. 9. Cocoon**

**Photographer:** Lees, David C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .





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**Fig. 2. Tissue feeding instar in mine**

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**Fig. 3. Position at rest**

**Photographer:** Lees, David C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .





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**Fig. 4. Position at rest**

**Photographer:** Lees, David C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



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**Fig. 5. Eggs laid on leaf of horse chestnut**

**Photographer:** Lees, David C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



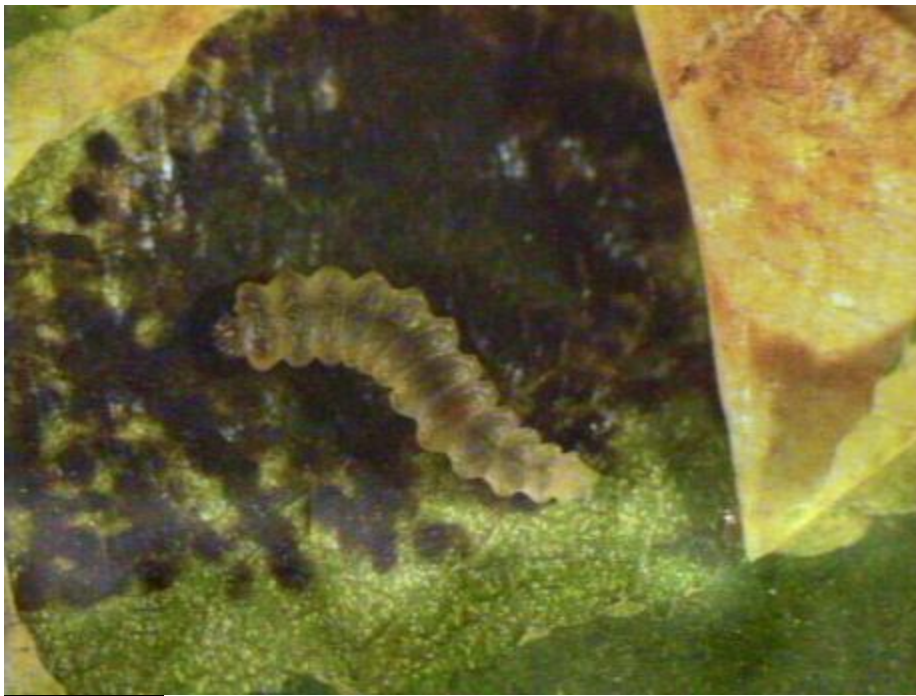
**Fig. 6. Tissue feeding larval instar**

**Photographer:** Lees, David C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



**Fig. 8. Pupa within cocoon**

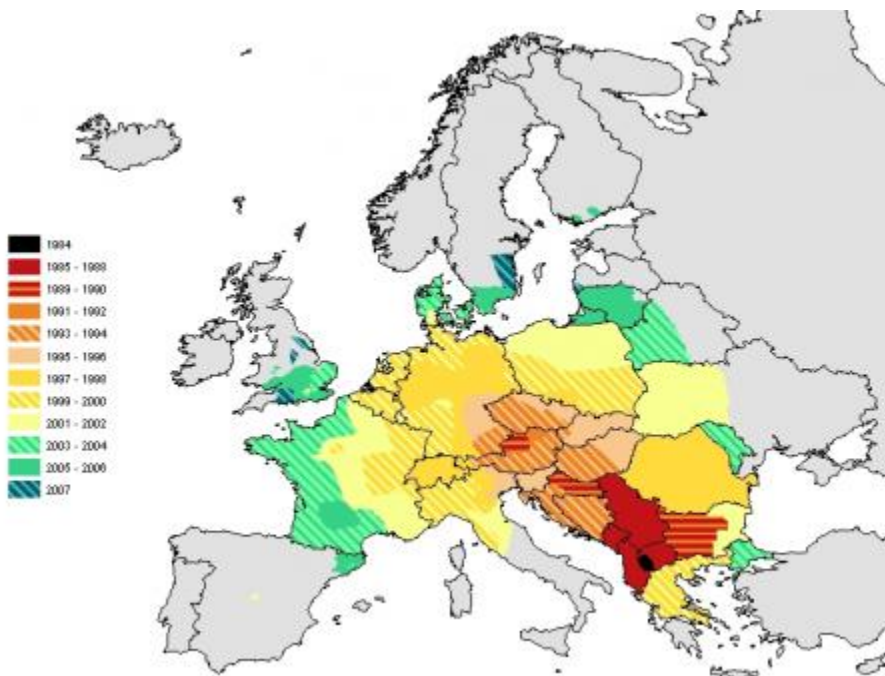
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**Fig. 10. Sap feeding instar**

**Photographer:** Heitland, W. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



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**Fig. 11. Incremental distribution of *Cameraria ohridella*, 1984-2007**

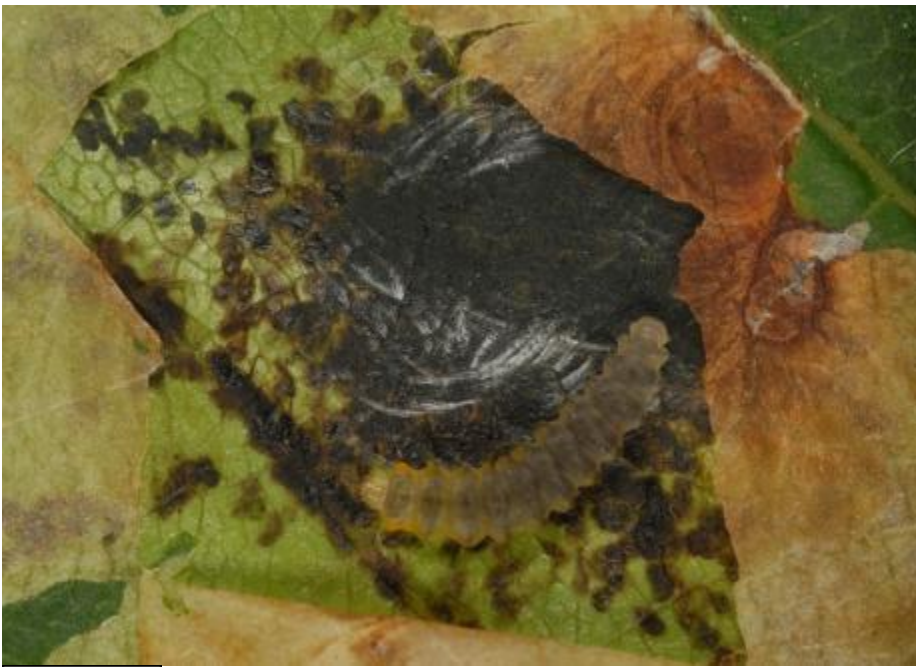
**Photographer:** Augustin, S. (Illustrator) **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



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**Fig. 7** *Cameraria ohridella* third and fifth larval instars, tissue feeding

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**Fig. 13** *Cameraria ohridella* first spinning larval instar

**Photographer:** Lees, D.C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .





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**Fig. 14** *Cameraria ohridella* second spinning larval instar

**Photographer:** Lees, D.C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



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**Fig. 12** *Cameraria ohridella* first larval instar, sap feeding with empty eggshell and start of mine

**Photographer:** Lees, D.C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .



**Fig. 15. *Cameraria ohridella* mines on sycamore, *Acer pseudoplatanus*, close to defoliated horsechestnut**

**Photographer:** Lees, D.C. **Submitted by:** Lees, D.C.; Lopez-Vaamonde, C.; Augustin, S., .