On the Place of Origin of *Cameraria ohridella* DESCHKA & DIMIC (Lepidoptera: Gracillariidae)

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Abstract

This contribution summarizes different theories on the place of origin of the horse chestnut leafminer *C. ohridella*. Potential regions include the Balkans, North America and Eastern Asia. The radiation of the genus *Cameraria*, the host range of the moth and the role of its natural enemies provide relevant information. Because the horse chestnut *Aesculus hippocastanum* is the main host tree of the leafminer, knowledge of the radiation of the genus *Aesculus* and its internal generic relationships should help us to narrow the search for the origin of the moth to certain areas. In the light of the present data, the region in the Balkan Mountains where the species was first discovered probably represents the origin of *Cameraria ohridella*.

Keywords: *Cameraria ohridella*, leafminer, origin, radiation, parasitism, horse chestnut, *Aesculus*, infestation, Lepidoptera.

Introduction

In 1989, *Cameraria ohridella* (Fig. 1) was reported for the first time in Central Europe at a location near Linz in Upper Austria (PUCHBERGER 1995). Since then it has enormously expanded its range and rapidly spread over Austria and its neighbouring countries. In 1999 the range of *C. ohridella* extended from Bologna (Italy) and the Balkan states in the south (HELLRIGL 1998) to Northern Germany (e.g. Berlin) and even to the Netherlands in the north. Presently, the horse chestnut...
leafminer has spread westward into France and Switzerland and eastward into Poland (Ch. Lethmayer, personal communication, 1999).

In addition to this rapid expansion, the moth is known to reach epidemic population densities within only a few years at newly infested locations. The larvae cause conspicuous damage to the leaves of the horse chestnut *Aesculus hippocastanum* L. These facts have made *C. ohridella* a general concern. Alarming reports about the endangered horse chestnut populations have promoted the leafminer’s reputation as one of the best known insect pests to the public.

Actually, however, little is known about the moth itself, especially its origin. It was discovered in 1985 at lake Ohrid in Macedonia (DESCHKA & DIMIC 1986), but it is not certain if this region in the Balkan Mountains is the place of origin of the species or merely the first find after possibly being introduced to Europe. The present paper does not purpose to furnish conclusive evidence on the leafminer’s origin, but will provide an overview and attempt to bring meaning to the currently available data. New facts which are pertinent to the investigation are presented and hypotheses on the origin of *C. ohridella* are discussed.

Area and origin of the genus *Cameraria*

The radiation of the genus *Cameraria* and the relationship between the species provides some information. The genus is widespread over the tropic, subtropic and the southern temperate zone of the holarctic region (OPLER & DAVIS 1981, DESCHKA 1993, KUMATA 1993, D.R. Davis, personal communication 1999, G. Deschka, personal communication, 1999). The mass center lies in the subtropic part of the nearctic region (southern USA and northern Latin America). Fifty-two species are described for North America, twelve species from the palaearctic region, from Malaysia (main part), China, Japan, India and Russia. Only one species, *C. ohridella*, is reported for Europe. Several Latin American species remain undescribed until now (D.R. Davis, personal communication 1999). The genus *Cameraria* is believed to be indigenous for the nearctic region and its Holarctic radiation indicates that it must have occurred before the separation of North America and Eurasia in the early Eocene (DESCHKA 1993). Glacial cooling in later Tertiary and Quarternary extinguished the genus in Europe with perhaps one exception.

The holarctic radiation of the genus *Cameraria* makes it difficult to restrict the search for the moth’s origin to a certain area. First of all, North America - with 52 of 74 known *Cameraria* species - is a possibility, but Davis (in PSCHORN-WALCHER 1997) states that *C. ohridella* shows clear differences to all American species making them unlikely close relatives of the horse chestnut leafminer. From this point of view *C. ohridella* must be an Old World species. However, the leafminer’s relationship to the Asian species has not yet been examined. In addition, it remains uncertain whether the Old World species belong to *Cameraria* (a revision is still lacking), so that the horse chestnut leafminer may not have close relatives in Asia.
either. In that case, *Cameraria ohridella* should be a relict species of the genus *Cameraria* in Europe, and the area of discovery should be more or less identical with the moth’s origin.

**Host range of Cameraria ohridella**

Members of the genus *Cameraria* are mostly monophagous (Deschka 1993). Therefore, the natural area of the host tree species should also be the origin of the leafminer. The main host tree of *Cameraria ohridella* is *Aesculus hippocastanum*. Natural populations of *A. hippocastanum* occur only in southeastern Europe, exactly the region where the horse chestnut leafminer was discovered. This is the best indication to believe that this area is the origin of the moth. However, *C. ohridella* is not totally restricted to *A. hippocastanum*, not even to the family Hippocastanaceae. Mines and larvae of the moth have been found on several *Aesculus* species and on *Acer pseudoplatanus* (Aceraceae). Successful development, from egg to adult, is possible on some of these trees (see below). Nevertheless, a strong preference for *A. hippocastanum* is evident, and infestation of other tree species seems to be an exception. Such observations are usually from sites very close to horse chestnut populations, especially where *A. hippocastanum* trees have already been defoliated and oviposition on leaves of the main host tree is no longer possible. Without exception, the infestation on other tree species is much lower than on *A. hippocastanum*. Nevertheless, the possibility remains that the original host tree of *C. ohridella* is not the horse chestnut but another closely related tree species. Therefore, radiation of the genus *Aesculus* and the relationship between its species are important aspects to consider.

**Area and origin of the genus Aesculus**

*Aesculus* shows a disjunct radiation in the Holarctic region. Presently, natural populations of *Aesculus* species are found in eastern Asia, eastern and western North America and in Europe. Nineteen species of *Aesculus* exist, including six species described by Fang (1981) but doubted by Xiang et al. (1998).

Based on the review by Hardin (1957, 1960), Xiang et al. (1998) divided the genus in six sections: “Pavia” in eastern North America, “Parviflora” in southeastern North America, “Californica” in western North America, “Parryana” in Mexico, “Aesculus” in Europe and Japan and “Calothyrsus” in eastern Asia. Presumably, *Aesculus* evolved in eastern Asia during the transition from Cretaceous to Tertiary. It has split into two lineages, one spreading southwards forming the current section “Calothyrsus”, the other one spreading westwards to Europe and eastwards to North America. The North American group has diverged into two lineages, which were subsequently divided into eastern and western populations due to drought stress in central North America. Climatic cooling during the late Tertiary
and early Quarternary eliminated the Eurasian section except in two "refugia", one in Japan and the other in the Balkans. These relicts are the recent species *A. turbinata* and *A. hippocastanum*.

During 1999, the authors examined several species of the genus *Aesculus* for infestation by *C. ohridella*. The results correspond with the relationship within the genus: Only *A. hippocastanum* is infested regularly by high population densities. The American *Aesculus* species *A. parviflora*, *A. pavia*, *A. flava* and *A. glabra* do not show any infestation (SKUHRAVY 1998), however, argues the reverse. Consequently, we could not prove that complete development occurs on these buckeyes. *Aesculus x carnea*, which is a hybrid of the American *A. pavia* with the European *A. hippocastanum* sometimes shows infestation, if planted near heavily infested horse chestnut trees (see Fig. 2). HELLRIGL (1998) has observed complete development on this form. *Aesculus flava* is often grafted on *A. hippocastanum*, which improves resistance against the cold climate in Austria. In such cases low infestation and even complete development of the moth was observed (see Fig. 3).

The Asian *A. indica* seems to be resistant against the moth (SKUHRAVY 1998); the other species of the section "*Calothyrsus"* and the remaining sections, "*Parryana"* and "*Californica"*, have not yet been examined for infestation.

In contrary, regular infestation and normal development of *C. ohridella* was found on *A. turbinata*, the closest relative to the horse chestnut, as shown in Fig. 4. Although the infestation is currently much lower than on *A. hippocastanum*, this observation is the only fact supporting the hypothesis that *C. ohridella* originated in Asia. In Japan, which is the natural distribution area of *A. turbinata*, three of the palearctic *Cameraria* species are common (M. Lödl, personal communication,
1999). Japan is thus an alternative hypothesis for the origin of the horse chestnut leafminer, especially if southeastern Europe can be definitely excluded.

Arguments against southeastern Europe as the area of origin

Several considerations weaken the hypothesis that the Balkan area is the origin of *C. ohridella*. HOLZSCHUH (1997) summarized the three most important points:

1.: In 1985, the leafminer was discovered on planted trees (not in autochthonous populations of *A. hippocastanum*) during a mass outbreak. DESCHKA (1993) reports that *C. ohridella* is able to develop population densities larger than any other leafminer he has experienced in his 30 years of practice.

2.: Parasitism in *C. ohridella* is very low compared with similar leafminers not only in Central Europe but also in Macedonia. Usually, related leafminer species show a high level of parasitism.

3.: Although *A. hippocastanum* has been spread by man all over Central Europe for the past two hundred years, the leafminer has not been able to follow its host during this period. This stands in sharp contrast to many cases in which leafminers have expanded to other countries and even continents within a few years.

These arguments, however, are mainly based on assumptions and lack an accurate empiric analysis. Regarding point one, it must be noted, that natural populations of *A. hippocastanum* have not been studied so far. Theoretically, the leafminer may never develop high population densities under natural conditions and therefore has remained undiscovered. Although entomological collections have a long tradition in the region of lake Ohrid, the small moth may have been overseen.

The statements about parasitism (point two) also remain questionable. In 1999, we attempted to examine the level of parasitism in samples from Macedonia. Unfortunately, most of the samples developed mold due to long transport, and the remaining material was too small for statistical analysis. Although only two of seven samples from Macedonia could be examined, the analysis provided interesting results. The leaves contained only pupae of *C. ohridella* and numerous empty mines of previously hatched moths and parasitoids. From a total of 123 mines, 14 parasitoids hatched, all belonging to a single species, *Pediobius saulius* WLK. (Eulophidae, Chalcidoidea). *Pediobius saulius* is a common parasitoid of leafminers, its larvae are endoparasitic and solitary. Thus, more than 11% of the larvae were attacked by this parasitoid species. Although *P. saulius* may be more important in Macedonia than in Central Europe (the species also occurs in Austria but plays a negligible role in the parasitoid spectrum of *C. ohridella*; see GRABENWEGER & LETHMAYER 1999), the relatively high abundance of the parasitoid in the two small
samples clearly shows, that the level of parasitism is not as low as estimated in previous papers. Without doubt, parasitism of *C. ohridella* in Macedonia and its neighbouring countries must be examined more closely before the region is to be excluded as a possible origin area.

The third point mentioned by HOLZSCHUH (1997) is currently the most reasonable, because *C. ohridella* is able to migrate long distances by passive flight (drifting with wind) and passive transport (anthropogenic). There should have been enough time for the moth to reach Central Europe in the last centuries. Therefore, the possibility that *C. ohridella* was recently introduced to Macedonia cannot be rejected at this point.

Host change of *Cameraria ohridella*

Another idea explaining the sudden appearance of *C. ohridella* in Macedonia has recently been presented by HELLRIGL (1998): The mass outbreak and the lack of parasitoids may be due to a possible host change of the leafminer. Such changes are known from other phytophagous insects and may be followed by unexpected radiation and / or very high population densities (e. g. TARMANN 1998). HELLRIGL (1998) supposes that the original host tree of *C. ohridella* might have been *Acer pseudoplatanus*, on which the moth is able to develop. The moth remained inconspicuous on this tree species, and its natural enemies have been able to control it efficiently. According to this line of argumentation, *C. ohridella* when changing the host host it rid itself of the parasitoids and opened up new radiation opportunities. High population densities reflect the lack of competition with other phytophagous insects on *Aesculus hippocastanum*. Thus, the origin of *C. ohridella* would be located in the Balkans, but on a different host tree species.

This hypothesis also has weak points: First, mines of *C. ohridella* rarely occur on *A. pseudoplatanus*, even in regions where horse chestnut trees have been infested for years. In our own investigations, most of the larvae died on *A. pseudoplatanus* in an early instar stage. In other studies, complete development has been observed, e.g. HELLRIGL (1998) or GREGOR et al. (1998). Nevertheless, these cases appear exceptional because infestation of *A. pseudoplatanus* only occurs in “emergency situations” for the moth, usually when oviposition sites on horse chestnut leaves are no longer available. Reasons why *C. ohridella* should have problems developing on its original host tree are not evident. Furthermore, *A. pseudoplatanus*, like the horse chestnut, has been a common tree in Central Europe for a long time. Nevertheless, it remains unclear why the horse chestnut leafminer did not spread over the whole region. At present, *C. ohridella* appears to be widening its host range by spreading from *A. hippocastanum* to other tree species.
Conclusions

Based on our present knowledge, the Balkans are still the most plausible place of origin of *Cameraria ohridella*. In this region, where the leafminer was originally discovered, natural populations of *Aesculus hippocastanum* still exist. The horse chestnut is the only host which is regularly infested and allows problem-free development of the moths. The suggestion that the horse chestnut leafminer is a relict species which has survived the Ice Age in southeastern Europe (like its host) remains a possibility. Nonetheless, the reason for the mass outbreak beginning Fifteen years ago and the sudden radiation across Europe remain unclear. In order to demonstrate that the Balkans are the origin area, future investigations should examine infestations of natural *A. hippocastanum* populations and determine the role of parasitism in these habitats. A possible host change of the moth should be considered only when these two aspects have been addressed.

North America, as a possible region of origin, can most likely be eliminated. Although more than two-thirds of the described *Cameraria* species are reported from the USA, they all seem to differ strongly from *C. ohridella*. In addition, many American *Aesculus* species are resistant to the horse chestnut leafminer, whose normal development is restricted at least.

If investigations on the infestation density and the parasitoid complex of natural *A. hippocastanum* populations exclude southeastern Europe as the origin of the horse chestnut leafminer, certain regions in East and Southeast Asia should be kept in consideration. Basically, *Cameraria* species are reported from Malaysia, China, Japan, India and Russia. Representatives of the buckeye genus growing in these regions (section “Calothyrsus”) have not been checked yet for infestation with *C. ohridella*, except *A. indica*, which seems to be resistant. The opposite is true for *Aesculus turbinata*, which is a close relative to *A. hippocastanum* and originates in Japan. Regular infestation and normal development of the moth have been observed on planted trees in Austria, yet infestation density is low. Therefore, natural populations of *A. turbinata* in Japan may be of interest to further investigations on the origin of the horse chestnut leafminer.

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