Different continents, same species? Resolving the taxonomy of some Holarctic Ancylis Hübner (Lepidoptera: Tortricidae)

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Abstract

Several species of Ancylis related to A. unguicella (Linnaeus) and A. geminana (Donovan) have been presumed by previous authors to be Holarctic. However, difficulty in identifying genitalic characters to define and separate these taxa has brought into question their true distribution and led to inconsistencies in their taxonomic treatment in Europe and North America. Here we use a combination of DNA barcode sequence data and morphology to resolve these taxonomic differences, determine the actual geographic range of these taxa, and describe three new species. In the A. unguicella group, only A. unguicella and A. uncella (Denis & Schiffermüller) are Holarctic in distribution. In the A. geminana group, none of the taxa are Holarctic in their distribution. Three species are described as new: A. christiandiana Huemer and Wiesmair, sp.n. (Austria, Germany); A. oregonensis Gilligan and Huemer, sp.n. (USA: Oregon); and A. saliana Gilligan and Huemer, sp.n. (USA: Florida). In addition, Ancylis carbonana Heinrich, syn.n., is synonymized with A. uncella; A. cuspidana (Treitschke), syn.rev., is synonymized with A. diminutana (Haworth); and A. diminutana Kearfott, stat.rev., and A. subarcuana (Douglas), stat.rev., are raised from synonymy.

Key words: christiandiana, DNA barcoding, Enarmoniini, oregonensis, saliana

Introduction

Tortricid taxonomy has long been plagued by inconsistencies in classification between the Nearctic and Palearctic faunas. Early workers in North America encountering potential new species had to determine if these taxa were undescribed or Holarctic in distribution, thus conspecific with species already described from Europe. This task was especially difficult prior to the use of genitalia in tortricid taxonomy, and decisions regarding conspecificity were based on wing patterns and life histories, although the latter was often unknown. The widespread use of genitalic characters to separate species began in the 1920’s, led by Pierce and Metcalfe (1922) in Europe and Heinrich (1923, 1926) in North America. Examination of the genitalia allowed these researchers to make tremendous advances in tortricid taxonomy, and reliance on the genitalia to define species and higher taxonomic groups increased to where it has become one of the most important characters sets in the classification of the Tortricidae (Horak 1999). Specifically, it has been the male genitalia that are believed to be of diagnostic value at the species level (Klots 1970), and taxa are often considered to be conspecific based on similarity in the male genitalia (Mutanen et al. 2012). Care should be taken, however, when relying on a single character set to infer taxonomy. Traditionally, reliance on the male genitalia as a species-specific character set was justified by the lock-and-key mechanism of genital evolution (e.g., Mikkola 1992), although sexual selection, where variation in the male genitalia is directly responsible for fertilization success (Eberhard 1985, Arnqvist 1997, Hosken and Stockley 2004) suggests that intraspecific variation in the genitalia is expected. Intraspecific variation in tortricid genitalia has been well documented in some groups (e.g., Mutanen et al. 2007, Gilligan and Wenzel 2008, Wright and Gilligan 2015).

The advent of molecular systematics, including DNA barcoding (Hebert et al. 2003), has led to the
development of new character sets with which to test species boundaries. Patterns in DNA sequence data can be used to determine “important” morphological characters for defining a taxon that would otherwise be undecipherable because of intraspecific variation or an apparent lack of interspecific variation (Mutanen et al. 2012, Brown et al. 2014, Gilligan et al. 2014b). This approach can also be used to determine if morphologically similar populations in North American and Europe are conspecific or separate species. Several recent studies (e.g., Humble et al. 2009, Mutanen et al. 2012, Landry et al. 2013) have used DNA barcoding to resolve issues surrounding Holarctic (or presumed Holarctic) Tortricidae. One group with presumed Holarctic species that are difficult to define using traditional male genitalic characters is the genus Ancylis Hübner.

Ancylis is the largest genus in the Enarmoniini with more than 140 described species (Brown 2005, Gilligan et al. 2014a). Members of the genus are found worldwide, with the majority of species in the Holarctic, Oriental, and Australian regions (Horak 2006). The genus was divided between Anchylopera Stephens and Ancylis until the late 1970’s based on an atrophied uncus in Anchylopera, but this character was found too variable to be diagnostic (Razowski 1989, 2003). The genus is currently defined by the hollow bladelike signa arising from a sclerotized area on the corpus bursae and possibly the structure of the sterigma (Horak 2006). A falcate or “hooked” apex of the forewing is characteristic for most species, although this character is shared by species in other genera.

In North America, approximately 35 species of Ancylis are present (Powell 1983), although the exact number is uncertain. One reason for this uncertainty is the number of taxa in species complexes that have seemingly identical (and variable) genitalia (Miller 1987, Gilligan et al. 2008). Another reason is the number of species that are assumed by various authors to be Holarctic; these include A. comptana (Frölich), A. diminutana (Haworth), A. geminana (Donovan), A. tinea (Hübner), A. uncella (Denis & Schiffermüller), and A. unguicella (Linnaeus) (Miller 1987, Razowski 2003, Brown 2005, Gilligan et al. 2008, Gilligan et al. 2014a). The majority of these species fall into two groups with the members of each group having similar male genitalia. In addition, each group contains new species, three of which are described here.

The European fauna is less diverse than the North American, including 24 species (Aarvik 2013). The taxonomic history of taxa, particularly of the Ancylis geminana group and the Ancylis unguicella group, is varied and represented differently in the European versus North American literature. Early European checklists (Stephens 1829) recognized Anchylopera biarcuana, A. diminutana, and A. uncella, treating A. geminana as a synonym of the latter. Wocke (1871) followed this arrangement (as Phoxopteryx) and also listed subarcuana as a variety of P. biarcuana and P. uncella as a junior synonym of P. uncella. Phoxopteris and Phoxopteryx were synonymized under Ancylis by Walsingham (1897). Rebel (1901) recognized A. unguicella, A. uncella (including A. uncella), A. biarcuana, and A. diminutana, listing A. geminana as a subspecies and subarcuana as a variety of A. biarcuana. It was nearly a century before an updated list of European Lepidoptera was published, during which time A. biarcuana and A. uncella were relegated to junior synonyms of A. geminana and A. uncella, respectively, and A. subarcuana was elevated to species level. Thus, Razowski (1996) recognized A. diminutana, A. geminana, A. subarcuana, A. uncella, and A. unguicella as separate species in the European checklist.

Early North American checklists (Fernald 1882, 1903) followed the European convention, treating both A. geminana and A. uncella as synonyms of A. uncella, and A. biarcuana as a separate species. North American checklists also included A. goodelliana and A. pacifica, and later (Barnes and McDunnough 1917), A. diminutatana, described as new by Kearfott in 1905 and “close to European biarcuana.” Heinrich (1923) was the first author to deviate from the European classification of Ancylis for North America. He described A. carbonana, stating that it was different from A. uncella (= A. uncella), and that the latter species “does not occur in our fauna.” He relegated Kearfott’s A. diminutatana to a junior synonym, stating that it was “nothing but the European diminutana redescribed under practically the same name.” Heinrich also speculated that “the so-called biarcuana Stephens” was the same as A. diminutana (although he did not list it as a synonym). Powell (1983) followed Heinrich for the most part, recognizing A. carbonana (with North American A. uncella as a synonym), A. goodelliana, A. unguicella, and A. pacifica. He also listed A. diminutana and included A. diminutana as a misspelling under that name. To further complicate matters, Brown (2005), while examining material primarily in the USNM, determined that A. diminutana does not occur in North America, and specimens determined as such were actually A. geminana. He also synonymized A. diminutana and A. subarcuana under A. geminana. This arrangement was preserved in Gilligan et al. (2014a) but neglected in Europe.

While examining COI DNA barcode sequences in the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007), we noticed several inconsistencies in the clustering of sequences from specimens identified as A.
The taxa treated here can be divided into two groups based primarily on the structure of the male genitalia. The first group, the *A. unguicella* group, contains *A. unguicella*, *A. pacificana*, *A. uncella*, *A. goodelliana*, and *A. oregonensis*. Of these, *A. unguicella* and *A. uncella* have a Holarctic distribution, the latter as a result of being synonymized here with *A. carbonana*.

Species in this group can be identified using a combination of wing pattern and genitalia. Male genitalia exhibit some intraspecific variation but are generally more diagnostic than in the *A. geminana* group. Female genitalia are relatively uniform but have a few species-specific characters. Shared characters include:

**Materials and methods**

We examined 559 adult specimens (415 ♂, 144 ♀) together with 77 associated genitalia preparations deposited in the following collections: American Museum of Natural History, New York, New York, U.S.A. (AMNH); Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada (CNC); Colorado State University, Fort Collins, Colorado, U.S.A. (CSU); Cornell University Insect Collection, Cornell University, Ithaca, New York, U.S.A. (CUIC); Essig Museum of Entomology, University of California, Berkeley, California, U.S.A. (EME); Florida State Collection of Arthropods, Gainesville, Florida, U.S.A. (FSCA); Landesmuseum Kärnten, Klagenfurt, Austria (LMK); Mississippi Entomological Museum, Mississippi State University, Starkville, Mississippi, U.S.A. (MEM); Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria (TLMF); and National Museum of Natural History, Washington, D.C., U.S.A. (USNM).

Images of adults were taken with Canon 100 mm and MP-E 65 mm macro lenses attached to a Canon 7D digital SLR or with an Olympus E 3 digital camera attached to an Olympus SZX 10 binocular microscope. Images of genitalia were taken with a Nikon DS-Fi1 digital microscope camera attached to a Nikon Labophot-2 compound microscope or with an Olympus E-1 Digital Camera attached to an Olympus BH2 microscope. All images were edited using Photoshop CS6 and some are composite stacks of many individual images created with Zerene Stacker. Forewing length (FWL) is defined as the distance from the base to the apex including the fringe, reported to the nearest half millimeter. Measurements were made with a stereomicroscope equipped with an ocular micrometer or a compound microscope using a slide micrometer. The number of observations supporting a particular statistic is indicated by “n =.” Dissection methods follow those presented in Brown and Powell (1991), and morphological nomenclature follows Horak (2006) and Gilligan *et al.* (2008).

Dried legs were prepared according to pre-described standards and processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) to obtain COI DNA barcodes using the standard high-throughput protocol (deWaard *et al.* 2008). DNA sequences > 200 bp from our material and public sequences from BOLD were considered for analysis. Further details including complete voucher data and images can be accessed in the public dataset “Lepidoptera—Ancylis” (dx.doi.org/10.5883/DS-LEANCYLIS) in the Barcode of Life Data Systems (BOLD; Ratnasingham & Hebert 2007). Degrees of intra- and interspecific variation of DNA barcode fragment were calculated under Kimura 2 parameter model of nucleotide substitution using analytical tools of BOLD systems v. 3.0. (http://www.boldsystems.org). A neighbor-joining tree of DNA barcode data was constructed under the Kimura 2 parameter model for nucleotide substitutions.

**Results and discussion**

**Ancylis unguicella group**

The taxa treated here can be divided into two groups based primarily on the structure of the male genitalia. The first group, the *A. unguicella* group, contains *A. unguicella*, *A. pacificana*, *A. uncella*, *A. goodelliana*, and *A. oregonensis*. Of these, *A. unguicella* and *A. uncella* have a Holarctic distribution, the latter as a result of being synonymized here with *A. carbonana*.

Species in this group can be identified using a combination of wing pattern and genitalia. Male genitalia exhibit some intraspecific variation but are generally more diagnostic than in the *A. geminana* group. Female genitalia are relatively uniform but have a few species-specific characters. Shared characters include:
FIGURE 1. Neighbor-joining tree of COI DNA barcode data obtained from BOLD (K2P model). Clusters representing morphologically distinct species are color-coded with the corresponding species name.
Male genitalia. Uncus bifid, well developed in all species except *A. oregonensis*. Socii large, membranous, setose pads. Valva with costal margin concave; saccular angle weakly to moderately developed; neck width relatively uniform; cucullus densely setose, outer margin convex, apex acute to broadly rounded. Caulis long; phallus 0.5 to equal length of valva; vesica with numerous deciduous lanceolate cornuti.

Female genitalia. Papillae anales moderately setose. Apophyses posteriores and apophyses anteriores approximately the same length. Lamella postvaginalis membranous, undefined; lamella antevaginalis sclerotized, projecting ventrally above ostium, often with slight median indentation, forming a funnel-shaped antrum that is sclerotized 0.4–0.6 length of ductus bursae (except in *A. oregonensis*). Colliculum present as two lateral sclerites of varying length continuous with anterior sclerotization of antrum. Ductus seminalis arising from near junction of ductus and corpus bursae. Corpus bursae large, oval; two blade- or horn-shaped signa present.

**Ancylis unguicella** (Linnaeus, 1758)

Figs. 2–6, 59–60, 75

*Phalaena (Tinea) unguicella* Linnaeus, 1758, *Systema Naturae* (10th ed.): 536.

*Phalaena unguicella* Clerck, 1759, *Icones Insectorum Rariorum* 1: pl. 12, fig. 7. [misspelling of unguicella]

*Pyralis unguiculana* Fabricius, 1775, *Systema Entomologiae*: 654. [unjustified emendation]


**Diagnosis.** *Ancylis unguicella* is one of few *Ancylis* with dark fasciate wing markings. In the Palearctic, *A. achatana* has a similar wing pattern, but the median fascia is not as well defined, and the male genitalia differ with a narrow valval neck and well-defined 90° saccular angle. The Nearctic *A. pacificana* is identical in wing pattern to *A. unguicella*, and the two species cannot be separated without dissection. In the male, the cucullus of *A. unguicella* is blunter with a nearly acute apex versus the elongate rounded cucullus in *A. pacificana*, and the phallus is longer (0.75 as long as valva in *A. unguicella*; 0.5–0.6 as long as valva in *A. pacificana*). In the female, the antrum of *A. unguicella* is wider posteriorly and the signa are smaller than in *A. pacificana*.

**Redescription.** Forewing. FWL 7–8.5 mm (n=102), 7–9 mm (n=8). Forewings are gray and brown, with a brown to dark brown median fascia that is complete from costa to dorsum, white costal strigulae, and silvery striae. Some individuals have tan or light gray-tipped scales interspersed throughout the entire wing, especially in interfascial areas. Male genitalia. Uncus bifid to approximately half its length. Valva with shallow basal excavation extending to middle of neck; saccular angle weakly developed with variable triangular terminal projection; neck of uniform width from sacculus to cucullus; cucullus blunt, densely setose, outer margin rounded with several rows of short stout setae, apex nearly acute; caulis 0.5 to 0.75 as long as phallus; phallus 0.75 as long as valva, with small triangular tooth just proximal to apex; vesica with ca. 40–60 deciduous lanceolate cornuti. Female genitalia. Antrum sclerotized to 0.5 length of ductus bursae, widened at ostium to near distance between apophyses anteriores. Corpus bursae large, oval, expanding abruptly from ductus bursae; signa blade-shaped, unequal in size.

**Molecular data.** BIN URI: BOLD:AAB3498. The intraspecific divergence of the barcode region is moderate with average 0.84% and maximum 2.36% (n=46). However, North American and European populations cluster separately with a minimum distance of 0.87%. The minimum distance to the nearest neighbor *A. mediofasciana* is 4.5%.

**Distribution.** *Ancylis unguicella* has a Holarctic distribution. In the Palearctic, it is found from Western Europe to Siberia, the Korean Peninsula, and Japan (Razowski 2003). In the Nearctic, it is present from Alaska and British Columbia east to Ontario and south to Colorado.

**Biology.** Adults are present from May to early July. Larvae feed from July to August on various species of *Erica* (Ericaceae) and on *Calluna* (Ericaceae). Pupation takes place in early spring after larval hibernation in the final instar (Bradley et al. 1979; Razowski 2001). *Ancylis unguicella* prefers heathland and moors.

**Remarks.** This species is identical in wing pattern to *A. pacificana*. In the Pacific Northwest, where *A. pacificana* is also present, species-level determinations should rely on the male genitalia. We were unable to locate any specimens of *A. unguicella* from California or Oregon. Despite the weak genetic divergence of North American populations, we treat them as conspecific due to the morphological conformity.

Ancylis pacificana (Walsingham, 1879)
Figs. 7–10, 61–62, 76


Diagnosis. Ancylis pacificana is identical in wing pattern to A. unguicella, and the two species cannot be separated without dissection. In the male, the cucullus of A. pacificana is more elongate with a rounded apex versus the shorter, blunt cucullus in A. unguicella, and the phallus (and caulis) is shorter in A. pacificana. In the female, the antrum of A. pacificana is narrower posteriorly and the signa are larger than in A. unguicella.

Redescription. Forewing. FWL ♂ 7.5–10 mm (n=18), ♀ 8.3 mm (n=1). Forewing description as in A.
Male genitalia. Uncus bifid to approximately half its length. Valva with shallow basal excavation extending to just beyond sacculus; saccular angle weakly to moderately developed with variable triangular terminal projection; neck of uniform width or slightly narrowed from sacculus to cucullus; cucullus elongate, densely setose, outer margin convex with several rows of short setae near the anal angle, apex rounded; caulis 0.5 as long as phallus; phallus 0.5–0.6 as long as valva, with small triangular tooth just proximal to apex; vesica with ca. 40–60 deciduous lanceolate cornuti. The length of the cucullus, the width of the valval neck, and the saccular terminal projections all vary between individuals; we have attempted to illustrate the range of variation in Figs. 58–59.

Female genitalia. Antrum sclerotized to 0.4 length of ductus bursae, widened at ostium to 0.5 distance between apophyses anteriores. Corpus bursae oval, expanding gradually from ductus bursae; signa large, blade- or horn-shaped, unequal in size.

Distribution. Because of its similarity with *A. unguicella*, the distribution of *A. pacificana* is difficult to determine from undissected museum specimens. Heinrich (1923) reported specimens from California, British Columbia, and Colorado, whereas Powell and Opler (2009) reported a distribution limited to montane habitats in Oregon and northern California. The specimens that we determined as *A. pacificana* were from California, Oregon, and British Columbia, although we discovered one male in the EME from San Bernardo, Sonora, Mexico. This suggests that the distribution of *A. pacificana* is more extensive than assumed by previous authors, although we have not confirmed *A. pacificana* from any other locations (including Colorado). In any event, undissected museum specimens identified as *A. pacificana* should be treated as suspect until verified using genitalic characters.

Molecular data. Unknown.

Biology. Adults are present May to July. The larval host is unknown, although Powell and Opler (2009) report adults associated with *Ceanothus*.

Remarks. Heinrich (1923) stated that *A. pacificana* was larger and less darkly marked than *A. unguicella*. We found that, whereas some specimens of *A. pacificana* are slightly larger, both species overlap in size. We also found smaller specimens of *A. pacificana* with dark markings (e.g., Fig. 9) that were incorrectly identified as *A. unguicella*. Species-level determinations of either species from the Pacific Northwest should rely on male genitalia.

*Ancylis uncella* (Denis and Schiffermüller, 1775)

Figs. 11–16, 63–64, 77–78


Diagnostic. Most individuals of *A. uncella* can be diagnosed by forewing pattern: the median fascia is brown to reddish brown, complete from costa to dorsum, and flanked on the dorsum and tornus by gray patches. Some *A. goodelliana* can appear similar (Fig. 18), but the median fascia is not expressed on the costa in that species.

Redescription. Forewing. FWL ♂ 5–9 mm (n=30), ♀ 6–8 mm (n=14). Forewings are brown to reddish brown and gray with white to gray costal strigulae. The brown to reddish-brown median fascia is complete from costa to dorsum in most individuals; occasionally the dorsal portion is broken before reaching the dorsum (Fig. 13), but in all cases the median fascia is expressed on the costa. Gray to light gray patches are present proximal to the median fascia on the dorsum and distal to the median fascia on the tornus; often median fascia extends into the distal gray patch (Fig. 12–13, 16). In some individuals the brown and gray areas of the wing are sharply contrasting (Fig. 11), while in others the gray is darker and subdued (Fig. 14). Black streaks are sometimes weakly expressed along the radius and cubitus (Figs. 12–14). Male genitalia. The male genitalia are identical to those of *A. pacificana* with the exception of the phallus, which is 0.7 as long as the valva, and the tooth on the phallus, which is at the apex (and difficult to see in some preparations). As with *A. pacificana*, the length of the cucullus, the width of the valval neck, and the saccular terminal projections all vary between individuals; we have attempted to illustrate the range of variation in Figs. 63–64. Female genitalia. Antrum sclerotized to 0.6 length of ductus bursae, widened at ostium to 0.5 distance between apophyses anteriores. Corpus bursae large, oval, expanding abruptly from ductus bursae; signa large, blade- or horn-shaped, unequal in size.
Molecular data. BIN URI: BOLD:AAA7191, BIN-sharing with *A. goodelliana*, with a minimum distance of 1.13%.

Distribution. With the synonymy of *A. carbonana, A. uncella* has a Holarctic distribution. In the Palearctic, it is found from the United Kingdom and France south to Romania and east to Siberia, the Korean Peninsula, and Japan (Razowski 2003). In the Nearctic, it is present across Canada from Ontario to Manitoba and Alberta, and in the U.S. from Maine south to Pennsylvania and Virginia.

Biology. Adults are present from late April to June, sometimes also in a small second generation in July and August (Razowski 2003). Larvae feed in July and August on *Betula* and *Erica* and pupate after hibernation in a cocoon spun in a dead leaf (Bradley *et al.* 1979).

Remarks. Heinrich (1923) described *A. carbonana* as different from *A. uncella* (= *A. uncella*) based on darker hindwings, a fainter mid-dorsal pale patch (on the forewing), a shorter phallus, and a narrower valva. We compared the holotype and several paratypes of *A. carbonana* with *A. uncella* from Europe and found that these characters vary to the extent that they will not reliably separate individuals from Europe and North America. Further, individuals of *A. uncella* from Europe and *A. carbonana* from Canada (identified as *A. carbonana, A. goodelliana,* or *A. uncella*) clustered together in the DNA barcode analysis (Fig. 1). Based on this evidence we synonymize *A. carbonana* with *A. uncella*. Ancylis goodelliana (Fernald, 1882)

Figs. 17–22, 65, 79


Diagnosis. The light gray to white costal margin and black streaks along the radius and cubitus of the forewing separate *A. goodelliana* from other *Ancylis* treated here. Some individuals of *A. uncella* appear similar, but the brown to reddish-brown median fascia is always expressed on the costa in *A. uncella*. Lighter (or worn) individuals of *A. diminuatana* may also appear similar, although the costa is usually not as pale in the distal half, and *A. diminuatana* lacks the black streak along the radius.

Redescription. Forewing. FWL ♂ 6–9.5 mm (n=16), ♀ 6.5–8.5 mm (n=4). Forewings are brown to reddish brown and gray with white costal strigulae near the apex. The costa is white to light gray from base to near apex, and the same color is present along the dorsum. No fasciae are defined, instead a brown to reddish-brown band runs from base to apex; the dorsal margin of this band is sinuate as a result of remnants of the median fascia extending towards the tornus. Two black streaks are present: one along the cubitus to ca. one-third the distance to the termen, and one along the distal two-thirds of the radius to the apex (most evident in Fig. 22). Male genitalia. Uncus bifid to more than half its length. Valva with basal excavation nearly absent; saccular angle weakly to moderately developed with variable triangular terminal projection; neck of uniform width or slightly narrowed from sacculus to cucullus; cucullus elongate, tapering towards apex, densely setose, outer margin convex with several rows of short setae near the anal angle, apex rounded. Caulis 0.5 as long as phallus; phallus 0.7 as long as valva, with small tooth at apex (difficult to see in some preparations); vesica with ca. 40–70 deciduous lanceolate cornuti. The length of the cucullus, the width of the valval neck, and the saccular terminal projections all vary slightly between individuals, although genital variation is not as pronounced as in other species in this group. Female genitalia. As in *A. uncella*.

Molecular data. BIN URI: BOLD:AAA7191, BIN-sharing with *A. uncella*, with a minimum distance of 1.13%.

Distribution. Most specimens of *A. goodelliana* are from eastern North America: Nova Scotia west to Ontario, and Wisconsin south to North Carolina and Florida. Heinrich (1923) reported this species from Manitoba and Colorado, and we examined one specimen from central Alberta in the CUIC, suggesting that it also present in the West. Historical records are difficult to confirm because of confusion with *A. diminuatana* in many collections.

Biology. Adults are present from the end of May through mid-August. The larval host is unknown.

Remarks. Worn specimens of *A. goodelliana* are easily confused with *A. diminuatana*, and the two are often mixed in collections. A genitalic dissection will easily separate *A. goodelliana* from all species in the *A. geminana* group. Gilligan *et al.* (2008) incorrectly illustrated the adult and male genitalia of *A. goodelliana* as “A.
Although *A. goodelliana* and *A. uncella* appear very similar based on COI barcode data (with a minimum distance of only 1.13%), the two species can be reliably separated by forewing pattern.

**Ancylis oregonensis** Gilligan and Huemer, sp.n.
Figs. 23–25, 66, 80

**Type material.** Holotype. ♂: “Oregon, Crescent Lake, Klamath Co., 4600’ 7.VII 1955, JFG Clarke” (USNM). Paratypes (9). United States: 3 ♂, 6 ♀ [same data as holotype], slides TGM630, TGM633 (USNM).

**Diagnosis.** *Ancylis oregonensis* is distinguished from all other species treated here by the discontinuous longitudinal line of the forewing, which is broken or obscured in the middle in most specimens. In individuals where the longitudinal line is nearly continuous (Fig. 25), the costal and dorsal halves of the forewing are not deeply contrasting. The male genitalia are also unique in this species, with the cucullus well-defined, the phallus as long as the valva, and the uncus reduced.

**Description.** Head, labial palps and thorax light brownish gray. **Forewing.** FWL ♂ 6.5–8.7 mm (n=4), ♀ 7.0–7.8 mm (n=6). Forewing is falcate. The costal half of the wing is a mix of light brownish gray, dark brown, and black. The costa is light grayish brown in the basal half becoming a mix of gray, brown, and dark brown in the apical half with remnants of dark brown costal strigulae in some individuals. The dorsal half of the wing is light brownish gray. The longitudinal line starts at A1+2, extends towards the termen, and is disrupted in the middle one-third of the wing by brownish gray scales of the dorsal half of the wing extending to the cubitus. Beyond the disruption the longitudinal line is usually well defined, continuing from CuA2, straight to the apex. Cilia at the apex dark brown to black with a white postapical strigula. Hindwing pale grayish brown. **Male genitalia.** Uncus bifid, reduced, ca. 0.5 as tall as wide. Valva with shallow basal excavation extending to neck; saccular angle strongly developed with triangular terminal projection; neck narrowed from sacculus to cucullus, ventral margin semicircular; cucullus well-defined, densely setose, outer margin convex with several rows of short setae, costa weakly convex. Caulis 0.25 as long as phallus; phallus as long as valva, with small triangular tooth at apex; vesica with ca. 45 deciduous cornuti. **Female genitalia.** Apophyses posteriores 0.75 as long as apophyses anteriores. Lamella postvaginalis membranous, undefined; lamella antevaginalis sclerotized, projecting ventrally above ostium; antrum weakly developed; colliculum two small lateral sclerites. Ductus seminalis arising at junction of ductus and corpus bursae. Corpus bursae large, oval; two horn-shaped signa present.

**Molecular data.** Unknown.

**Distribution.** *Ancylis oregonensis* is known only from the type locality, Crescent Lake, located on the eastern side of the Cascades in Klamath County, Oregon.

**Biology.** The only collection data are from the type series, and all specimens were collected on the same night in early July. The larval host is unknown.

**Etymology.** The name signifies that this species has only been recorded from Oregon.

**Ancylis geminana group**

The *A. geminana* group contains *A. geminana*, *A. christiandiana*, *A. diminutana*, *A. diminuatana*, *A. subarcuana*, and *A. saliana*. *Ancylis diminuatana* and *A. subarcuana* are elevated from synonymy with *A. geminana*, and *A. christiandiana* and *A. saliana* are described as new. As a result of these taxonomic changes, none of the species in this group is considered to be Holarctic in distribution.

Species identification in this group is difficult and usually relies on minor differences in wing pattern. Male genitalia are variable and useless in discriminating species; we illustrate each species to display the range of variability in this group. Female genitalia are uniform with species-specific characters for only a couple taxa. Shared characters include:

**Forewing.** Fasciae are undefined; instead the wing is divided longitudinally along the radius and/or cubitus into a darker costal half and a lighter dorsal half, creating a two-toned appearance in some species. The border between the costal and dorsal halves creates a sinuate “longitudinal line,” often bordered in white, which runs from base to apex. The shape and degree of expression of the longitudinal line is often useful in diagnosing species.
Male genitalia. Uncus bifid to 0.75–0.9 its total length, well developed in all species. Socii large membranous setose pads. Valva with costal margin concave to nearly straight; saccular angle moderately to strongly developed with variable triangular terminal projection; neck width variable, from moderate to wide; cucullus with rounded dorsal lobe and narrow fingerlike ventral lobe, outer margin concave to straight, variably setose with rows of short setae along dorsal lobe and outer margin. Caulis 0.5–0.7 as long as phallos; phallus 0.4–0.5 as long as valva; vesica with > 100 deciduous lanceolate cornuti.

Female genitalia. Papillae anales moderately setose. Apophyses posteriores the same length or 0.75 as long as apophyses anteriores. Lamella postvaginalis membranous, undefined; lamella antevaginalis sclerotized, projecting ventrally above ostium, often with slight median indentation, forming a weakly sclerotized funnel-shaped antrum. Colliculum present as two small lateral sclerites continuous with anterior sclerotization of antrum. Ductus seminalis arising posterior to junction of ductus and corpus bursae. Corpus bursae large, oval; two blade- or horn-shaped sigmas present.

Variation. The shape of the male valva varies greatly. The width of the neck, and corresponding degree of development of the dorsal lobe of the cucullus, can vary extensively within species (e.g., Figs. 70–71, 73–74) or even within the same individual (e.g., Fig. 71). The shape of the ventral lobe of the cucullus also varies within species and individuals. Note that the appearance of valval shape is influenced by the method of slide preparation; any tilting or twisting of the genitalia during mounting will alter the appearance of the cucullus and the saccus. The male genitalia figures presented here (Figs. 67–74) illustrate the range of variability found within this group; however, none of the variability is specific to a particular species and any of the figures could represent any of the species treated here.

Ancylis geminana (Donovan, 1806)

Figs. 26–31, 67, 81


Diagnosis. Ancylis geminana is distinguished by the grayish brown coloration on the costal half of the forewing, which is lighter on the costa and darker towards the longitudinal line, and the uniform curvature of the longitudinal line. It is most similar to A. christiandiana from which it differs by the distinctly curved longitudinal line and the more variegated light and dark wing pattern. The smaller A. diminutana is reddish brown with a longitudinal line similar to A. christiandiana.

Molecular data. BIN URI: BOLD:AAE1223. The intraspecific divergence of the barcode region is low with average 0.28% and maximum 0.8% (n=23). The minimum distance to the nearest neighbor A. christiandiana is 3.82%.

Redescription. Forewing. FWL ♂ 7.5–9.5 mm (n=10), ♀ 7–8 mm (n=2). The costal half of the wing is a mix of grayish brown, dark brown, and black. The costa is lighter grayish brown with darker markings towards the longitudinal line. The dorsal half of the wing is light brownish gray to near white. The longitudinal line is continuous from base to just below the apex and is often bordered in white dorsally. The line starts at A1+2, curves evenly up to the cubitus, back down to CuA3, and then up to radius, angling down slightly to reach the termen near M1. Small black streaks are often present on R5 just proximal to the termen. Male genitalia. As described for the group. Female genitalia. As described for the group with the following modifications: apophyses posteriores and apophyses anteriores approximately the same length; antrum weakly sclerotized to the posterior 0.15 of the ductus bursae; and ductus seminalis arising in the anterior 0.3 of the ductus bursae.

Distribution. Ancylis geminana is distributed across much of Western Europe to Asia Minor, Mongolia, Siberia, China, and Japan (Razowski 2003).

Biology. Adults are present from May to August with suspected occasional bivoltinism (Razowski 2001, 2003). However, our data as well as various alternative literature sources (e.g. Schütze 1931) support a single generation of adults primarily in May and June. The reported larval host is willow (Salix spp., Salicaceae)
(Razowski 2003), although this species prefers different kind of hygrophilous to mesophilous woods such those found in riverine forests.

**Remarks.** *Phalaena geminana* was described from material collected on one occasion in Kent. Donovan (1806: pl. 370, fig. 1, 1) figured two slightly deviating specimens, indicating that the species was described from more than a singleton. No type material could be found in the collections of the Natural History Museum (London, UK), but the precise color figures of the original description leave no doubt of the identity.

Prior to the release of the first world tortricid catalogue (Brown 2005), the majority of *Ancylis* in North America with a wing pattern similar to species in the *A. geminana* group were identified as *A. diminutana*. Brown (2005) realized that *A. diminutana* did not occur in North America, and determined that specimens in the USNM under that name were actually *A. geminana*. Thus, he synonymized *A. diminutana* (formally determined to be nothing more than *A. diminutana* from North America by Heinrich) with *A. geminana*. He also included *A. subarcuana* as a synonym of *A. geminana*.

DNA barcode data has helped greatly in solving this taxonomic chaos. Figure 1 shows that *A. geminana* is clearly separate from *A. subarcuana*, and both are only found in the Palearctic. The remaining specimens from North America, mostly misidentified as *A. carbonana*, match the type of *A. diminutana*. All three species can be reliably separated from each other using forewing pattern.

**Ancylis christiandiana** Huemer and Wiesmair, sp.n.

Figs. 32–34, 68, 82


Paratypes (20). Austria: 1 ♂, same data as holotype, but barcode sample ID BC TLMF Lep 03395, gen. slide TOR 464 ♂ P. Huemer (coll. Helmut Deutsch, Bannberg, Austria); 1 ♂, ditto, but barcode sample ID BC TLMF Lep 03396, gen. slide 07/098 ♂ H. Deutsch (coll. Helmut Deutsch, Bannberg, Austria); 1 ♂, ditto, but Griffer See, Bruchwald, 490 m, AT-BMN 31 14,721609 E / 46,697111 N, 27.5.2016, leg. Dr. C. Wieser (LMK); 1 ♂, ditto, but 3.6.2016 (LMK); 1 ♂, Kärnten, Finkenstein, S Höfling, Finkensteiner Moor W, 536 m, 13°52′45″E, 46°34′06″N, 27.5.2016, leg. Huemer (TLMF); 2 ♂, ditto, but 28.5.2016 (TLMF); 1 ♂, Carinthia, Lavant Au, Aufweitung Aich, Insel, 385 m, AT-BMN 31 14,856502 E / 46,728070 N, 31.5.2016, leg. Dr. C. Wieser (LMK); 1 ♂, Carinthia, St. Paul/L. bei Aich, 395 m; AT-BMN 31 14,860402 E / 46,72273 N, 21.5.2014, leg. D. Wieser (LMK); 1 ♀, Carinthia, Flughafen, Witternitz, Rückhalteb. 3, 440 m, 26.5.2008, AT-BMN 31 14,354825E / 46,642159N, leg. Dr. C. Wieser, Kärntner Landesmuseum, gen. slide TOR 478 ♀ P. Huemer (LMK); 1 ♂, ditto, but barcode sample ID BC TLMF Lep 06853, gen. slide TOR 462 ♂ P. Huemer (LMK); 1 ♀, ditto, but 23.6.2008 (LMK); 1 ♀, ditto, but Rückhalteb. 1, AT-BMN 31 14,355872 E / 46,642029 N, 26.5.2008 (LMK); 2 ♂, ditto, but Rückhalteb. 4, AT-BMN 31 14,353762 E / 46,642417 N, 26.5.2008 (LMK); 1 ♂, ditto, but 24.6.2008 (LMK); 1 ♀, Carinthia, Großedlinger Teich, 420m, 14.6.2005, AT-BMN 31 14,843800 E / 46,795742 N, leg. Dr. C. Wieser, Kärntner Landesmuseum, barcode sample ID BC TLMF Lep 06854 (LMK); 2 ♂, Carinthia, Ebersdorf, Sablatnigmoor, Lichtfalle 1, 550m, 5–8.6.1989, leg. Dr. C. Wieser, Kärntner Landesmuseum, gen. slide T390 ♂ C. Wieser (LMK); Germany: 1 ♂, Schwaben, Dillingen a.D., Wertingen, Wertinger Ried, 10.6.2016, leg. Heindel, barcode sample ID BC ZSM Lep ID 71187 (coll. Richard Heindel, Günzburg, Germany).

**Diagnosis.** *Ancylis christiandiana* is similar to *A. diminutana* and *A. geminana*, but all three species can be distinguished by a combination of wing pattern, coloration, and size. The costal half of the forewing is dark grayish brown in *A. christiandiana* versus lighter reddish brown in *A. diminutana*. The longitudinal line is more angulate in *A. christiandiana* and reaches the termen in a diagonal shallowly curved line near the apex, whereas the longitudinal line in *A. geminana* is distinctly curved, and the coloration of the forewing in *A. christiandiana* is rather monotonous and less contrasting than in *A. geminana*. Both *A. christiandiana* and *A. geminana* are larger than *A. diminutana*. The tubular shape of the antrum with a straight posterior edge of the lamella antevaginalis is possibly diagnostic in *A. christiandiana*; in *A. geminana* the posterior part of the lamella antevaginalis is weakly convex whereas in *A. diminutana* it is concave and the antrum is funnel shaped.

**Description.** Head, labial palpi and thorax light grayish brown. Labial palpi and head with scattered black scales.
Forewing. FWL ♂ 8.1–9.1 mm (n=6), ♀ 7.6 mm (n=1). Forewing is falcate. The costal half of the wing is a mix of grayish brown, dark brown, and black. The costa is light grayish brown with darker markings towards the apex. The dorsal half of the wing is light brownish gray to near white, with several black dots present on the dorsum. The longitudinal line is continuous from base to apex and is bordered in whitish gray dorsally. The line starts at A$_{1+2}$, curves up to the cubitus, angles back down to CuA$_2$ and then runs in a diagonal line straight to the apex. A row of black scales runs along the termen. The cilia at the apex are black with a white postapical strigula; other cilia are pale on the basal half and dark on the apical half. Hindwing is gray. Male genitalia. As described for the group. Female genitalia. As described for the group with the following modifications: apophyses posteriores and apophyses anteriores approximately the same length; posterior edge of the lamella antevaginalis straight; and antrum tubular.

Molecular data. BIN URI: BOLD:AAV7672. The intraspecific divergence of the barcode region is 0% (n=5). The minimum distance to the nearest neighbor A. geminana is 3.85%.

Distribution. Ancylis christiandiana is known from a few localities in southern Austria and Germany, but it is probably more widespread and expected to occur at additional sites.

Biology. The few adults known to date have been collected in late May and June at light. The larval host is unknown but this species likely feeds on willow (Salix spp.) like other members of the group. Ancylis christiandiana seems to prefer hygrophilous woodland.

Etymology. The species name christiandiana is an artificial compound form of the forenames of two colleagues who contributed to this study, Christian Wieser and Andi [Andreas] Segerer.

Ancylis diminutana (Haworth, 1811)
Figs. 35–38, 69, 83


Diagnosis. Ancylis diminutana is distinguished by the reddish-brown coloration on the costal half of the forewing and the shape of the longitudinal line, which curves broadly from the cubitus down to CuA$_2$, and then angles straight to the apex. Both A. christiandiana and A. geminana are similar: A. geminana is grayish brown and the longitudinal line is evenly curved; and A. christiandiana is larger, lacks the reddish brown color of the forewing and the longitudinal line is more angulate.

Redescription. Forewing. FWL ♂ 6–8 mm (n=16), ♀ 6–7 mm (n=5). The costal half of the wing is reddish brown. The costa is lighter in some specimens, but only at the base. The dorsal half of the wing is brownish gray in the median portion, becoming lighter gray to near white at the tornus and along the termen. The longitudinal line, which is often bordered in white dorsally, starts at A$_{1+2}$, curves up to the cubitus, back down to CuA$_2$, and then runs in a diagonal line straight to the apex. Small black streaks are often present on R$_5$ just proximal to the termen. Male genitalia. As described for the group. Female genitalia. As described for the group with the following modifications: apophyses posteriores 0.6–0.7 as long as apophyses anteriores; antrum weakly sclerotized just below the ostium; and ductus seminalis arising in the anterior 0.3–0.4 of the ductus bursae.

Molecular data. BIN URI: BOLD:AAB6876. The intraspecific divergence of the barcode region is low with average 0.1% and maximum 0.64% (n=21). The minimum distance to the nearest neighbor A. geminana is 4.73%.

Distribution. Ancylis diminutana is locally distributed from the northwestern, northern and central parts of Europe (Razowski 2003) to central Siberia (Sinev 2008).

Biology. Adults are present from May to June and from July to August (Schütze 1941). The larval host is willow (Salix spp.) (Razowski 2003). The species prefers different kind of hygrophilous to mesophilous woods such as those found in riverine forests.

Remarks. Tortrix diminutana was described from an unspecified number of specimens without precise locality data from Great Britain. According to Sattler (in litt.) no type material could be found in the collections of the Natural History Museum (London, UK). However, the original description precisely points to the comparatively small size and the reddish brown color of the costal half.

Phoxopteris cuspidana was described from an unspecified number of specimens collected in Hungary and
Germany (Saxonia). The species was previously synonymized with *A. geminana*. However, photographs of two type specimens (courtesy of Laszlo Ronkay) verify that the species fully agrees with typical *A. diminutana* both from the small wingspan and the reddish color of the costal half of the forewing. We therefore formally synonymize *P. cuspidana* with *A. diminutana*. To serve stability we furthermore designate the specimen with following labels as the lectotype: “TREITS. 3280” “cuspidana 3280” “Micropraep. upen. No. 1087 Kuznetsov, 1983” “Lectotypus m Phoxopteris cuspidana Tr. design. Kuznetsov, 1983” (Hungarian Natural History Museum, Budapest, Hungary).

The taxonomic confusion surrounding *A. diminutana* is detailed in the *A. geminana* species account. DNA barcode data (Fig. 1) and consistent differences in wing pattern clearly demonstrate that the Nearctic *A. diminutana* is a separate species from *A. diminutana*.

**Ancylis diminutana** Kearfott, 1905
Figs. 39–43, 44–46 (complex), 70–71, 84


**Diagnosis.** *Ancylis diminutana* is distinguished by its “three-toned” forewing, which is pale tan on the costa, reddish brown to dark brown in the remainder of the costal half, and gray in the dorsal half. In most specimens, the shape of the longitudinal line is also distinctive, as it curves only slightly towards the cubitus before reaching CuA\textsubscript{2} (Figs. 39 – 41); however, in some specimens the longitudinal line curves abruptly to the cubitus and down to CuA\textsubscript{2} (Fig. 42). Other similar species (*A. geminana*, *A. diminutana*) appear two-toned, with contrasting costal and dorsal halves of the forewing. Also, the longitudinal line in these other species is more sinuate. Because of the pale tan costa, some specimens of *A. goodelliana* (*A. unguicella* group) appear similar to *A. diminutana*, but the two species have very different genitalia (Figs. 70–71, 84 versus Figs. 65, 79).

**Redescription.** Forewing. FWL ♂ 4.5–7.5 mm (n=44), ♀ 5.5–8 mm (n=16). The costa is pale tan in the basal 0.5–0.75 of the wing. The remainder of the costal half is brown to reddish brown, becoming darker at the longitudinal line. The dorsal half is pale gray to brownish gray. The longitudinal line starts at A\textsubscript{1+2} at the base of the wing, curves only slightly towards the cubitus before reaching CuA\textsubscript{2}, and then angles in a diagonal line to the apex. In some specimens the longitudinal line curves abruptly to the cubitus and down to CuA\textsubscript{2} before angling to the apex. Small black streaks are often present just proximal to where the longitudinal line intersects M\textsubscript{1}. Male genitalia. As described for the group. Female genitalia. As in *A. diminutana*.

**Molecular data.** BIN URI: BOLD: AAA7190. The intraspecific divergence of the barcode region is moderate with average 0.32% and maximum 1.28% (n=87). The minimum distance to the nearest neighbor *A. subarcuana* (BIN AAB3492) is 3.53%.

**Distribution.** In Canada, *A. diminutana* is distributed from Quebec west to Alberta and British Columbia. In the U.S., *A. diminutana* is distributed from New Hampshire and Massachusetts, south to North Carolina, west to Nebraska, and possibly beyond. Kearfott (1905) included specimens from Colorado in his type series although we have not located any specimens that we could confirm as *A. diminutana* from that state. We did identify a single female from California and specimens from Washington (discussed below) that we would confirm as this species.

**Biology.** Label data suggests that *A. diminutana* is bivoltine in the East, with adults present May though early July and again mid-August through September. Several specimens from the USNM appear to be reared from willow (*Salix* spp.).

**Remarks.** *Ancylis diminutana* has been consistently misidentified in North America, first as *A. diminutana* and then as *A. geminana*. Specimens of *A. diminutana* in BOLD consistently misidentified as *A. carbonana* (Fig. 1) demonstrate some of the dangers in relying on only DNA data for determinations—it is obvious from the online photographs that none of these specimens is *A. carbonana*. The DNA data do clearly separate this group of Nearctic *A. diminutana* from the Palearctic *A. diminutana*.

We have identified several specimens from the American West that most closely match *A. diminutana* but are unlikely to be the same species. Figures 43–44 illustrate two specimens from Washington (Fig. 43, Everett; Fig. 44, Yakima). The Everett specimen (and another from the same date and locality) appears to be a typical *A. diminutana* with slightly darker markings; however, the Yakima specimen, and a similar specimen from Walla
Walla (not illustrated), appears more two-toned, and the longitudinal line is much more sinuate. Similarly, the specimen in Fig. 45 from Silverton, Colorado, is nearly black and white with a sinuate longitudinal line. Two other specimens (not illustrated) from Colorado match this phenotype. The specimen in Fig. 46 from Alaska is also unusual with subdued markings and a sinuate longitudinal line. Other specimens (not illustrated) from the Humboldt Mountains in northwest Nevada and Provo, Utah have wing patterns similar to those in Figs. 45–46. Unfortunately, none of these specimens were collected recently enough to obtain quality DNA sequence data. Thus, we hesitate to describe any additional species until additional diagnostic characters are discovered and include all of these phenotypes as a potential species complex with *A. diminuatana*.

**Ancylis saliana** Gilligan and Huemer, sp.n.
Figs. 47–52, 72, 85


**Diagnosis.** *Ancylis saliana* is distinguished by the shape of the longitudinal line, which extends along A_{1+2} before angling abruptly back towards the base of the wing, and then continuing down to CuA_{2} and straight towards the apex. This shape approximates a “wave” or “hook” in most specimens that is easy to distinguish from the weakly sinuate line in *A. diminuatana*. In specimens of *A. diminuatana* where the longitudinal line curves more abruptly to the costa (e.g., Fig. 42), *A. saliana* can be distinguished by the pale tan or brown coloration in the dorsal half of the wing versus gray in *A. diminuatana*.

**Description.** Head, labial palpi and thorax tan. Second and third segment of labial palpi with patches of brown scales. Forewing. FWL ♂ 5.9–6.8 mm (n=4), ♀ 6.5–7.7 mm (n=8). Forewing is falcate. The costal half of the wing is a mix of light tan, brown, and yellowish brown. The costa is light tan becoming brown towards the apex with remnants of costal strigulae. The dorsal half of the wing is pale tan with some brown markings. The longitudinal line runs from the base of the wing along A_{1+2}, angles abruptly back above the cubitus towards the base of the wing, and then continues down to CuA_{2}, and straight towards the apex. Small black streaks are often present on R_{5} just proximal to the termen, which has a row of dark brown scales. Some specimens (Fig. 52) have black scales interspersed in the costal half of the wing along the margin of the longitudinal line and in the dorsal half of the wing. Cilia at the apex dark brown with a white postapical strigula, other cilia are pale tan. Hindwing is pale grayish brown. *Male genitalia*. As described for the group. *Female genitalia*. As described for the group with the following modifications: apophyses posteriores 0.7 as long as apophyses anteriores; antrum sclerotized to the posterior 0.3 of the ductus bursae; and ductus seminalis arising in the anterior 0.3 of the ductus bursae.

**Molecular data.** Unknown.

**Distribution.** *Ancylis saliana* is only known from few localities in Florida.

**Biology.** The majority of adults were collected from January to May. A single collection in September from the type locality suggests two generations. The larval host is unknown.

**Etymology.** The species name is a variation of the Latin “sali” for “waves,” referring to the shape of the longitudinal line in most specimens.

**Remarks.** Although it is somewhat troubling that we could find no genitalic differences from *A. diminuatana*, we believe that the consistent shape of the longitudinal line and lack of gray in the dorsal half of the wing sufficiently distinguishes *A. saliana* as a separate species.
Ancylis subarcuana (Douglas, 1847)

Figs. 53–58, 73–74, 86


**Diagnosis.** Ancylis subarcuana is distinguished by its grayish forewing and subdued markings. The costal and dorsal halves of the forewing are not contrasting, and the expression of the longitudinal line is obscured at the base and apex of the wing. The longitudinal line is continuous from the base of the wing to the apex or termen in *A. geminana*, *A. christiandiana*, and *A. diminutana*, and the costal and dorsal halves of the forewing are contrasting to nearly two-toned in those species. Some individuals are dark brown with reduced markings (Fig. 58).

**Redescription.** Forewing. FWL ♂ 6–8.5 mm (n=15), ♀ 6–8 mm (n=10). The costal half of the wing is pale grayish tan at the costa, becoming brown towards the longitudinal line. The dorsal half of the wing is light brownish gray. The longitudinal line arises from below a dark brown to black mark near A_{1,2}, runs up to the cubitus, down to CuA_{1} beneath another dark brown to black mark, and then up towards the apex, becoming obscured again before reaching the termen. A small black dash is often present just proximal to where the longitudinal line intersects M. The male in Fig. 58 from northern Finland is typical of specimens from that region that are dark brown with only a remnant of the longitudinal line. *Male genitalia.* As described for the group.

*Female genitalia.* As in *A. diminutana*.

**Molecular data.** BIN URI: BOLD:AAB3492, BOLDABX6097. The intraspecific divergence of the barcode region is moderate when considering both BINs, with average 0.72% and maximum 2.34% (n=9). Within BIN BOLD:AAB3492 average distance is only 0.19% with maximum 0.76%. The minimum distance of this cluster to the nearest neighbor BIN BOLDABX6097 is 2.25%.

**Distribution.** Razowski (2001, 2003) reported *A. subarcuana* as distributed from the United Kingdom through Northern Europe to the Baltic States and parts of central Europe, and according to Sinev (2008) also in the northwestern part of European Russia. We also examined specimens from northern Italy.

**Biology.** Adults are on the wing in two generations, from April to May and from July to August (Razowski 2001). The larval host is *Salix repens* (Razowski 2003) and, according to Wegner (2015), also *Salix aurita*. In northern Europe the species prefers dunes, heathland and marshy pinewood, in southern parts it was found in alluvial river zones.

**Remarks.** Anchylopera subarcuana was described from a single specimen collected on May 12, 1844 near Wimbledon (England, GB). According to Sattler (in litt.) no type material could be found in the collections of the Natural History Museum (London, UK). However, the original description with attached color figure leaves no doubt of the identity.

DNA barcode data (Fig. 1) and consistent differences in wing pattern clearly separate *A. subarcuana* from *A. geminana*. Species status is furthermore supported by unique larval characters as described already by Schütze (1931) but largely neglected in subsequent literature (e.g. Bradley et al. 1979). The taxonomic confusion surrounding species in this group is detailed under the *A. geminana* account.

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