Bucculatrix ainsliella Murtfeldt, a new North American invader already widespread on northern red oaks (*Quercus rubra*) in Western Europe (Bucculatricidae)

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Abstract. *Bucculatrix ainsliella* Murtfeldt, 1905 is for the first time reported from Europe: the Netherlands, Belgium, and adjacent Germany. DNA barcodes confirm its identity. It is the first North American lepidopteran species feeding on northern red oak *Quercus rubra* ever found in Europe, and only the second North American oak-feeding insect found in Europe. The species has regularly been found in the Netherlands and northern Belgium since 2006, and in 2011 also in Nordrhein-Westfalen in Germany, adjacent to the Dutch border, but the earliest records are from the Netherlands, Amersfoort in 1989 and 1990. Early stages, leafmines, and the adult are described, illustrated, and diagnosed against oak-feeding *Bucculatrix ulmella* Zeller, 1848 and other similar species. The biology and distribution are discussed. This species can be abundant in Europe, but significant damage has not been observed.

Zusammenfassung. *Bucculatrix ainsliella* Murtfeldt, 1905 wird hier zum ersten Mal aus Europa gemeldet. DNA Barcodes bestätigen die Identität. Die bisherigen Fundorte liegen in den Niederlanden, Belgien und im angrenzenden Deutschland. Die in Nordamerika häufige Art lebt an Eichen (*Quercus* spp.), darunter auch an Roteichen (*Quercus rubra*). Nachdem bereits eine Blattlaus den Sprung über den Ozean geschafft hat, ist *B. ainsliella* nun die zweite Insektenart, die jetzt in Europa an den bereits im 17. Jahrhundert eingeführten Roteichen vorkommt. Die ersten Nachweise stammen von Amersfoort in den Niederlanden und wurden 1989 – 1990 gemacht. In Belgien taucht die Art 2006 auf, und in Nordrhein-Westfalen wird sie 2011 erstmals gefunden. Die Art ist mittlerweile in den Niederlanden und Belgien weit verbreitet und häufig, jedoch ohne Schäden anzurichten. Die Beschreibung und Abbildungen von Larvenstadien, Puppen und Blattminen werden vorgelegt und mit denen von *B. ulmella* Zeller, 1848 verglichen, die ebenfalls an Eiche lebt. Biologie und Verbreitung der Art werden ausführlich diskutiert.

Introduction

Northern red oak (*Quercus rubra* L.) was introduced into Western Europe at the end of the 17th century and became an economically important and widely planted timber tree in Central and Western Europe during the 19th and 20th century (Bauer 1953; Göhre & Wagenknecht 1955; Goßner et al. 2009; Magni Diaz 2004). Many authors noted that the number of insect species feeding on red oak in Europe is still very small and consists mainly of relatively polyphagous species (Csóka & Szabóky 2005; Goßner & Bräu

2004; Turčáni et al. 2009). This is in sharp contrast to the very rich entomofauna on the indigenous European deciduous oaks (in Northern and Western Europe mainly *Q. robur* L. and *Q. petraea* (Matt.) Liebl.), on which hundreds of herbivore species are known to feed (for Britain 423 species are cited: Kennedy & Southwood 1984; for Germany 699: Brändle & Brandl 2001). The difference can probably be explained by the phylogeny of the genus *Quercus*: the red oak belongs to a phylogenetically separate part of the genus *Quercus*, the section Lobatae (commonly known as "red oaks"), only known from the New World, whereas all European deciduous oaks belong to the so called "white oaks" (*Quercus* sensu stricto) that include both North American, European, and Asian species (Manos et al. 1999). Both groups of oaks harbour different faunas in North America (e.g,. Robinson et al. 2002), and in other studies it was shown that introduced oaks belonging to the same taxonomic group as native oaks received a considerably higher number of herbivores than oak species from different taxonomic groups (e.g., Connor et al. 1980). In the late 20th century, the first, and hitherto only, North American insect attacking *Q. rubra* was recorded from Europe, the aphid *Myzocallis* (*Lineomyzocallis*) *walshii* Monell, 1879 (Hemiptera, Aphidoidea). It has since become invasive and problematic in city areas (Havelka & Stary 2007; Modic 2010; Osiadacz & Wieczorek 2006; Perez Hidalgo et al. 2009; Pons & Lumbierres 2010). As far as we know until now, no species of Lepidoptera restricted to red oaks have been found in Europe. We here report first records of the oak skeletoniser *Bucculatrix ainsliella* Murtfeldt, 1905 from the Netherlands, Belgium, and Germany.

One of us (KJH) collected *Bucculatrix* specimens in a light trap in his garden in Wezep (Netherlands, province Gelderland) that he did not recognise and thus presented to JCK for dissection and identification. Because he also could not recognise these specimens as belonging to any species known from the Netherlands, photographs of the male genitalia were sent to WM, who identified it as the North American species *Bucculatrix ainsliella* in 2011. After that, we started looking for early life stages. From the life history in its original distribution area, we knew we had to look for a species likely feeding on *Q. rubra*, the only red oak that is commonly planted in the Netherlands. The search started in Wezep, near KJH's house, where *Q. rubra* is common. We found larvae and cocoons at two sites. After confirming the identity by breeding adult moths from the larvae and cocoons, these findings prompted a press release on 13 July 2011 (http://www.naturalis.nl/nl/over-ons/pers/persberichten/2011/eerste-vestiging-amerikaanse-eikenmot-europa) and a short online story in Dutch on a website for Microlepidoptera (van Nieukerken & Doorenweerd 2011).

Very soon after this media coverage, it became apparent that various records of this species were already available as misidentified or unidentified records on national observers' websites (http://waarneming.nl/contact.php; http://waarnemingen.be/index.php), and several collectors, including some of us, were able to record the species from more localities after knowing where and what to look for. Finally, searching collection holdings resulted in recognising several older specimens, including some from 1989 and 1990.

Bucculatricidae is a rather small family with 297 described species (van Nieukerken et al. 2011), most belonging to the very uniform genus *Bucculatrix* Zeller, 1839. In

Europe, 55 species are known (Mey 2010), in North America more than 100 (Braun 1963; Opler 1974; Rubinoff & Osborne 1997), the majority feeding on Asteraceae. Whereas there is only a single native *Bucculatrix* species feeding on oaks in Europe (*B. ulmella* Zeller, 1848, a confusing name, since it does not feed on *Ulmus*), there are at least 11 species associated with oaks in North America, which usually only feed on a single *Quercus* species or a limited group of either white or red oaks (Braun 1963). Most *Bucculatrix* species mine in their first larval instar, and later feed externally on the parenchyma between veins, making small windows in the leaf. The ribbed cocoon is one of the best characters and apomorphies for the genus. There is no single work treating all European species, and only a few papers can be used for the identification of a subset (Bengtsson & Johansson 2011; Langmaid et al. 2007; Mey 1999; Seksjaeva 1993; Svensson 1971), but a survey of European species is in preparation (Z. Tokár, personal information). All North American species are treated by Braun (1963), except the few that were described later (Opler 1974; Rubinoff & Osborne 1997). Baryshnikova (2008) provided the first phylogenetic analysis of the genus.

Material and Methods

Material

Specimens were either taken as adults collected at light, using various methods, or as larvae or cocoons from *Quercus rubra* trees and shrubs. Later in the year, larvae and cocoons were also found on fallen leaves, and cocoons were observed on tree trunks. Rearing in small plastic containers proved easy for the summer generation, although many parasitoids emerged as well. The material is either deposited in the collections of the Naturalis Biodiversity Centre, Leiden, or in private collections. Many records were identified from photographs provided by the observers. All data on specimens and observations of *B. ainsliella* are given in Table 1, and for barcoded specimens (also of other species) data are uploaded to the BOLD project "Lepidoptera of the Netherlands – public [NLLA]" (http://www.barcodinglife.com), where also Genbank Accession numbers can be found.

Morphological methods

Genitalia were dissected in the usual way (van Nieukerken 1985; Robinson 1976), males were stained with phenosafranin and females with chlorazol black. Because the valvae in the male genitalia of these species cannot be spread, we folded them downwards, whereas the socii remain in their posterior position (following Svensson 1971). Photographs of moths, leafmines, genitalia slides, and wing slides were taken with a Zeiss AxioCam digital camera attached, respectively, to a Zeiss Stemi SV11 stereomicroscope, a motorised Zeiss SteREO Discovery.V12 or a Zeiss Axioskop H, using Carl Zeiss AxioVision software. In the field, various digital cameras were used. Measurements of genitalia and mines were taken from photographs with AxioVision software, and measurements of moths were taken with the stereomicroscope provided

with a calibrated eyepiece graticule. The distribution map was prepared with the program "Klasse" (Anonymous 2011).

DNA barcoding

DNA was extracted destructively from larvae preserved in 96% ethanol or adult legs. Extractions were carried out with the Qiagen DNeasy Blood and Tissue kit. A 658 bp fragment of the mitochondrial COI gene was amplified using as primers Lep-F and Lep-R (Hebert et al. 2004), often tailed with T7 promotor [TAATACGACTCACTATAGGG] and T3 [ATTAACCCTCACTAAAG]. Amplification was performed in volumes of 25 µl. The PCR cycle consisted of 3 min initial denaturation at 94°C, 15 sec denaturation at 94°C, 30 sec at 50°C, 40 sec extension at 72°C for 40 cycles. After completion of all cycles, there was a final extension at 72°C for 5 min. A negative control with no template was included for each series of amplifications. The amplified products were separated on a 1% agarose gel and visualized under UV following staining with ethidium bromide before clean-up and sequencing.

PCR clean-up and bi-directional sequencing was outsourced to MACROGEN Europe on an ABI 3730XL. The chromatograms were checked with Sequencher (Gene Codes Corporation) and the resulting sequences were aligned by eye with reference to amino acids in BIOEDIT 7.0.9.0 (Hall 2004). Neighbor-joining (NJ) trees based on DNA barcode sequences of all available specimens, supplemented with publicly available sequences of Bucculatricidae, were calculated with PAUP* 4.0b10 (Swofford 2003), using uncorrected P distance (Srivathsan & Meier 2012). Inter- and intraspecific distances between the COI barcodes were calculated with the species delimitation plug-in v1.04 by Brad Masters & Howard Ross for Geneious (Drummond et al. 2011).

Results

Bucculatrix ainsliella Murtfeldt Figs 1, 3–7, 13, 14, 17–19, 21–23, 26–30, 35

Bucculatrix ainsliella Murtfeldt 1905: 218. Holotype male: USA, Minnesota, Olmstead, cocoons, on/near black oak [*Quercus velutina*], C.N. Ainslie, Type 65035 (USNM). [not examined]

B. ainsliella; Gibbons & Butcher 1961: 681 [biology], Braun 1963: 167 [redescription, taxonomy], Gelok et al. 1999: 111 [recorded from British Columbia, phenology].

Material. See Table 1.

Diagnosis. Adults of *Bucculatrix ainsliella* can be distinguished from *B. ulmella*, the other European oak-feeding species, by the more monochrome grey forewing with the prominent elongate blackish brown spot on dorsum with white edging, the longer forewings and the distinct separation of dark and pale areas in the frontal tuft. Further, *B. ainsliella* is slightly larger. *B. ulmifoliae* (Hering, 1931) from *Ulmus* is also rather similar, has a rather similar frontal tuft, but the dorsal spot is more square and often much smaller, and the antennal annulation is regular. In living specimens, the spot in *B. ainsliella* is distinctly rounded and rendered more apparent by white edging. In European collections, *B. ainsliella* specimens were misidentified as *B. bechsteinella* (Scharfen-

Figs 1, 2. *Bucculatrix* species reared from *Quercus rubra*, Wezep, adult habitus. **1.** *B. ainsliella*, male, RMNH.INS.544410. **2.** *B. ulmella*, female, RMNH.INS.544416. Right antenna in Fig. 2 reconstructed from left antenna. Scales 2 mm.

berg, 1805), *B. demaryella* (Duponchel, 1840), and even *B. cidarella* (Zeller, 1839). These species have smaller dorsal spots than *B. ainsliella* and different antennal annulation. Photographs on observers' websites had been identified earlier as *B. ulmella*, *B. albedinella* (Zeller, 1839) or *B. noltei* Petry, 1912. Among other European *Bucculatrix* specimens, *B. ainsliella* usually stands out by its larger wingspan and elongate wings with the distinct spot. Annulation of antenna and legs also separate *B. ainsliella* and *ulmella* from various other Palaearctic species.

The male genitalia of *B. ainsliella* are large, bear a double row of cornuti in the bulbous basal part of the phallus, and the valva has a hooked apex. The male genitalia of *B. ulmella* are much simpler and smaller, and those of *B. ulmifoliae* can be recognised by the terminally hooked phallus and short socii (Fig. 16). Female genitalia are immediately recognisable by the extremely long ductus bursae, several times longer than the abdomen, presence of spines in ductus, and peculiarly shaped ostium and surrounding sclerotisations.

Description. Adult (male, female) (Figs 1, 3–7). Forewing length 3.7–4.0 mm (male), 3.4–3.9 mm (female), wingspan 7.6–8.8 mm (male), 7.6–8.4 mm (female). Head: frons white, irrorate with some pale grey scales, vertex with tuft of hairscales clearly separated in ferruginous central band and white lateral bands; neck tufts and collar white; labial palpus hardly visible, white. Antenna with 56–62 segments in both sexes; first flagellar segment strongly notched in male; scape dorsally white, irrorate with greyish brown scales, ventrally shining white with greenish reflections, flagellum dorsally greyish white, strongly annulated dark brownish grey, ventrally white, vaguely annulated; annulation regular until 23 segments before tip, after that with characteristic pattern as follows: segment formula (d=dark segment, w=white segment): 3d-1w-5d-1w-1d-1w-5d-1w-1d-4w (Fig. 7). Thorax and tegulae white, irrorate with greyish brown scales, thorax with two dark brown posterior spots. Legs: white on inner side; fore- and midfemur, -tibia and first segment of tarsus dark brownish grey with whitish irroration on outer side; hindfemur: whitish with pale grey irroration; tarsus segments 2–4 of all legs white with dark brownish grey apical rings, tarsus segment 5 white, apically tipped dark brownish grey, spurs dark greyish brown on outer side, white on inner side. Forewing white, heavily irrorate with ochreous-grey to dark grey scales,

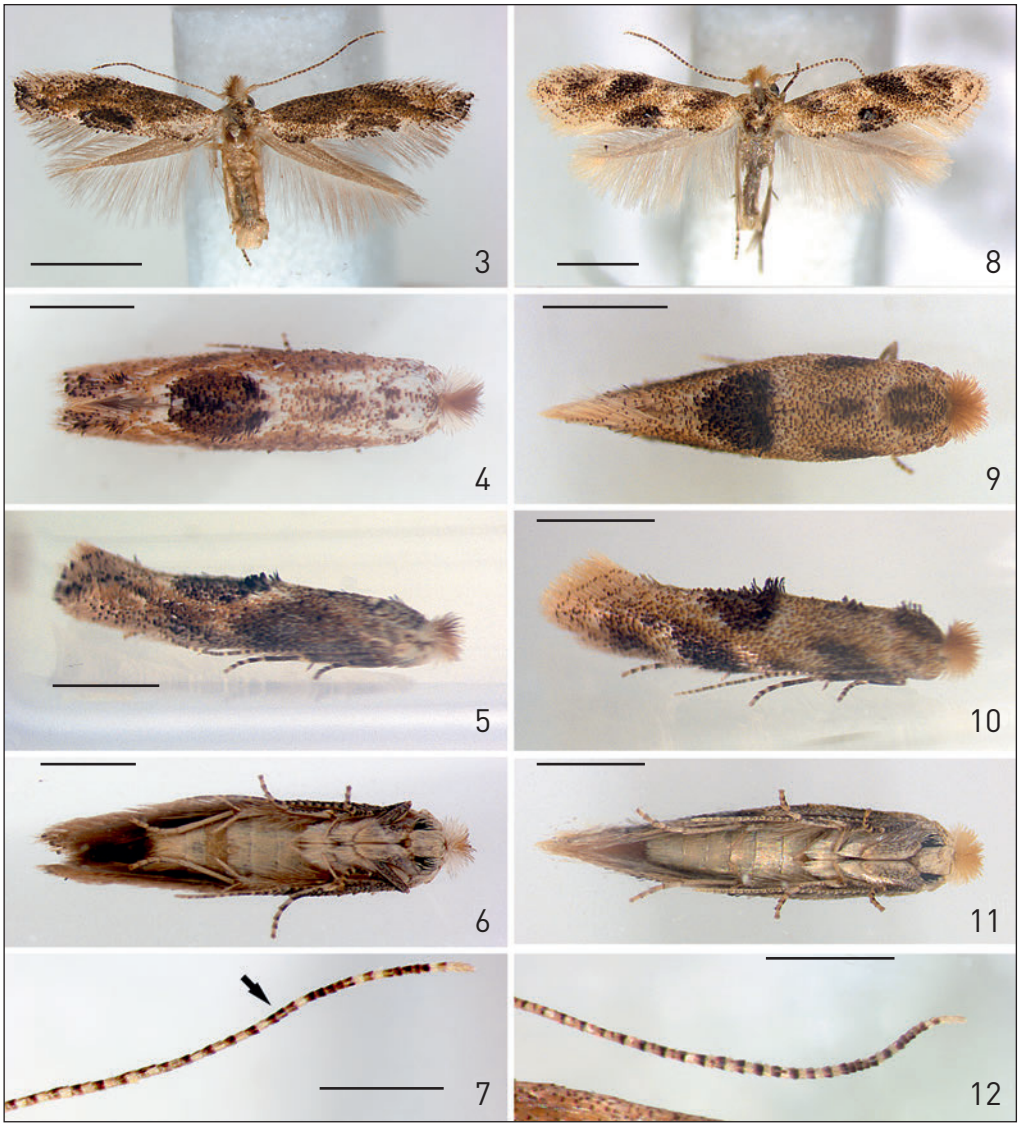
especially from fold to costa, a large blackish brown elongate spot on dorsum from just before 1/2 to 2/5, in- and outwardly edged whitish, a blackish brown inward oblique streak from costa at one-half to tornus, outwardly edged with white, tufts of raised blackish brown scales at dorsum near base, at inner edge of elongate spot and at dorsal end of inward oblique streak, two blackish brown cilia lines encircling apex, cilia pale grey. Hindwing shining grey, cilia pale grey. Underside: forewing shining dark grey, more ochreous towards apex, outer cilia line distinctly visible, hindwing shining grey. Abdomen dorsally shining grey, laterally shining pale grey, ventrally shining white, anal tuft white; abdomen in female widened posteriorly, covered with one broad anal tuft; in male tapering, anal tuft smaller, not completely covering external genitalia.

Male genitalia (Figs 13–14). In size almost twice as large as genitalia of *B. ulmella.* Socii long and slender, setose, narrowing apically, tip rounded. Vinculum more or less rounded, wider in the middle. Valva long (435–465 μm), broad at base, narrowing distally with narrowest part just beyond one-half, apex rounded and with a short and slightly bent latero-ventral hook. Phallus long (ca. 650–730 μm), bulbous at base, distal part tubular, one and a half times length of basal part, slightly narrowing distally and upwardly bent. Vesica with double row of eight long spiny cornuti.

Female genitalia (Figs 17–19). Anal papillae setose, posterior apophyses short, anterior apophyses absent. Tergite 8 with centrally elevated group of special scales. Ostium tubular, opening more or less triangular; connected laterally on sternum 8 to two semicircular excavations, broadly connected in the middle. Ductus bursae narrow and extremely long (almost 5 mm), coiled, ca. twice as long as abdomen, abruptly widening before entering corpus bursae and with anterior rows of spines, more or less along midline. Corpus bursae elongate, signa forming ring around posterior half, comprising rows of spined ribs, spines directed anteriorly.

Immature stages (Figs 21, 26–30). *Larva*. Early instar in mine yellow, with brown head capsule and prothoracic plate (Fig. 21). Free-living larva up to 5 mm long (Fig. 26), with pale yellowish green body; prothoracic and anal plates concolourous, head slightly more pale brownish. Pinacula not distinguishable, major setae appearing dark against light body. Rear end of the body tapering towards long anal prolegs (typical for the genus); the four abdominal prolegs relatively long. The free-living larvae are easily distinguished from those of *B. ulmella* by the absence of colouration. Larvae of *B. ulmella* are greyish green, with several indistinct darker longitudinal lines, and with about eight whitish spots on each body segment. *Pupa* (Figs 28–30). Only exuviae were studied (one on slide). Tenth abdominal segment (A10) with one pair of lateral tubercles, similar to most *Bucculatrix* species, but unlike *B. thoracella* (Thunberg, 1794) which has two pairs. Tergites A3–7 with 2–3 rows of rather coarse spines anteriorly, amidst a strong network of microspines (Figs 29, 30). Macroscopically, T2 seems also to have an indistinct row of spines, but this appears to be an indistinct row (or almost absent) when studied in a slide under high magnification (Fig. 29). *B. ulmella* has only single rows of large spines, none on T2, and the microspines are less strong (see also below).

Biology. Hostplants: *Quercus velutina* Lam. (eastern black oak) and *Q. rubra* L. (northern red oak). Single records on chestnut oak (*Quercus montana* Willd.) (Drooz



Figs 3 – 12. *Bucculatrix* species, comparison between oak feeding species in mounted and live specimens. **3 – 7.** *B. ainsliella*, female, Wezep, RMNH.INS.544411 (**3** and **7**), RMNH.INS.544412 (**4 – 6**). **8 – 12.** *B. ulmella*, male, 't Harde, RMNH.INS.544414 (**8 – 11**), female, as Fig. 2 (**12**). **7** and **12** show aberrant antennal annulation pattern, extra group of 3 dark segments in *B. ainsliella* arrowed. Some photos were mirrored for reasons of comparison. Scales 1 mm, 2 mm (**4**), 0.5 mm (**7** and **12**).

1960, cited by Gibbons & Butcher 1961), a white oak, and chestnut (*Castanea* sp.) (labels cited by Braun 1963) should be confirmed because of their different taxonomic placement. Since cocoons can be placed on any surface, records of cocoons alone are not sufficient proof for host records. In Europe only recorded from *Quercus rubra*.

Life history. The egg is deposited on the upperside of the leaf, adjacent to (but never on) a major vein. The empty eggshell is oval in outline, and has a cockled sur-

face, making it iridescent under magnification. The mine (Figs 21–23) is a full-depth gallery, more than 1 cm in total length (11–14 mm); except for the last few mm, the gallery is strongly contorted. The sides are not straight but rather scalloped or jagged. The larval exit is on the leaf underside. For most of its width, the gallery, larval chamber excluded, is filled with lumpy, brownish-black frass. The mining larva does not cross major veins. The mine itself is indistinguishable from that of *B. ulmella*, but consistently longer in the few measured mines.

The free-living larvae window or skeletonise the underside of the leaves by consuming the softer tissue between the minor veins. Skeletonised patches of several mm in diameter in northern red oak leaves are a good indication of the presence of *Bucculatrix*, but we are not sure how to discriminate between *B. ainsliella* and *ulmella*.

The larva makes two "moulting cocoons", usually in vein axils on a leaf underside and the final instar larva fashions an oval, ribbed cocoon, with 5–8 ribs, without a "picket fence" (or palisade, see Braun 1963). Most cocoons lie adjacent to a major vein, at the underside of the leaf, or at the leaf margin or the margin of a leaf hole. Unlike *B. ulmella*, which has a somewhat dirty yellow cocoon, the cocoon of *B. ainsliella* is bright white.

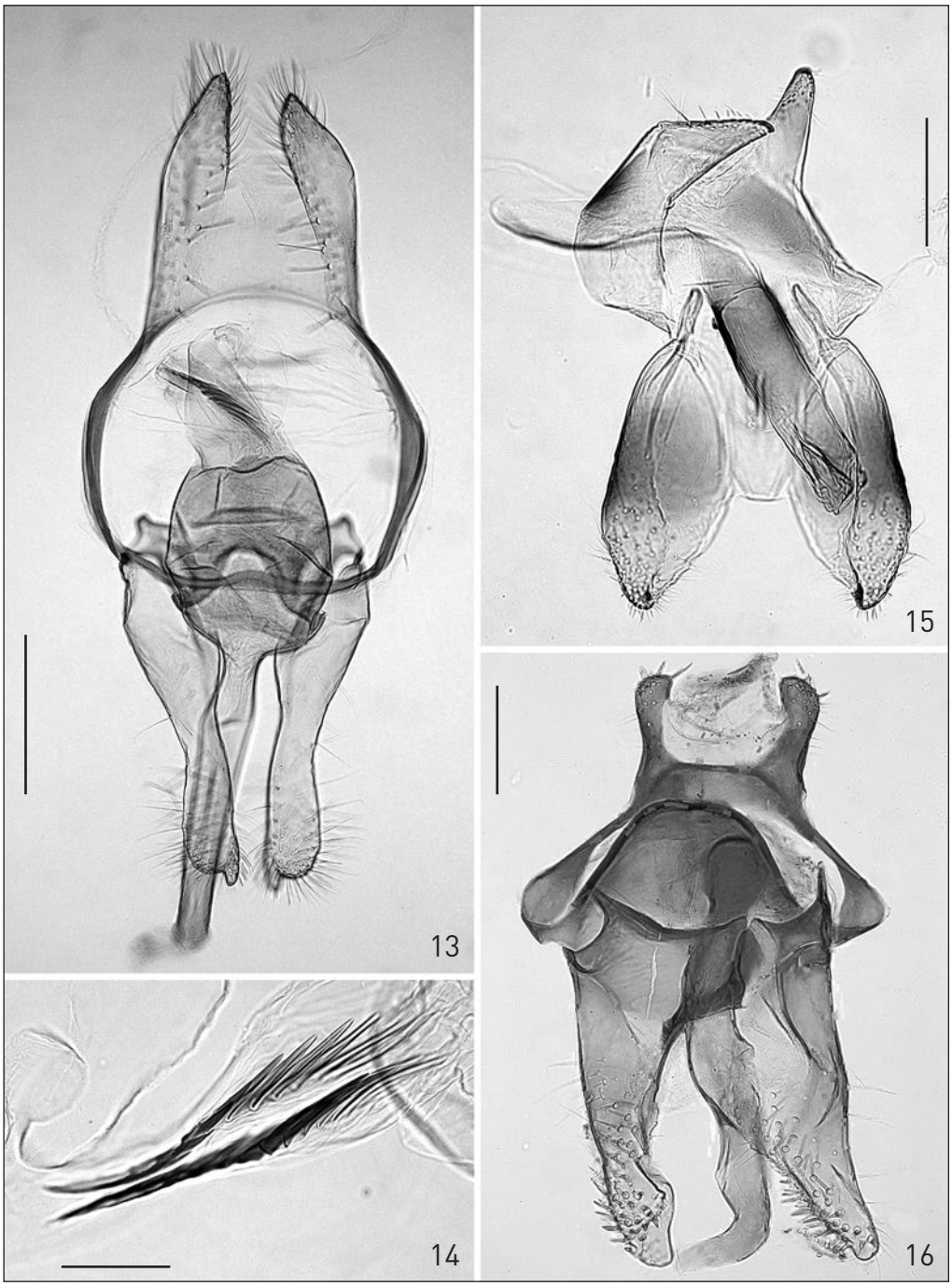
Voltinism. In North America recorded as bivoltine: larvae occur from mid April to early July and again from early August through mid-October. Cocoons of the first generation occur from late June to August, with moths flying from early July on, those of the second generation from October. Hibernation occurs in the pupal stage, on fallen leaves, trunks or other debris. Adults fly in spring mostly in April and early May, the summer generation from early July to August, in southern localities in the US until September (Braun 1963; Gelok et al. 1999; Gibbons & Butcher 1961). So far, the European records fit this general pattern (Table 1). Adults were found on the wing from mid-April to early October, thus a third generation might be a possibility.

Parasitoids. In the field, we very often observed cocoons with an exit hole of a parasitoid (see e.g., Ellis 2012, photo of cocoon), but until now, only a few hymenopterans have been reared from cocoons in Europe. They were all Ichneumonidae, two specimens belonging to the subfamily Campopleginae, and one to the genus *Gelis* Thunberg, 1827. The latter are often hyperparasitoids. In British Columbia and Canada the majority of parasitoids were also Ichneumonidae, but many Chalcidoidea were reared as well (Gelok et al. 1999).

From the native area of *B. ainsliella* the following parasitoids are recorded: Braconidae: *Pholetesor ornigis* (Weed, 1887), *Stiropius bucculatricis* (Ashmead, 1889); Eulophidae: *Chrysocharis* Forster, 1856 (unidentified species), *Cirrospilus cinctithorax* (Girault, 1916), *Cirrospilus flavicinctus* Riley, 1883, *Pnigalio maculipes* (Crawford, 1913); and Eurytomidae: *Eurytoma solenozopheriae* Ashmead, 1887 (Yu 2012).

Distribution (Fig. 35). Widespread in eastern North America, from the southern end of the Appalachians in South Carolina northward to the coastal area of New England, Nova Scotia, west to Oregon and Minnesota (Braun 1963), introduced into British Columbia in western Canada (Gelok et al. 1999).

Here, we record the species as new for Europe and currently found in The Netherlands, Belgium, and Germany. It is likely to be more widespread in Germany, and



Figs 13 – 16. *Bucculatrix* species, male genitalia. **13**, **14.** *B. ainsliella*, slides JCK7310 (= RMNH.INS. 544410), JCK3157. **15.** *B. ulmella*, JCK1898. **16.** *B. ulmifoliae*, slide JCK5549. Scales 200 µm (**13**), 100 µm (**15**, **16**), 50 µm (**14**).

should be searched for in France, Denmark, and other countries. Details of the records are presented in Table 1. The oldest specimens are from 1989–1990, and there is a gap in records between the 1989–1990 findings from Amersfoort and those in the Veluwe from 2003 onwards.

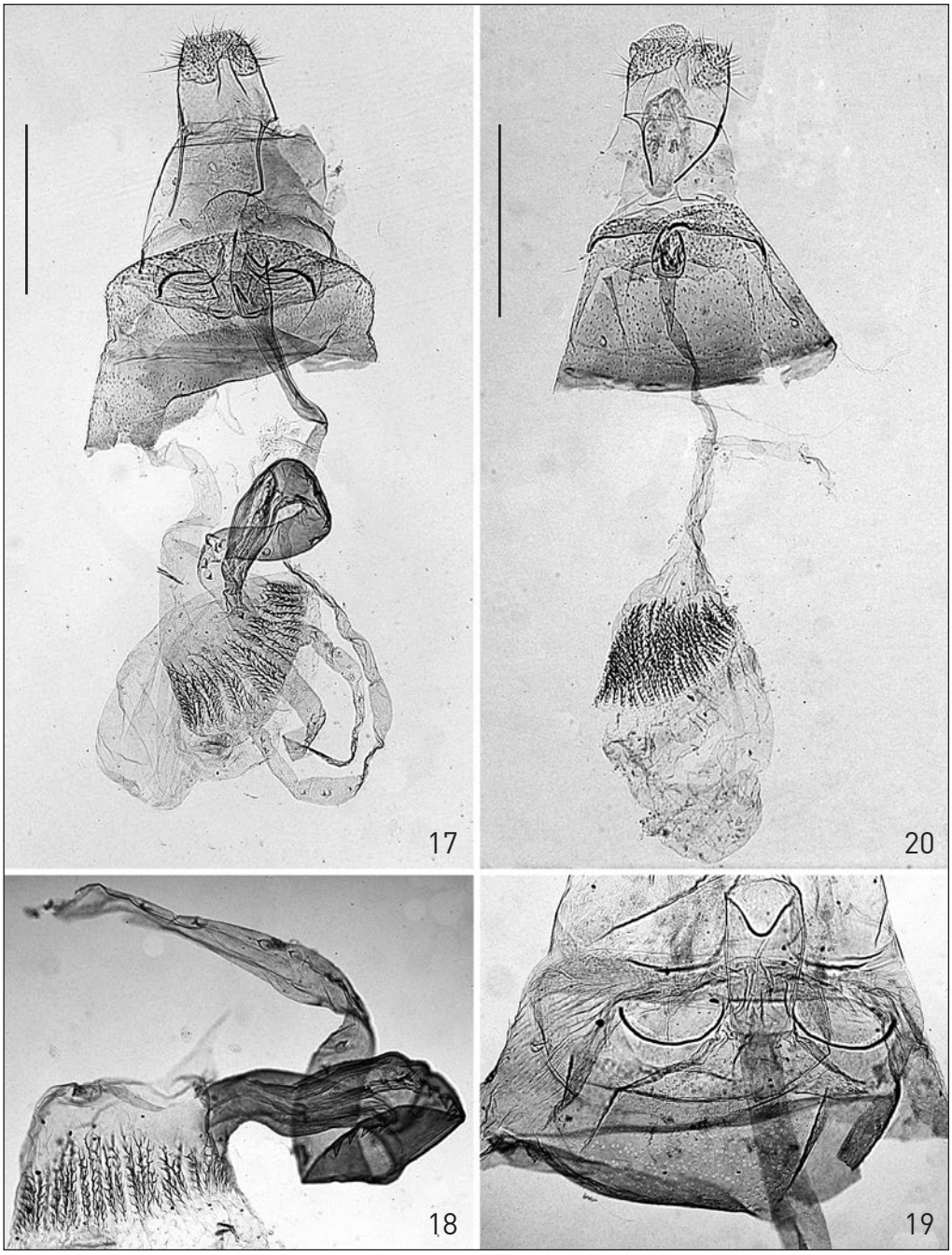
Damage. In North America, the species, known widely as the Oak Skeletonizer, can have outbreaks which lead to damage: trees that sustain repeated attacks are weakened and suffer crown thinning and die-back; ornamental trees appear especially vulnerable (Gibbons & Butcher 1961; Hanson & Walker 2004; Solomon et al. 2000). The prepupal larvae of *B. ainsliella* can be a nuisance when they are abundant because of their habit of descending along a silken thread (Gelok et al. 1999) and/or spinning cocoons over a variety of surfaces.

Remarks. The characteristic annulation of the antennae was also described by Braun (1963), but slightly different (probably an observation error). The pattern we see is constant in all specimens examined, and constantly different from *B. ulmella* that lacks the first group of three dark segments. The annulation pattern may be an interesting diagnostic character for the separation of *Bucculatrix* species. Braun described a comparable pattern for *B. pomifoliella* Clemens, 1860 and a slightly different one in *B. platyphylla* Braun, 1963; an illustration of European *B. demaryella* shows a similar pattern as well (Bengtsson & Johansson 2011).

***Bucculatrix ulmella* Zeller** **Figs 2, 8–12, 15, 20, 24, 25, 31–34**

Bucculatrix ulmella Zeller 1848: 289. Syntypes: [GERMANY, POLAND]: Berlin, Glogau [Glogow], "an Baumstämmen, besonders an Eichen" (types probably in London). [not examined]

Comparative notes. Adult (male, female) (Figs 2, 8–12) smaller than *B. ainsliella*: with forewing length ca. 3.1–3.4 mm, wingspan 6.7–7.6 mm. Antennal segments ca. 52–61, terminal segment formula: 5d-1w-1d-1w-5d-1w-1d-4w (Fig. 12), missing the first group of three dark segments present in *B. ainsliella*; first flagellar segment in male hardly notched. Head with tuft of scales completely ferruginous or yellow, only some pale scales may be seen laterally, but not banded as in *B. ainsliella*. Forewings with strong ochreous to ferruginous ground colour, black maculation variable, a squarish dorsal spot usually present. Male genitalia (Fig. 15) small. Socii short and triangular; valvae ca. 210–230 μm long, without apical hook. Phallus a short tube without cornuti. Female genitalia (Fig. 20) with short ostium, oval opening, no semicircular excavations. Ductus bursae slender, only slightly longer than corpus bursae, less than 1 mm long, without spines. Corpus bursae with signum comprising very closely set spined ribs, with very long spines, directed anteriorly.
Immature stages (Figs 24, 31–34). *Larva*. The free-living larva is basically greyish green, with several indistinct darker longitudinal lines, and with about eight whitish spots on each body segment. Larva in mine yellow (Fig. 24). *Pupa* (Figs 32–34). A10 with one pair of lateral tubercles. Tergites A3–7 with a single anterior row of rather coarse spines, in contrast to *B. ainsliella* that has 2–3 rows per seg-



Figs 17 – 20. *Bucculatrix* species, female genitalia. **17 – 19.** *B. ainsliella*, slides JCK7744 (**17**) and JCK 7734 (**18**, **19**). **20.** *B. ulmella*, JCK7732. Scales 500 µm.

ment. Microspines less conspicuous than in *B. ainsliella*. See also Patočka & Turčáni 2005.

Biology. Hostplants: *Quercus faginea* Lam., *Q. petraea* (Matt.) Liebl., *Q. pubescens* Willd., *Q. robur* L., *Q. rubra* L., *Q. trojana* Webb, and *Castanea sativa* Miller (Ellis 2012).
Life history: Very similar to *B. ainsliella*. Mines (Figs 24, 25) in principle inseparable, but smaller, with length of measured mines always less than 10 mm (ca. 8–9 mm), both on *Q. robur* and *Q. rubra*. Cocoon dirty yellow.

Distribution. Throughout Europe where oaks occur, yet to be recorded from Spain, Slovenia, Bosnia, Albania, and Bulgaria (Corley et al. 2006; Mey 2010).

Remark. The confusing name *B. ulmella* was suggested by Mann to Zeller (1848), who quoted Mann (in litt.) as describing that hundreds of caterpillars went down on threads from elms (*Ulmus*) near Vienna. Zeller also quoted Mann's description of the mine from *Ulmus*. Zeller identified the moths that he found on oak trunks as the same species, an understandable mistake, since the species that Mann described is probably *B. ulmifoliae*, a species externally rather similar to *B. ulmella*.

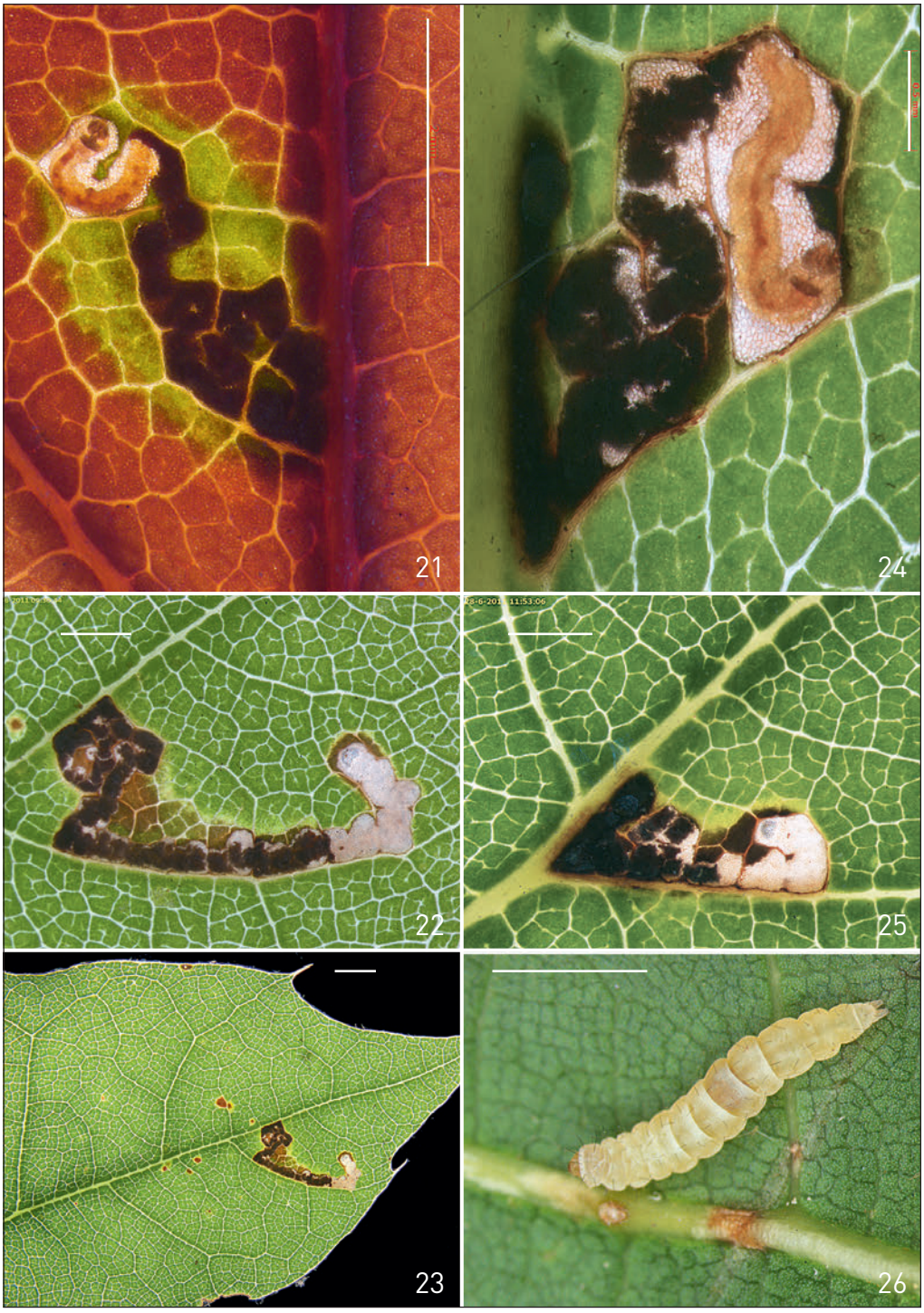
DNA barcodes

A neighbor-joining tree (Fig. 36) of DNA barcodes of our specimens of *B. ainsliella* combined with some other species from the Netherlands, plus publicly available barcodes of *Bucculatrix* (http://www.barcodinglife.com), demonstrate the conspecifity of Dutch and North American specimens. *B. ainsliella* is represented by 19 specimens, five from the Netherlands [NLLA] and 14 from North America, which collectively form a monophyletic cluster with an average (uncorrected) intraspecific distance of 0.7%. The Dutch specimens are represented by several haplotypes that are scattered over this cluster. The closest neighbour to *B. ainsliella* in this dataset of COI barcodes, which is lacking many species of *Bucculatrix*, is the North American *B. canadensisella* Chambers, 1875 at an average distance of 7.9%. This distance can be considered as relatively large for a distance to the nearest neighbour, when compared to other leafmining Lepidoptera (e.g., van Nieukerken et al. 2012a). The average intraspecific distances in *B. canadensisella* are 1.1%. *B. ulmella* is the nearest neighbour to *B. ainsliella* if the comparison is limited to European species, at an average distance of 8.0%. The average intraspecific distances in the available *B. ulmella* are 0.5%. This makes the identification of *B. ainsliella* by COI barcodes reliable.

Discussion

Lepidoptera on *Quercus rubra*

From the scarce literature data it appears that the northern red oak has a poor entomofauna in Europe, with few oak specialists. Polyphagous external feeding caterpillars, such as Tortricidae: *Archips xylosteana* (Linnaeus, 1758); Lasiocampidae: *Malacosoma*



Figs 21 – 26. *Bucculatrix* species, leafmines and larvae on *Quercus rubra*. **21 – 23**, **26.** *B. ainsliella*, Elmpt (21, RMNH.INS.18752), Wezep, Engelandseweg (**22**, **23**), Wezep, Patrijzenlaan (**26**). **24**, **25.** *B. ulmella*, Wezep, Wezeper Hei, (24 = RMNH.INS.18466). Scales 1 mm (**22**, **25**), 2 mm (**23**, **26**).

neustria (Linnaeus, 1758); Geometridae: *Operophtera brumata* (Linnaeus, 1758), *Erannis defoliaria* (Clerck, 1759), *Ectropis crepuscularia* (Denis & Schiffermüller, 1775), and *Colotois pennaria* (Linnaeus, 1761); Notodontidae: *Phalera bucephala* (Linnaeus, 1758) and *Thaumatopoea processionea* (Linnaeus, 1758); and Erebidae (Lymantriinae): *Lymantria dispar* (Linnaeus, 1758), *Calliteara pudibunda* (Linnaeus, 1758), *Euproctis chrysorrhoea* (Linnaeus, 1758), *E. similis* (Fuessly, 1775), and *Orgyia antiqua* (Linnaeus, 1758) have been recorded as defoliators on red oaks in Europe (Csóka & Szabóky 2005; Göhre & Wagenknecht 1955; Goßner & Hausmann 2009). Leafminers were rarely recorded, e.g., *Tischeria ekebladella* (Bjerkander, 1796) (Tischeriidae, Csóka & Szabóky 2005). While searching *Bucculatrix* mines in 2011, but also earlier, we have observed several more specialised oak-feeding leafminers on *Quercus rubra*, but usually in very low numbers, e.g., the Nepticulidae *Stigmella roborella* (Johansson, 1971), *S.* cf. *ruficapitella* (Haworth, 1828), *S. basiguttella* (Heinemann, 1862), *Ectoedemia albifasciella* (Heinemann, 1871), and the Gracillariidae *Caloptilia* sp., *Acrocercops brongniardella* (Fabricius, 1798), and *Phyllonorycter lautella* (Zeller, 1846). Only few of these were we able to rear, but since we did see completed mines, we think it most likely that all of the above can utilise this host. Apart from the lepidopteran leafminers, we also observed in June 2011 many old mines of the leaf-mining weevil *Orchestes quercus* (Linnaeus, 1758).

During our survey on the "Veluwe" near Wezep, we found larvae and cocoons of *Bucculatrix ulmella* (identity of mines proven by DNA barcodes) on *Q. rubra* at a locality where this species is common on indigenous *Quercus robur*, and where both trees grow intermingled. However, we have no evidence of the presence of *B. ulmella* on *Q. rubra* elsewhere. Further observations are needed to determine if both species occur syntopically more widely in Europe.

Quercus rubra has commonly been ignored by entomologists, because it is an exotic tree. This has, no doubt, contributed to the delayed detection of *B. ainsliella*, which has been present in Europe since at least 1989. Even though the general notion that *Q. rubra* has a poor entomofauna in Europe is definitely true and can be explained by the taxonomic separation between red and white oaks, it is also clear that there are gaps in our knowledge. Hopefully, with this new knowledge entomologists will also give attention to red oak trees so that a more complete record of insects associated with this species in Europe can be obtained.

Import of *Bucculatrix ainsliella*

The oldest known records from Europe originate from Amersfoort, province of Utrecht, the Netherlands. The (planted) forests in this area often consist entirely of *Quercus rubra*. An accidental introduction of *B. ainsliella*, therefore, could easily have been followed by establishment on its native hostplant. Close to Amersfoort is the former US Air Force Base Soesterberg, only closed in 2008. It is conceivable that moths or cocoons were transported by Air Force aircraft, or by military personal, living in this area. Cocoons of the hibernating generation, spun over virtually any surface in the vicinity of infested red oaks, including parked cars (Gelok et al. 1999), and which are present for more than six months in any year, are the likely source of the intro-

Figs 27 – 34. *Bucculatrix* species, cocoons and pupal exuviae of males. **27 – 30.** *B. ainsliella*, Wezep, Engelandseweg, RMNH.INS.544410. **31 – 34**. *B. ulmella*, 't Harde, RMNH.INS.544414. **29**, **33.** Details of spines on T2 and 3. **30**, **34.** Details of spines on T6 and 7.

duction. However, it may also be a sampling artefact that our first records are from near Amersfoort, and transport via containers on ships is another potential source of the original introduction. For another North American leaf-mining moth in Europe, *Macrosaccus robiniella* (Clemens, 1859) (as *Phyllonorycter robiniella*), it was suggested that either transport by air or by freight containers was the most likely source

Table 1. Specimens and observations of *Bucculatrix ainsliella* in Europe.

Stage, number	Registry #	Province	Locality	Date
2 cocoons, several mines		NL-DR	Boschoord	25-9-2011
3 adults ep, 4 mines, including 1 larva, 12 cocoons		NL-DR	Havelterberg	18-7-2011
cocoon with exuviae		NL-DR	Holtinge, Holtingerveld	21-7-2011
adult		NL-DR	Lhee, Dwingelderveld, Lheederzand	19-8-2011
cocoons and mines		NL-FR	Burgum	28-10-2011
cocoons and mines		NL-FR	Leeuwarden, Kleine Wielen	5-10-2011
cocoons and mines		NL-FR	Leeuwarden, Kleine Wielen	24-10-2011
cocoon on trunk of *Q. rubra*		NL-FR	Tytsjerk, Groot Vijversburg estate	24-10-2011
1 male, 2 females		NL-GE	Beekbergen, Engeland	1-8-2011
1 female		NL-GE	Beekbergen, Engeland	5-8-2011
1 adult		NL-GE	Beekbergen, Engeland	9-10-2011
1 female e.p., 4 cocoons,		NL-GE	Bennekom	19-7-2011
1 adult		NL-GE	Hoenderloo, De Rampe	18-9-2011
cocoons		NL-GE	Hoenderloo, Hoge Veluwe	30-10-2011
1 female		NL-GE	Twello	15-7-2003
1 male		NL-GE	Twello	18-7-2005
1 male		NL-GE	Twello	16-7-2007
1 male		NL-GE	Twello	21-8-2010
1 male		NL-GE	Twello	el 17-9-2009
1 male		NL-GE	Wezep	15-8-2009
1 male	RMNH.INS. JCK.7310	NL-GE	Wezep	29-4-2010
1 male	RMNH.INS. JCK.7513	NL-GE	Wezep	20-8-2010
1 male		NL-GE	Wezep	21-8-2010
1 male		NL-GE	Wezep	20-4-2011
1 male		NL-GE	Wezep	22-4-2011
cocoons		NL-GE	Zwolse Bos, Wezep-Heerde	18-7-2011
1 male	RMNH. INS.544410	NL-GE	Wezep, Engelandseweg	27-6-2011
1 female	RMNH. INS.544411	NL-GE	Wezep, Engelandseweg	27-6-2011
1 female	RMNH. INS.544412	NL-GE	Wezep, Patrijzenlaan	27-6-2011
> 250 cocoons, mines		NL-LI	Brunssumerheide, Heikop	15-8-2011
10 cocoons		NL-LI	Meinweg, Elfenmeer	16-8-2011
±150 mines, cocoons, several ♂ ♀ ep,		NL-LI	Meinweg, Vlodrop Station	31-7-2011

Abbreviations of countries and provinces: **BE** – Belgium: **AN** – Antwerpen, **LI** – Limburg, **OV** – Oost-Vlaanderen, **WV** – West-Vlaanderen. **DE** – Germany, Nordrhein-Westfalen. **NL** – Netherlands: **DR** – Drenthe, **FR** – Friesland, **GE** – Gelderland, **LI** – Limburg, **NB** – Noord-Brabant, **NH** – Noord-Holland, **OV** – Overijssel, **UT** – Utrecht.

Table 1. Table continued.

Leg	Method	Genitalia slide	Source	Longitude	Latitude
T. Muus			observation	52.90006	6.22525
T. Muus & S. Corver	ep	TM1159	coll. Muus	52.779	6.195
J. van Roosmalen			coll. Roosmalen. photograph *	52.811	6.248
J. Ebink	al		photograph *	52.823	6.412
G. Sinnema			photograph *	53.196	6.002
G. Sinnema			photograph *	53.217	5.886
G. Sinnema			photograph *	53.217	5.886
G. Sinnema			photograph *	53.215	5.907
L. Knijnsberg, J. van Roosmalen & A. Wijker	al		coll. Roosmalen. photograph *	52.158	5.95
L. Knijnsberg, J. van Roosmalen & A. Wijker	al		coll. Roosmalen. photograph *	52.158	5.95
J. van Roosmalen	al		coll. Roosmalen. photograph *	52.158	5.95
C. Geris	ep		coll. Muus *	52.011	5.681
L. Knijnsberg, A. Wijker	al		photograph *	52.121	5.911
W.N. Ellis			coll. Ellis	52.12	5.86
J. Wolschrijn		JCK7744	Coll Wolschrijn	52.2425	6.1084
J. Wolschrijn			Coll Wolschrijn	52.2425	6.1084
J. Wolschrijn			Coll Wolschrijn	52.2425	6.1084
J. Wolschrijn			Coll Wolschrijn	52.2425	6.1084
J. Wolschrijn	ep		Coll Wolschrijn	52.2425	6.1084
K.J. Huisman	al	JCK7310	RMNH	52.4544	5.9847
K.J. Huisman	al	JCK7513	Coll Huisman	52.4544	5.9847
K.J. Huisman	al	JCK7515	Coll Huisman	52.4544	5.9847
K.J. Huisman	al		RMNH	52.4544	5.9847
K.J. Huisman	al		Coll Huisman	52.4544	5.9847
K.J. Huisman	al		Coll Huisman	52.4544	5.9847
K.J. Huisman			observation	52.426	6.038
C. Doorenweerd & E.J. van Nieukerken	ep	JCK7310	RMNH	52.45017	5.98397
C. Doorenweerd & E.J. van Nieukerken	ep		RMNH	52.45017	5.98397
C. Doorenweerd & E.J. van Nieukerken	ep		RMNH	52.45529	5.98532
A. Schreurs	ep		coll Schreurs	50.928	6.006
A. Schreurs & M. van Stiphout			coll Schreurs	51.18	6.128
A. Scheurs & R. Seliger	ep		coll. Scheurs & Seliger	51.152	6.155

Method: al – at light, ep – reared from larva or cocoon.

* – details to be found at http://waarneming.nl/soort/view/211390

** – details to be found at http://waarnemingen.be/soort/view/211390

Table 1. Table continued.

Stage, number	Registry #	Province	Locality	Date
adults ep, cocoons		NL-LI	Meinweg, Vlodrop Station	2-7-2011
adult		NL-LI	Meinweg, Vlodrop Station	22-7-2009
1 female e.p., cocoon on *Cytisus scoparius*		NL-LI	Meinweg	ep 15-4-2007
leafmines		NL-LI	Meinweg, Roermond	4-9-2011
adult		NL-LI	Sint-Odiliënberg	9-9-2009
5 cocoons		NL-LI	Vijlenerbosch	13-8-2011
mines		NL-LI	Wellerlooi, De Hamert	1-8-2011
cocoons, e.p. 1 adult		NL-LI	Wellerlooi, De Hamert	2-8-2011
several mines and cocoons		NL-NB	Malpieven	17-7-2012
several adults		NL-NB	Nuenen	21-7-2010
several adults		NL-NB	Nuenen	11-7-2010
several adults		NL-NB	Nuenen	24-5-2011
several adults		NL-NB	Nuenen	27-6-2011
several mines and cocoons		NL-NB	Plateaux	18-7-2012
cocoon		NL-NH	Amstelveen, Gaasperplaspark	2011
1 male		NL-OV	Onna	20-7-2011
mines, 1 cocoon		NL-OV	Enschede, De Tip	24-7-2012
adult		NL-OV	Zwolle	19-4-2009
1 male		NL-UT	Amersfoort-Zuid	28-9-1989
1 male		NL-UT	Amersfoort-Zuid	30-4-1990
1 female		NL-UT	Amersfoort-Zuid	5-8-1990
1 male		NL-UT	Amersfoort-Zuid	15-8-1990
adults		NL-UT	Baarn, De Vuursche	7-5-2011
1 mine		NL-UT	Soest - Monnikenbos	19-7-2012
adult		BE-AN	Balen, Rosselaar	29-7-2010
adult		BE-AN	Berchem	12-5-2006
adult		BE-AN	Edegem	11-5-2011
cocoons		BE-AN	Meerhout	10-9-2011
adult		BE-AN	Mol, Molse zandputten	27-9-2011
adult		BE-AN	Mortsel	23-7-2010
adult		BE-LI	Lommel, Grote Barreel	3-10-2011
50 cocoons		BE-LI	Zutendaal	8-6-2011
10 cocoons, heavily parasited		BE-OV	Knesselare, Drongengoedbos	16-9-2011
adult		BE-WV	Torhout, Groenhove area	30-7-2011
Several mines and cocoons, 2 ep		DE	Rosenthal	31-7-2011
cocoons, vacated mines		DE	Elmpter Wald, near Dutch border	15-10-2011
cocoons, vacated mines, 1 larva		DE	Elmp, 2 km S, Dutch borderpole 938	16-10-2011

Abbreviations of countries and provinces: **BE** – Belgium: **AN** – Antwerpen, **LI** – Limburg, **OV** – Oost-Vlaanderen, **WV** – West-Vlaanderen. **DE** – Germany, Nordrhein-Westfalen. **NL** – Netherlands: **DR** – Drenthe, **FR** – Friesland, **GE** – Gelderland, **LI** – Limburg, **NB** – Noord-Brabant, **NH** – Noord-Holland, **OV** – Overijssel, **UT** – Utrecht.

Table 1. Table continued.

Leg	Method	Genitalia slide	Source	Longitude	Latitude
K.J. Huisman	ep		Coll Huisman	51.152	6.155
T. Muus	al		coll. Muus	51.152	6.155
W. Wittland		Tokár 607	coll. ÖZK	51.152	6.155
V. Middelman & R. Vos			photograph *	51.182	6.046
E. Clerx	al		photograph *	51.143	6.002
A. Schreurs				50.77	5.953
W.N. Ellis			coll. Ellis	51.518	6.172
W.N. Ellis			coll. Ellis	51.512	6.173
C. Doorenweerd, H. Dries & T. Muus			RMNH	52.18958	5.29524
C. Nolte	al		photograph *	51.47	5.551
C. Nolte	al		photograph *	51.47	5.551
C. Nolte	al		photograph *	51.48	5.56
C. Nolte	al		photograph *	51.48	5.56
C. Doorenweerd & C. Van Steenwinkel			RMNH	51.27108	5.40085
T. Hakbijl			RMNH	52.31	4.99
T. Muus			coll. Muus	52.775	6.149
J.C. & P.M. Koster			RMNH	52.257	6.969
G. Veurink	al		photograph	52.523	6.049
K.N. Nieuwland	al	JCK3157	RMNH	52.13881	5.38087
K.N. Nieuwland	al		RMNH	52.13881	5.38087
K.N. Nieuwland	al		RMNH	52.13881	5.38087
K.N. Nieuwland	al		RMNH	52.13881	5.38087
L. Knijnsberg, J. van Roosmalen & A. Wijker	al		coll. Roosmalen. photograph *	52.186	5.232
H. Soetekouw			photograph	52.15	5.335
Ludwig Jansen	light trap		photograph **	51.172	5.143
			photograph **	51.181	4.425
			photograph	51.153	4.438
C. van Steenwinkel			photograph **	51.108	5.053
C. van Steenwinkel	al		photograph **	51.215	5.112
			photograph	51.167	4.45
H. Dries.	al		photograph **	51.23	5.374
C. Snyers			coll. Snyers	50.933	5.577
S. Wullaert			coll. Wullaert	51.146	3.454
T. Vermeulen	light trap		photograph **	51.072	3.134
A. Scheurs & R. Seliger	ep		coll. Seliger	51.131	6.132
E.J. van Nieukerken			RMNH	51.2222	6.0749
E.J. van Nieukerken			RMNH	51.19332	6.16207

Method: al – at light, ep – reared from larva or cocoon.
* – details to be found at http://waarneming.nl/soort/view/211390
** – details to be found at http://waarnemingen.be/soort/view/211390

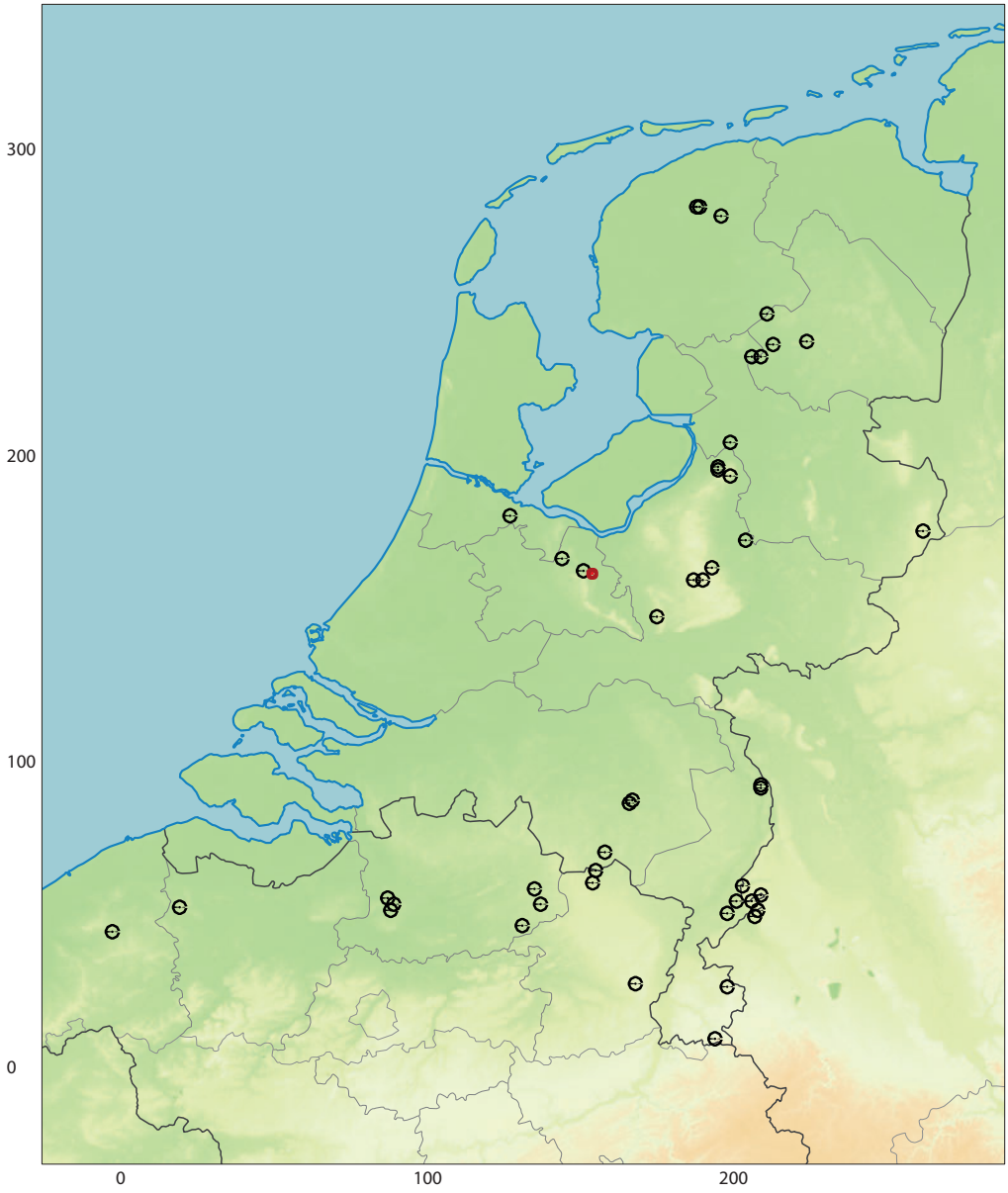


Fig. 35. *Bucculatrix ainsliella*, records in the Netherlands, Belgium and Germany. Red dot denotes first record in 1989 in Amersfoort. For details see Table 1.

(Whitebread 1990). The fact that we found different COI barcode haplotypes even from specimens at a single locality, suggests that multiple individuals have been imported. With the current rate of transportation of goods and people between Western Europe and North America and the ease with which *B. ainsliella* larvae can attach themselves to almost any surface, in combination with the ideal habitat away from home that has been created in Europe by widespread planting *Q. rubra*, it seems that it was only

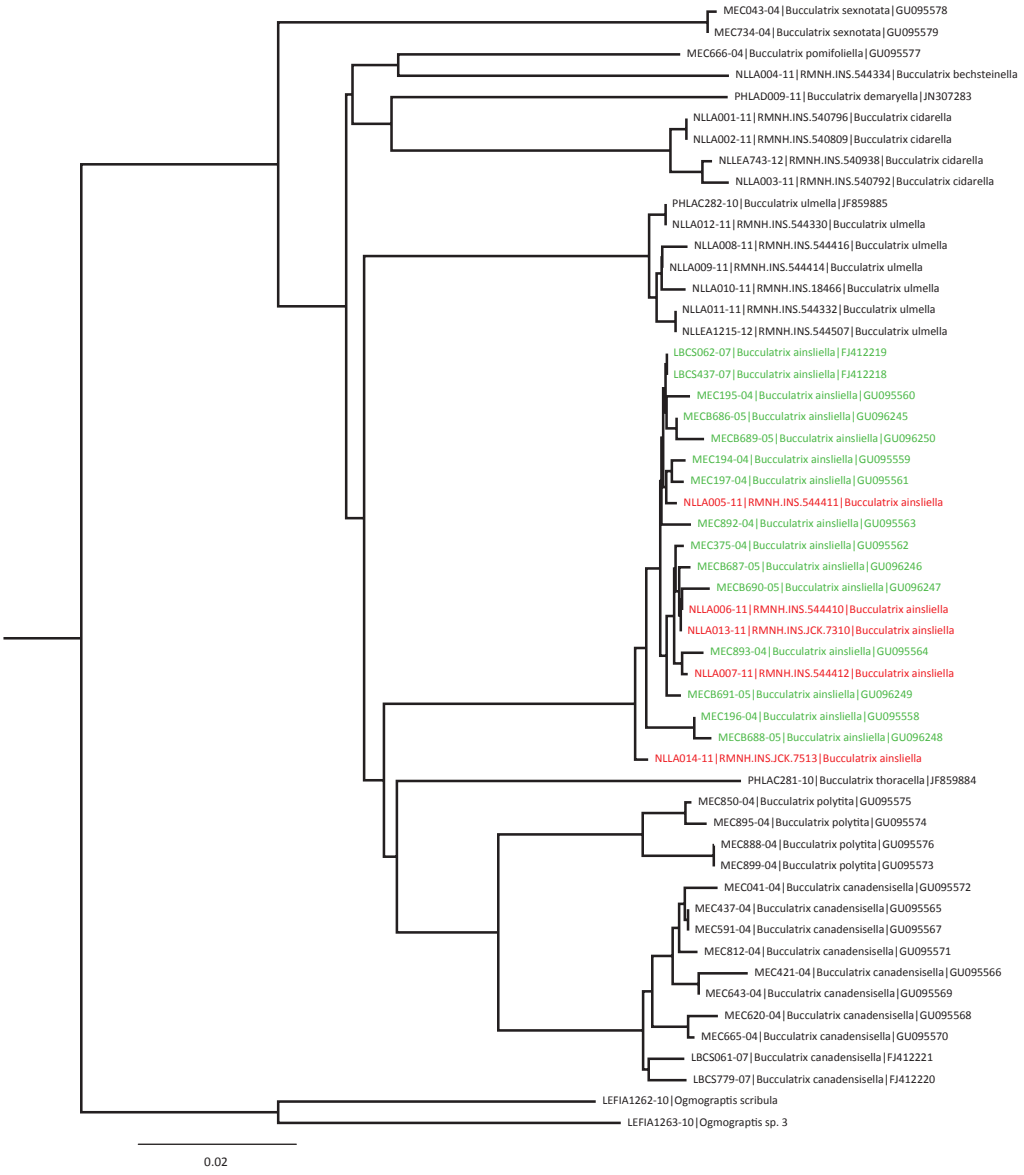


Fig. 36. Neighbor-joining tree of DNA barcodes of Bucculatricidae, using uncorrected P distance. The Australian *Ogmograptis scribula* Meyrick, 1935 is used as outgroup. Red records are Dutch specimens of *B. ainsliella*, green ones are from North America. The following are also North American species: *B. sexnotata* Braun, 1927, *B. pomifoliella* Clemens, 1860, *B. polytita* Braun, 1963, *B. canadensisella* Chambers, 1875. The remainder are European species. Details on vouchers of specimens with a "RMNH.INS" registry number can be found in the BOLD project "Lepidoptera of the Netherlands – public [NLLA]" (http://www.barcodinglife.com). Other public sequences are from other projects, and can be recognised here by the added Genbank Accession number.

a matter of time before this American moth established itself in Europe. There are ever-increasing examples of North American micromoths invading and successfully

establishing in Europe. Examples of recent introductions are in Heliozelidae: *Antispila oinophylla* Van Nieukerken & Wagner, 2012 on *Vitis* (van Nieukerken et al. 2012b), a species of *Coptodisca* on *Juglans* (Bernardo et al. 2012); in Gracillariidae: *Parectopa robiniella* (Clemens, 1863) and *Macrosaccus robiniella* both on *Robinia pseudoacacia* (Whitebread 1990), *Phyllocnistis vitegenella* Clemens, 1859 on *Vitis* (Posenato et al. 1997); in Argyresthiidae: *Argyresthia thuiella* (Packard, 1871) on *Thuja* and other Cupressaceae; and in Gelechiidae: *Coleotechnites piceaella* (Kearfott, 1903) on *Picea* (Lopez-Vaamonde et al. 2010).

Risks?

In North America *Bucculatrix ainsliella* is known to have severe outbreaks from time to time. Especially in British Columbia, where it is introduced, the species has become a nuisance in urban areas due to its abundance, especially when prepupae balloon down from trees and make their cocoons everywhere. In natural habitats, outbreaks are probably a natural phenomenon, followed by years of lower densities when parasitoid populations control their numbers. A similar alteration has been observed in the birch leaf skeletoniser *B. canadensisella* on *Betula* species, which underwent several outbreaks that lasted for two to three years (Friend 1927). In Europe, outbreaks are known from the expanding native species *B. thoracella* on *Tilia* (Kuchlein & Frankenhuyzen 1994), and we have observed similarly abundant ballooning larvae from *Tilia* trees in cities in the Netherlands. Although *B. ainsliella* can be common in places in the Netherlands, we have not yet seen an indication of an outbreak or indications of real foliar damage. Many of the northern red oak trees where we found *B. ainsliella* on, were more visibly damaged by caterpillars of indigenous polyphagous caterpillar and beetle species.

We urge forest entomologists and lepidopterists throughout Europe to look for this species (adults, mines, or cocoons) in order to be able to more fully understand its range expansion across the Palaearctic.

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