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Micro wonders: updates and insights into diversity of Nepticulidae from previous fieldwork in Armenia

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In the current paper, we provide a complete list of 32 Nepticulidae species discovered in Armenia, along with photographic samples of detected leaf mines. For the first time, we include photographic documentation of the male genitalia structures of the Armenian *Glaucolepis melanoptera* (van Nieukerken & Puplesis) and the previously little-known, formerly Central Asian *Stigmella klimeschi* Puplesis and *S. kuznetzovi* Puplesis. Moreover, our molecular analyses have confirmed the occurrence of *S. aceris* (Frey) and *Glaucolepis melanoptera* in Armenia and justified the description of two species, *Stigmella inopinoides* Dobrynina, 2024 and *Etainia caucasi* Remeikis, 2024.

Keywords: Caucasus fauna, leaf mines, male genitalia, mitotypes, pygmy moths

INTRODUCTION

Nepticulidae, also known as pygmy moths, are a phylogenetically primitive yet highly specialised family of Lepidoptera. Adults are characterised by a distinct and easily recognisable appearance, while larvae are known for their mining of plant tissues, primarily leaves. The majority of nepticulid species exhibit highly pronounced stenophagy, i.e. they are predominantly monophagous. This family has been extensively studied in monographic reviews (Scoble, 1983; Johansson et al., 1990; Puplesis, 1994; Puplesis &

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Diškus, 2003), including recent works focusing particularly on Neotropical America (Puplesis & Robinson, 2000; van Nieukerken et al., 2016; Stonis et al., 2022). In 2022, a targeted fieldwork was conducted in Armenia.

Armenia is a scenic mountainous country situated in the Armenian Highlands of the Southern Caucasus in Western Asia, between latitudes 38° and 42° N and longitudes 43° and 47° E (National Statistical Service of the Republic of Armenia, 2007). The country features mostly two ecological ecoregions, namely, the Eastern Anatolian montane steppe and the Caucasian mixed forests, which include the Caucasian oak (*Quercus macranthera*) (Dinerstein et al., 2017). Due to its location, Armenia experiences a highland continental climate characterised by hot, dry summers and cold, snowy winters, with winter temperatures typically ranging between −5°C and −10°C.

Recently, a catalogue of the Lepidoptera of Iran, a country directly south of Armenia, was published, which lists 29 species of Nepticulidae and at least one or possibly a couple of unconfirmed species (Rajaei et al., 2023). In contrast, the fauna of pygmy moths of Armenia was largely unknown, with only two species previously identified: *Stigmella armeniana* Puplesis (Puplesis, 1994) and *Glaucolepis melanoptera* (van Nieukerken & Puplesis) (van Nieukerken & Puplesis, 1991). A similar lack of knowledge exists regarding the nepticulid faunas of neighbouring Georgia and Azerbaijan. In 2024, we published the first comprehensive review of the Nepticulidae of Armenia (Stonis et al., 2024b). During the review of the said publication, prompted by suggestions from an anonymous reviewer, we omitted some significant research material due to concerns about their complexity and readability raised by the reviewer. Now, alongside additional commentary on the results of our fieldwork in Armenia, we present the first photographic documentation of three previously little-known species and insights into the taxonomic status of certain species discovered in Armenia.

MATERIALS AND METHODS

Materials. In 2022, approximately 600 nepticulid specimens were collected (with about 300 pinned) during targeted fieldwork in Armenia under the Agreement of Scientific Cooperation between the Scientific Center of Zoology and Hydroecology of the National Academy of Sciences of Armenia and the State Research Institute Nature Research Centre and as part of a collaborative research project with Dr Mark Kalashian (a co-author of this publication). Except for specimens of *Glaucolepis melanoptera* (van Nieukerken & Puplesis), all collected species were new records for Armenian fauna. Although the previously described Armenian species *Stigmella armeniana* Puplesis was not found during our fieldwork, we re-examined and documented its type series in Stonis et al. (2024b).

Our field collections in Armenia led to the discovery of new species, including seven described in Stonis et al. (2024b), and one, *S. colchica* Stonis & Diškus, a *Prunus*-feeding species with a wide geographical distribution from southern Russia and Georgia to Turkey and Armenia, described in Stonis et al. (2024a).

Collecting sites. In 2022, fieldwork was conducted at seven localities of Armenia (Figs 1–11). The habitats of these localities were classified strictly according to the EUNIS habitat classification (Davies et al., 2004), which was adapted for Armenia by Fayvush & Aleksanyan (2016), with codes provided in brackets: (1) Sevan, Tsovagyugh, Gegharkunik Province, 2000 m, 40°36'08''N, 44°57'45''E (G1.C); (2) Antarut, Aragatsotn Province, 1780–1985 m, 40°22'36''N, 44°16'03''E – 40°21'50''N, 44°16'25''E (G1.A1D2, F7.4I211); (3) Victory Park, Yerevan, 1142 m, 40°11'47''N, 44°31'17''E – 40°11'41''N, 44°31'25''E (I2.1) and Jrvezh Forest Park, outskirts of Yerevan, Kotayk Province, 1515 m, 40°11'07''N, 44°37'11''E (G4.F, C1.3); (4) Garni, Kotayk Province, 1312–1355 m, 40°07'18''N, 44°45'17''E – 40°06'41''N, 44°43'55''E and Garni, Ararat Province, 1371 m, 40°07'27''N, 44°45'40''E (G1.2, F5.342, E1.2H1,

Figs 1, 2. General location and collecting sites. 1 – Armenia, a landlocked country in the Southern Caucasus, with major collecting sites of the fieldwork 2022: (1) Sevan, Tsovagyugh, Gegharkunik Province, 2000 m, habitats near Lake Sevan; (2) Antarut, Aragatsotn Province, 1780–1985 m, on the southern slope of the Mt Aragats, mainly in oak (*Quercus macranthera*) forests; (3) Victory Park, the western area of Yerevan city, and Jrvezh Forest Park, outskirts of Yerevan, Kotayk Province, 1515 m; (4) Garni, various sites in Kotayk and Ararat provinces, c. 1350 m, on the sides of a gorge at the confluence of the rivers Goght and Azat; (5) Yeghegis, Vayots Dzor Province, 1574 m, on the southern slopes of the Vardenis Range; (6) Jermuk, Vayots Dzor Province, 2000 m, on southern slopes of the Vardenis Range; (7) Noravank (Gnishik River Canyon), Vayots Dzor Province, 1468 m, on the northern slopes of the Vayots Dzor (formerly Daralagyaz) Range; 2 – Geghard, a lush locality close to Garni (see #4 in Fig. 1)

Figs 3–11. Fieldwork in Armenia, 2022. 3 – Arman Khachatryan, a field assistant, attracting moths by light from a Philips bulb ML 220–230 V, 160 W; 4 – Viktorija Dobrynina, a collector and a co-author; 5 – a light trap set for collecting; 6 – Jonas R. Stonis, a collector and a co-author, and Garik Voskanyan, a field assistant, attracting moths by fluorescent lanterns powered by D batteries of a dry cell; 7, 8 – a lightweight LepiLED lamp operated with a 5–13 V voltage DC from powerbank batteries; 9 – some leaf mines and cocoons in glass tubes; 10, 11 – Artur Barseghyan, a field assistant, during collecting in Noravank, a remote site

H3.2H); (5) Jermuk, Vayots Dzor Province, 2000 m, 39°50'25.8"N, 45°40'07.6"E (G1.A1D2, H3.2H); (6) Yeghegis, Vayots Dzor Province, 1574 m, 39°52'10"N, 45°22'12"E (G1.2, H3.2H); (7) Noravank, Gnishik River Canyon, Vayots Dzor Province, 1468 m, 39°40'57"N, 45°14'10"E (F9.141, F9.3142, FB.41, F5.343, F5.347, H2.6H, H3.2E2). Extensive photographic documentation of all collecting sites was provided in Stonis et al. (2024b).

Collecting methods. During our fieldwork in Armenia, we attracted moths using a Philips bulb ML 160 W 220–230 V (Fig. 3), suspended in front of a white screen and powered by electric mains. In areas without access to electric mains, we utilised traditional fluorescent lanterns powered by D dry cell batteries (flashlight batteries) (Figs 4–6, 10, 11) (Stonis et al., 2022), along with a modern LepiLED lamp (Figs 7, 8). The LepiLED lamp, specifically designed for sampling nocturnal insects, is lightweight and compact, operating on 5–13 V DC voltage from powerbank batteries (Brehm, 2017).

Specimen dissection and documentation. The methods and protocols for specimen setting, species identification and description were extensively detailed by Puplesis (1994) and Stonis et al. (2022). Male genital capsules were removed after abdomen maceration in 10% KOH and subsequent cleaning, mounted with the ventral side facing up. In many cases, the phallus was removed and mounted alongside the genital armature. Abdominal pelts were not retained for preservation in this study. Permanent preparations on microscope slides were photographed and examined using a Leica DM2500 microscope equipped with a Leica DFC420 digital camera. Adults were measured and examined using a Lomo stereoscopic microscope MBS-10, and images were captured with a Leica S6D stereoscopic microscope paired with a Leica DFC290 digital camera. For illumination of the studied adult specimens, a stereomicroscope ring light LED 60 was used: it was attached directly to the stereomicroscope lens; the intensity of illumination was adjustable; colour temperature ranged from 7000 to 11000 K; illumination at 100 mm distance was 8000 Lux. Images of *Stigmella colchica* were taken by Sigitas Podėnas (NRC) with a Canon EOS R5 digital camera through a Canon MP-E 65 mm macro lens and through Mitutoyo M Plan Apo 10× and 20× lenses mounted on the same camera, and were stacked using Zerene Stacker (PMax algorithm). Photographs of leaf mines and host plants were captured using a Samsung Galaxy S21 smartphone. SEM photography was performed with a scanning electron microscope FEI Quanta 250 (NRC).

Molecular analysis. Genomic DNA extraction, amplification of the mtDNA COI partial sequences, and purification of the PCR product were performed according to Orlovskytė et al. (2023). Sequences were obtained in BaseClear B. V. (Leiden, The Netherlands) with the ABI 3730xl 96-capillary DNA analyzer (Applied Biosystems, Foster City, CA, USA). They were manually double-checked and edited, if necessary, with the BioEdit v. 7.2.5 program (Hall, 1999). The obtained 543–657 base pairs (bp) long sequences were deposited in the NCBI GenBank database (Benson et al., 2013) under accession numbers PP977019–PP9977026. The sequences of the closest species (all or only of different mitotypes) were added to the analysis from the BOLD database (Ratnasingham & Hebert, 2007). *Pseudopostega cucullata* Stonis & Vargas, 2020 (Opostegidae) was included as an outgroup.

The MEGA v.7 program (Kumar et al., 2016) was used to calculate pairwise distances, select the best nucleotide substitution model and construct the maximum likelihood (ML) tree based on a GTR+G+I model and 10 000 bootstrap replications. The Bayesian phylogenetic analysis was performed using the Markov chain Monte Carlo (MCMC) method under a GTR+G+I model and run for 5–12 million generations with the MrBayes v. 3.2.3 software (Ronquist, Huelsenbeck, 2003). Species delimitation was carried out by the ASAP (Puillandre et al., 2020) and the bPTP (Zhang et al., 2013) methods. The Fasta format was converted to Nexus by ClustalX2 (Larkin et al., 2007). Genetic diversity parameters were estimated with the DnaSP v.6 program (Rozas et al., 2017). The mitotype network was constructed using the Median Joining (Bandelt et al., 1999) and TCS (Clement et al., 2002) Networks with the PopArt v.1.7 software (Leigh & Bryant, 2015).

Abbreviation for institutions and specimen depository. BRG – Biosystematics Research Group, currently based at the NRC, Vilnius, Lithuania; MfN – Museum für Naturkunde, Berlin; formerly known as the Museum der Naturkunde für Humboldt Universität zu Berlin or Museum für Naturkunde/Leibniz-Institut für Evolutions und Biodiversitätsforschung, Berlin, Germany; NRC – the State Research Institute Nature Research Centre, Vilnius, Lithuania.

RESULTS

Updated checklist of Nepticulidae species currently known for the fauna of Armenia

Before our recent taxonomic review (Stonis et al., 2024b), knowledge of the Nepticulidae diversity in Armenia was extremely limited. One species, *Stigmella armeniana* Puplesis, 1994, was described based on a few specimens collected in the country by Povilas Ivinskis (Puplesis, 1994). The primary description of another species, *Glaucolepis melanoptera* (van Nieukerken & Puplesis, 1991), also included one atypical, non-type specimen from Armenia (van Nieukerken & Puplesis, 1991). It is worth noting that an earlier report of *Stigmella inopinata* Laštůvka & Laštůvka, 1990, based on specimens collected by Friedrich Kasy in Armenia (Laštůvka & Laštůvka, 1990, 1997), was re-evaluated by Stonis et al. (2024b), and similarly, in our current study, was identified as a case of misidentification. Therefore, the publication by Stonis et al. (2024b) dealt with 31 species, including seven new species. However, the previously mentioned publication did not yet include *Stigmella colchica* Stonis & Diškus. This species feeds on plums (*Prunus* spp.) and has a wide geographical distribution in the Caucasus and likely extends further into western Asia. Stonis et al. (2024a) described it separately based on material primarily from Georgia as well as from Southern Russia and Northeastern Turkey. This description also included two paratype specimens collected from Sevan, Armenia. Therefore, the Nepticulidae fauna of Armenia currently comprises 32 species.

Due to the dry season, collecting leaf mines was not very successful during our fieldwork in 2022 (Fig. 9). However, some samples of leaf mines in Armenia was discovered and documented in Figs 12–41 (as well as some adults in Figs 42–50).

Using SEM photography, we documented for the first time some morphological structures of adult specimens collected in Armenia (Figs 51–61). It is well-known (Johansson et al., 1990) that the head of Nepticulidae possesses a large and compound frontal tuft of erect piliform scales and a paired collar consisting of either piliform (Fig. 52) or lamellar scales (Fig. 53). The first segment of the antenna, the scape, is greatly enlarged, forming the so-called eye cap; these structures were documented based on Armenian specimens (Figs 51–61). The flagellum of the antenna (Figs 54, 55) is adorned with unique branched *sensilla vesiculoclada* in pygmy moths (van Nieukerken & Dop, 1987); however, these sensilla were concealed in our studied sample due to the covering scales (Fig. 54). It is also well-known that the male abdomen possesses a pair of distinctive genital plates ventrally, often accompanied by anal tufts of piliform or slender lamellar scales; however, the quantity and shape of these tufts can vary. The *Ectoedemia* (*Zimmermannia*) *longicaudella* Klimesh from Armenia we examined exhibited an unusual shape of anal tufts (Figs 56, 57). Females of Nepticulidae typically have a non-prominent, short, and rounded ovipositor; however, occasionally it may be truncated or extended and slender. The documented specimens from Armenia show a conservative morphology of the abdomen, with a short and rounded ovipositor (Figs 58, 59).

Some species discovered in Armenia were previously known solely from Central Asia and had never been documented photographically. Therefore, here we present the first photographic documentation of the male genitalia of two formerly Asian species (*Stigmella klimeshi* Puplesis (Figs 62–67), *S. kuznetzovi* Puplesis (Figs 68–72)). Also, we document for the first time the male genitalia of *Glaucolepis melanoptera* (van Nieukerken & Puplesis) based on specimens collected in Armenia (Figs 73–77).

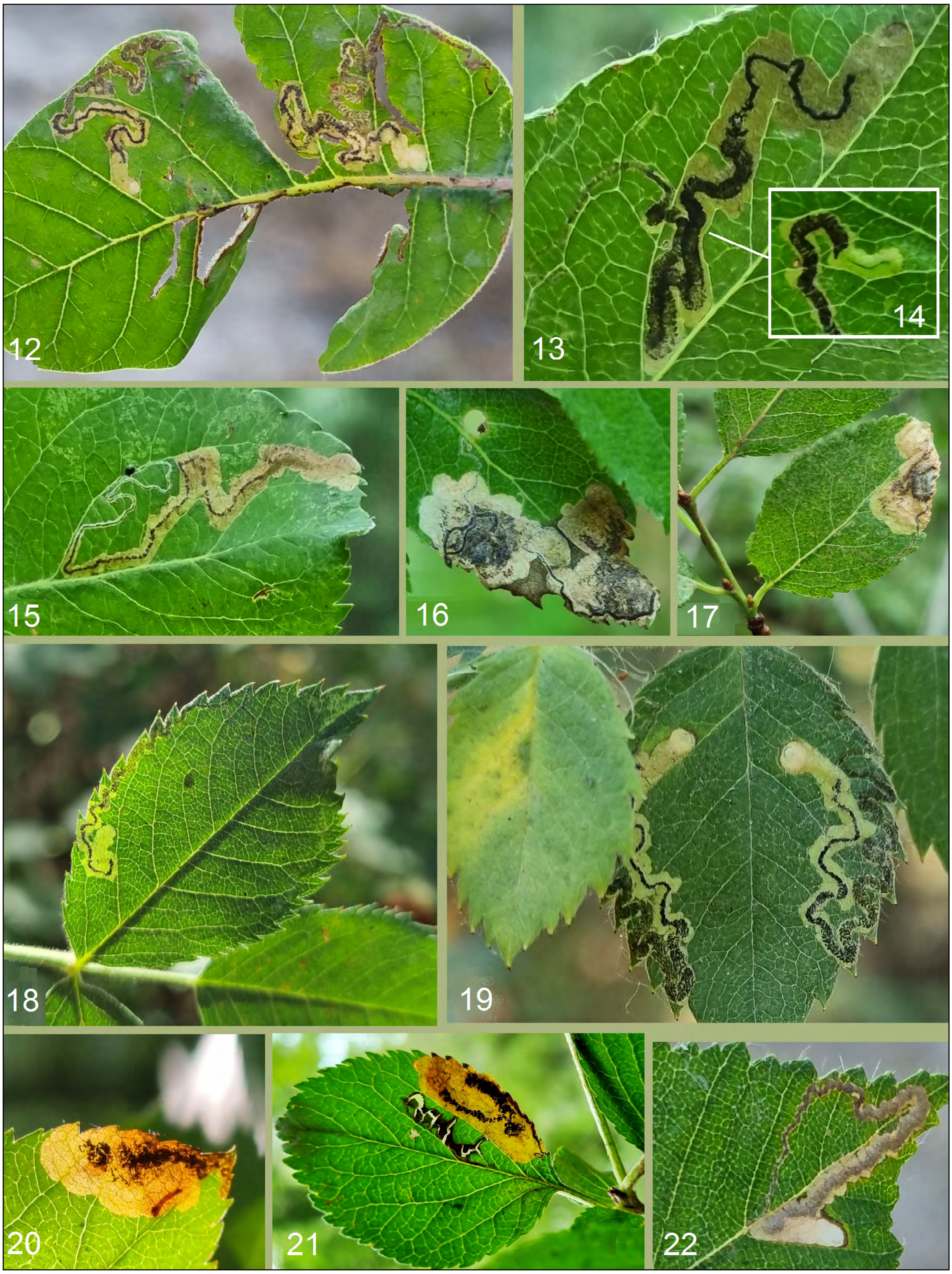
Below, we provide a list of all currently known species of Nepticulidae discovered in Armenia (details on the species distribution and potential host plants can be found in Stonis et al., 2024a, 2024b).

1. *Simplimorpha promissa* (Staudinger, 1870)
2. *Stigmella confusella* (Wood & Walsingham, 1894)
3. *Stigmella malella* (Stainton, 1854)
4. *Stigmella klimeschi* Puplesis, 1988
5. *Stigmella armeniana* Puplesis, 1994
6. *Stigmella kopetdagica* Puplesis, 1994
7. *Stigmella muricatella* (Klimesch, 1978)
8. *Stigmella armi* Stonis, Dobrynina & Remeikis, 2024
9. *Stigmella nivenburgensis* (Preissecker, 1942)
10. *Stigmella aceris* (Frey, 1857)
11. *Stigmella garnica* Stonis, Dobrynina & Remeikis, 2024
12. *Stigmella hybnerella* (Hübner, 1796)
13. *Stigmella inopinoides* Dobrynina, 2024
14. *Stigmella viscerella* (Stainton, 1853)
15. *Stigmella magicis* Stonis & Dobrynina, 2024
16. *Stigmella ararati* Stonis, Dobrynina & Remeikis, 2024
17. *Stigmella carpinella* (Heinemann, 1862)
18. *Stigmella lemniscella* (Zeller, 1839)
19. *Stigmella kuznetzovi* Puplesis, 1994
20. *Stigmella colchica* Stonis & Diškus, 2024
21. *Stigmella dorsiguttella* (Johansson, 1971)
22. *Stigmella roborella* (Johansson, 1971)
23. *Stigmella basiguttella* (Heinemann, 1862)
24. *Bohemannia pulverosella* (Stainton, 1849)
25. *Ectoedemia* (*Zimmermannia*) *longicaudella* Klimesch, 1953
26. *Ectoedemia mahalebella* (Klimesch, 1936)
27. *Fomoria septembrella* (Stainton, 1849)
28. *Trifurcula subnitidella* (Duponchel, 1843)
29. *Trifurcula vardenisi* Stonis, Dobrynina & Remeikis, 2024
30. *Glaucolepis melanoptera* (van Nieukerken & Puplesis, 1991)
31. *Glaucolepis hamirella* (Chrétien, 1915)
32. *Etainia caucasi* Remeikis, 2024

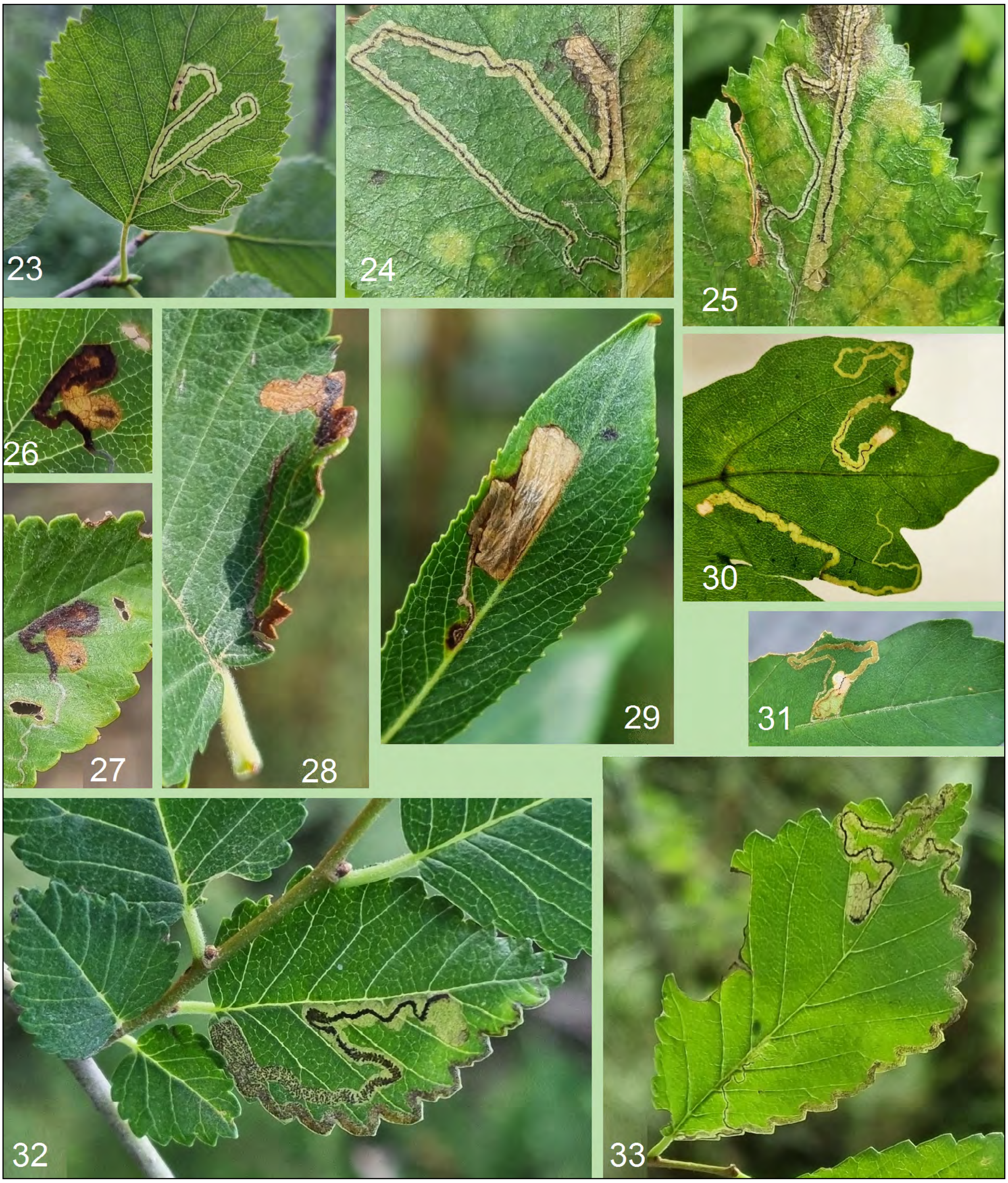
Molecular justification of *Stigmella aceris* (Frey), a species discovered in Armenia

Stigmella aceris (Frey, 1857) is an *Acer*-feeding, leaf-mining species known to be widespread in Europe from Spain and Italy to Norway, central European regions of Russia, and the Balkans. This species has also been recorded from Georgia (the Caucasus) (Puplesis, 1994) and Iran (Rajaei et al., 2023). During our fieldwork, we collected the following material: 1 ♂, Yerevan, Victory Park, 1141 m, 40°11'41''N, 44°31'12''E, at light, 1.viii.2022, leg. J. R. Stonis, genitalia slide no. DV126 (MfN); 2 ♂, 1 ♀, same locality, 19.viii.2022, leg. J. R. Stonis, genitalia slide no. RA1109♂ (MfN); 1 ♀, Ararat Province, E of Garni, 1371 m, 40°07'27''N, 44°45'40''E, at light, 22.viii.2022, leg. J. R. Stonis (MfN). It should be noted that despite the great abundance of old (vacant) leaf mines (especially in Victory Park), all specimens were collected in August using a light trap, but no feeding larvae were detected during our study in Armenia. Examination of external characteristics of the available series showed that the specimens from Armenia are characterised by a usually glossy dark collar and absence or weak development of a transverse fascia on the forewing. However, dissection of genitalia structures did not indicate any obvious differences from European specimens (for illustrations of the genitalia of European specimens, we recommend Johansson et al. (1990) and Puplesis (1994)). To clarify the status of the Armenian series, we sequenced a couple of specimens to compare the obtained and published sequences of this species.

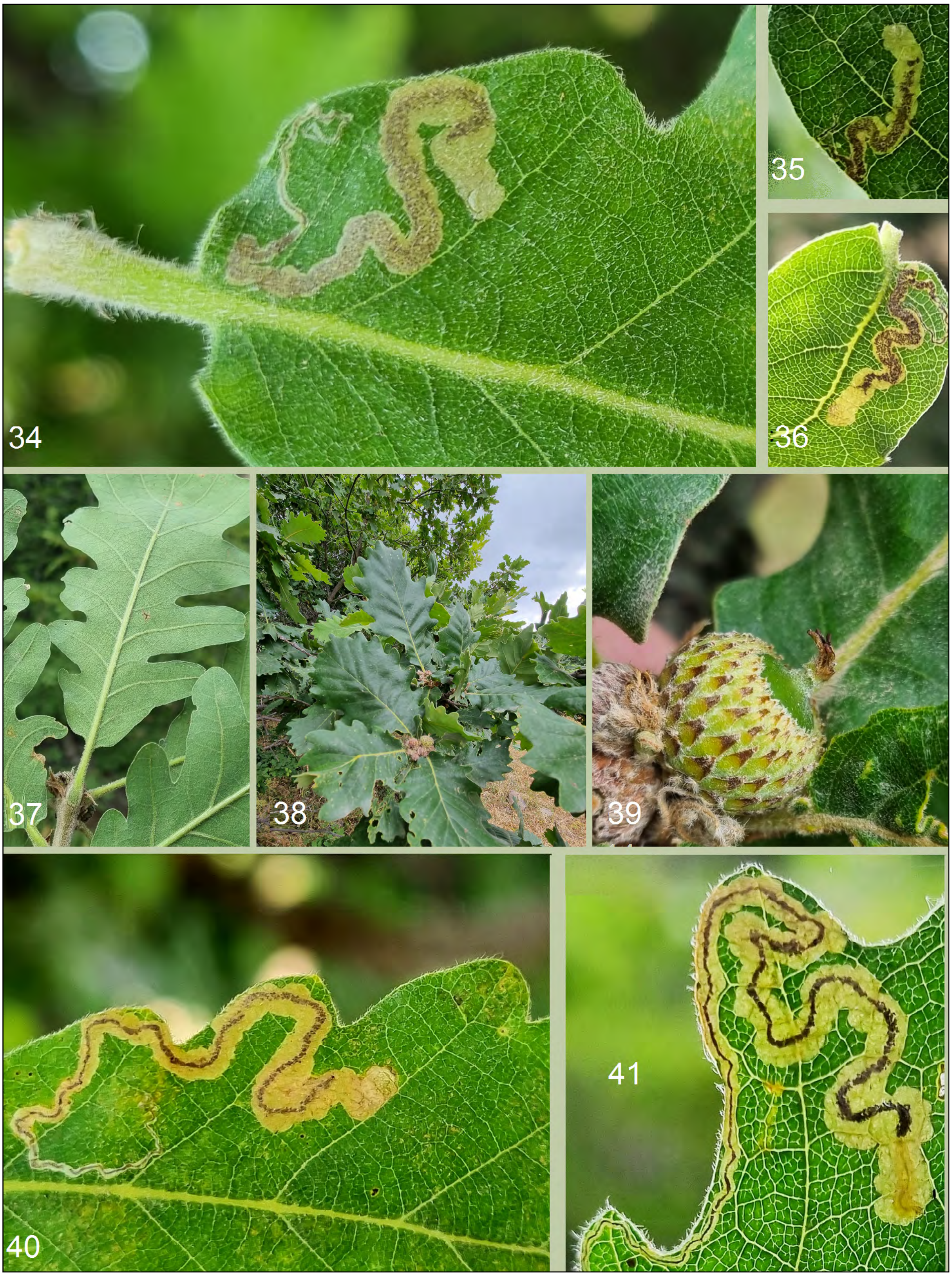
Up to now, 14 *S. aceris* COI-5' mitotypes have been published, all from specimens collected in the European continent. The two new



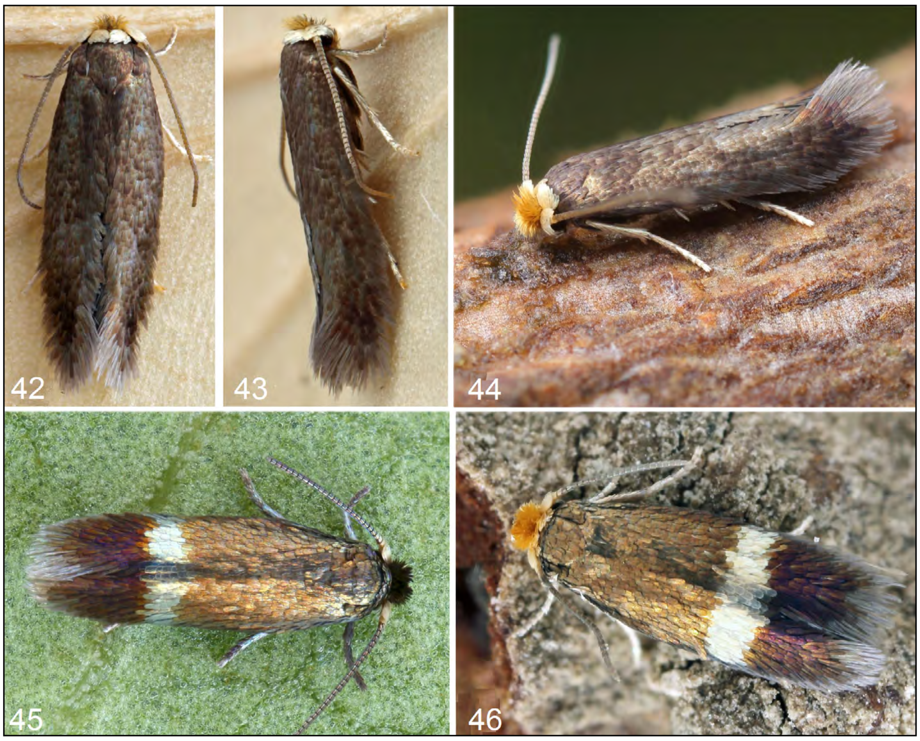
Figs 12–22. Some leaf mines of Nepticulidae discovered in Armenia. 12 – *Simplimorpha promissa* (Staudinger) on *Cotinus coggygria*; 13, 14 – *Stigmella* sp. on *Pyrus* sp.; 15 – *S. malella* (Stainton) on *Malus* sp.; 16, 17 – *S. colchica* Stonis & Diškus on *Prunus divaricata*; 18, 19 – *Stigmella* sp. on *Rosa* sp.; 20, 21 – *Bohemannia pulverosella* (Stainton) on *Malus* sp.; 22 – *Stigmella carpinella* (Heinemann) on *Carpinus orientalis*



Figs 23–33. Some leaf mines of Nepticulidae detected in Armenia. 23–25 – *Stigmella confusella* (Wood & Walsingham) on *Betula litwinowii*; 26–28 – *S. viscerella* (Stainton) on *Ulmus* sp.; 29 – *Stigmella* sp. of the *Stigmella salicis* species group on *Salix* sp.; 30, 31 – *Stigmella aceris* (Frey) on *Acer* sp.; 32, 33 – *S. lemniscella* (Zeller) on *Ulmus pumila* (=*U. microphylla*)

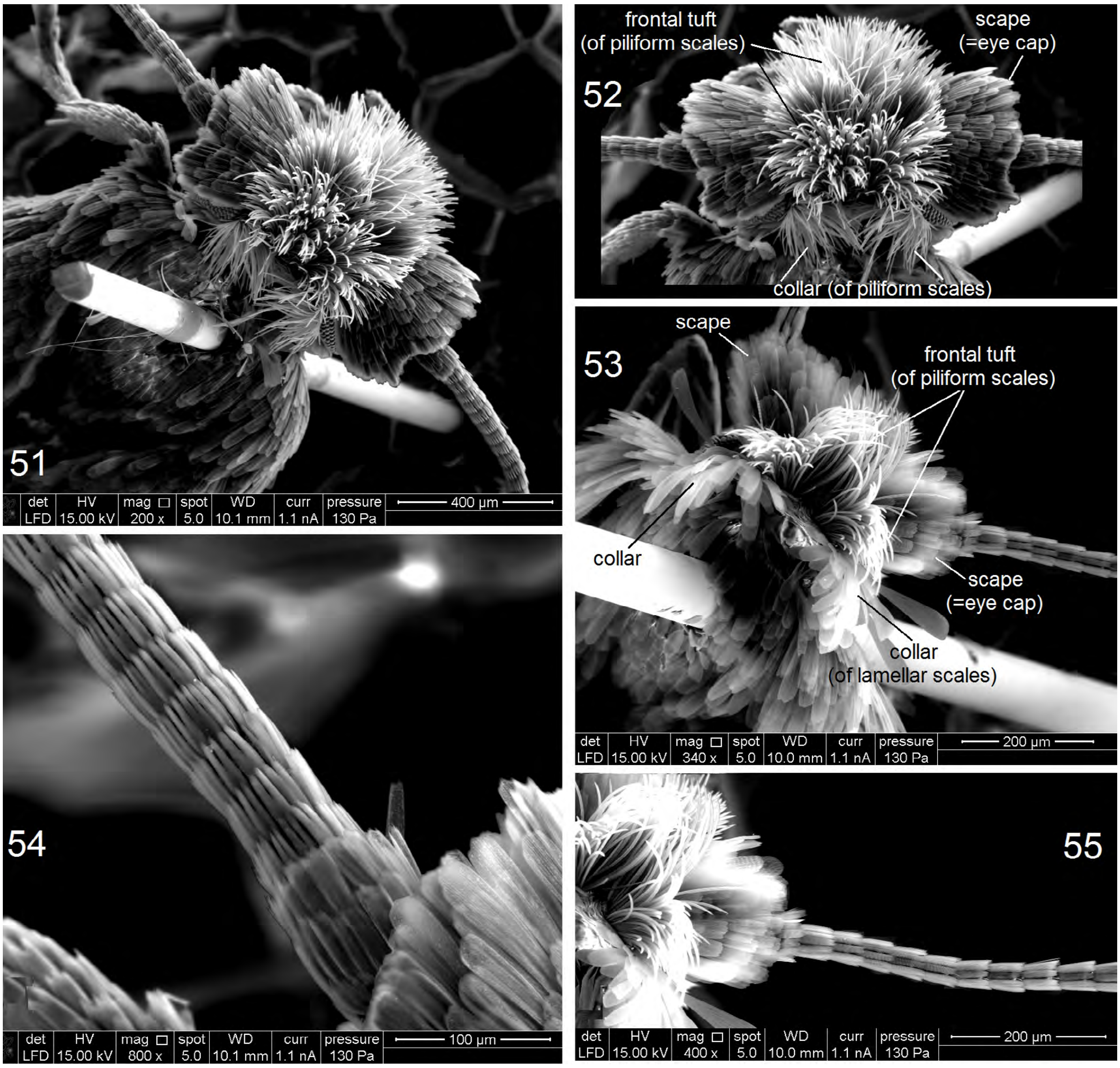


Figs 34–41. Some leaf mines of Nepticulidae on the Caucasian oak from Armenia. 34–36 – *Stigmella* sp. of the *S. ruficapitella* species group; 37–39 – Caucasian oak *Quercus macranthera* Fisch & C. A. Mey ex Hohen, a native host plant; 40, 41 – *Stigmella roborella* (Johansson)

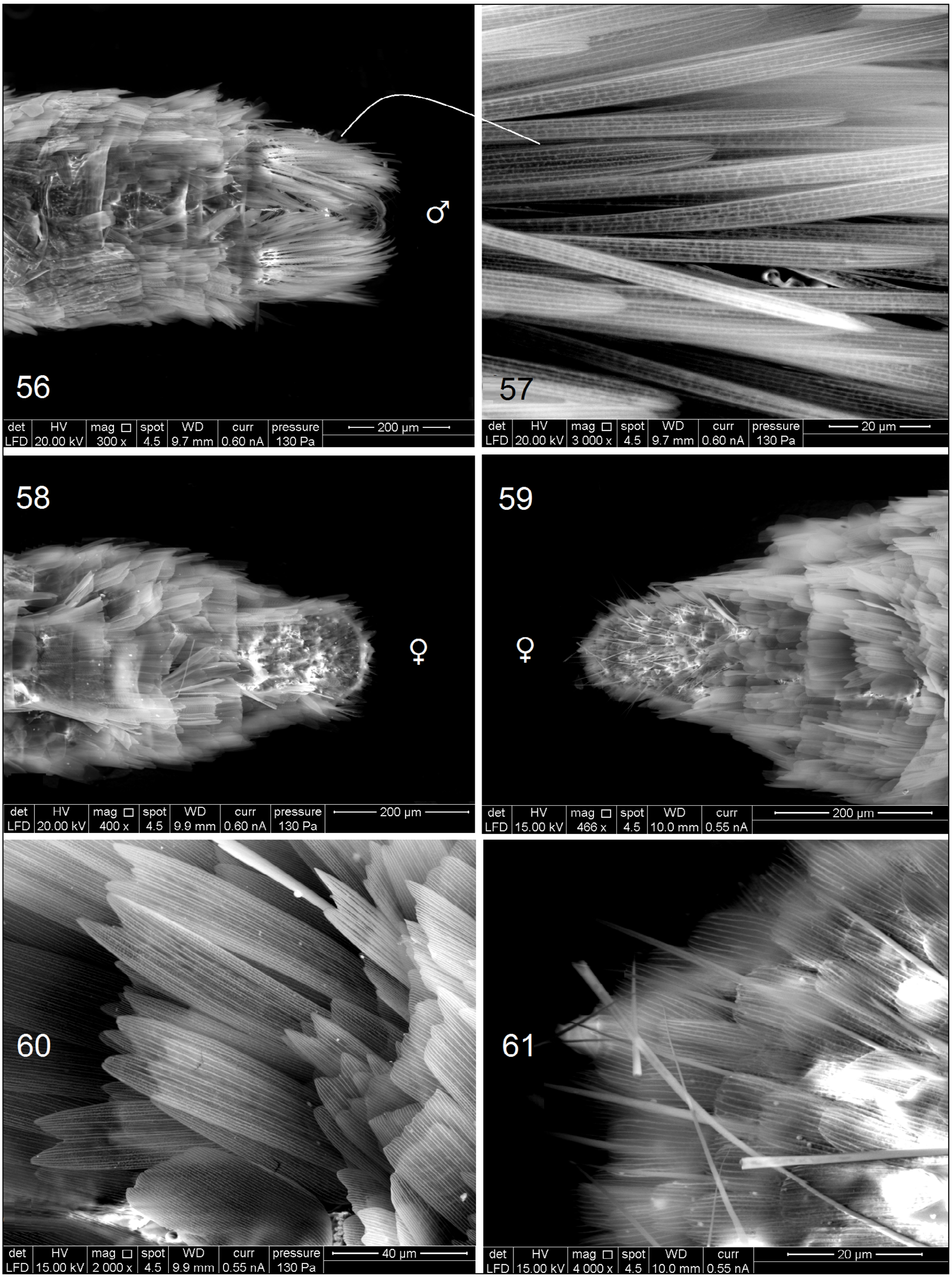


Figs 42–46. Adults of Nepticulidae of the species discovered in Armenia. 42–44 – *Stigmella roborella* (Johansson); 45, 46 – *S. hybnerella* (Hübner) (courtesy of Patrick Clement, Cornwall, U.K.)

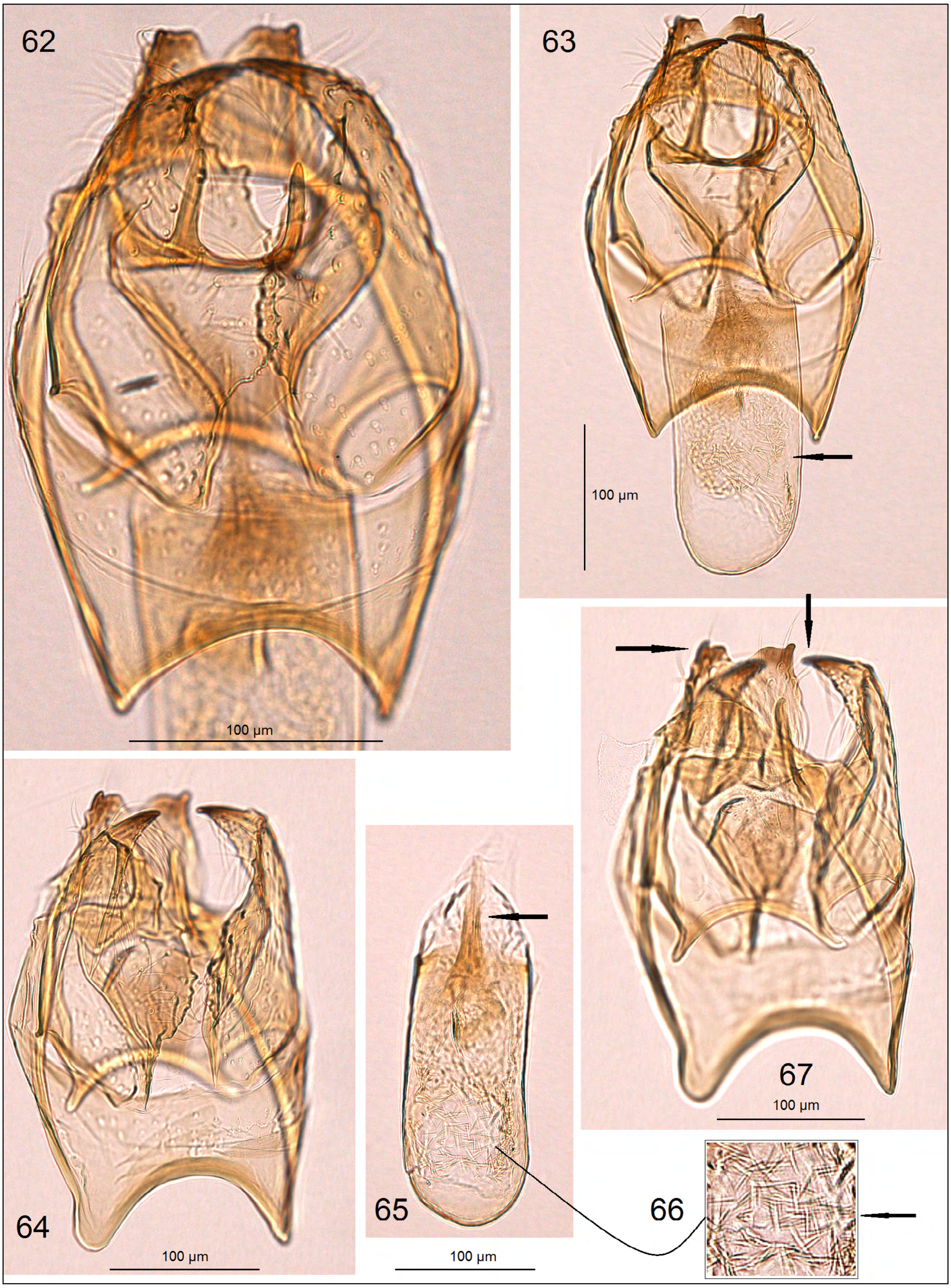
Figs 47–50. Adults of *Stigmella colchica* Stonis & Diškus. 47, 48 – a general view; 49, 50 – fringe (courtesy of Sigitas Podėnas, NRC)



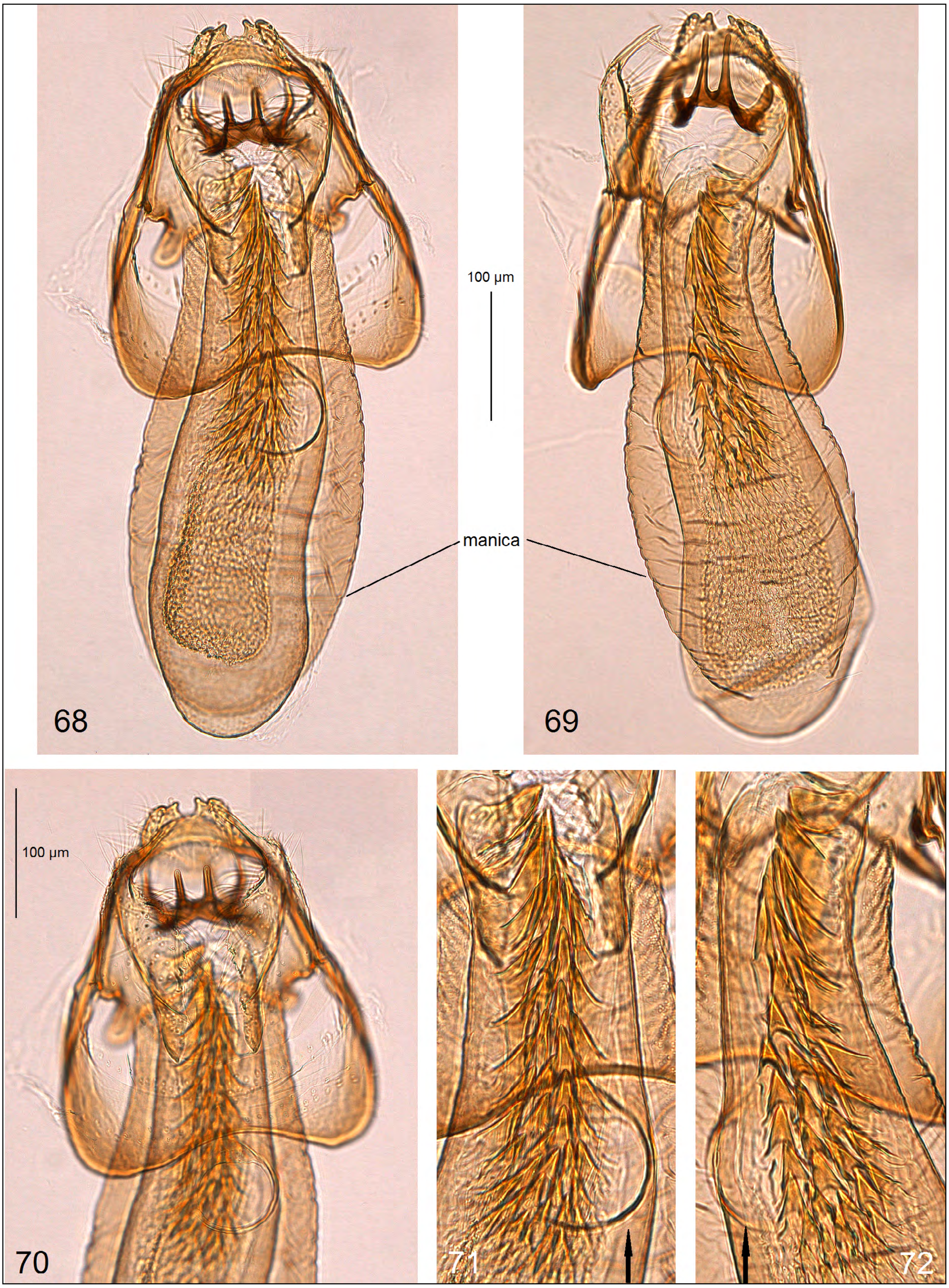
Figs 51–55. SEM photography of the head of Nepticulidae species discovered in Armenia. 51, 52 – *Ectoedemia* (*Zimmermannia*) *longicaudella* Klimesch, Antarut, 12.viii.2022; 53–55 – *Stigmella roborella* (Johansson), Antarut, 2.viii.2022



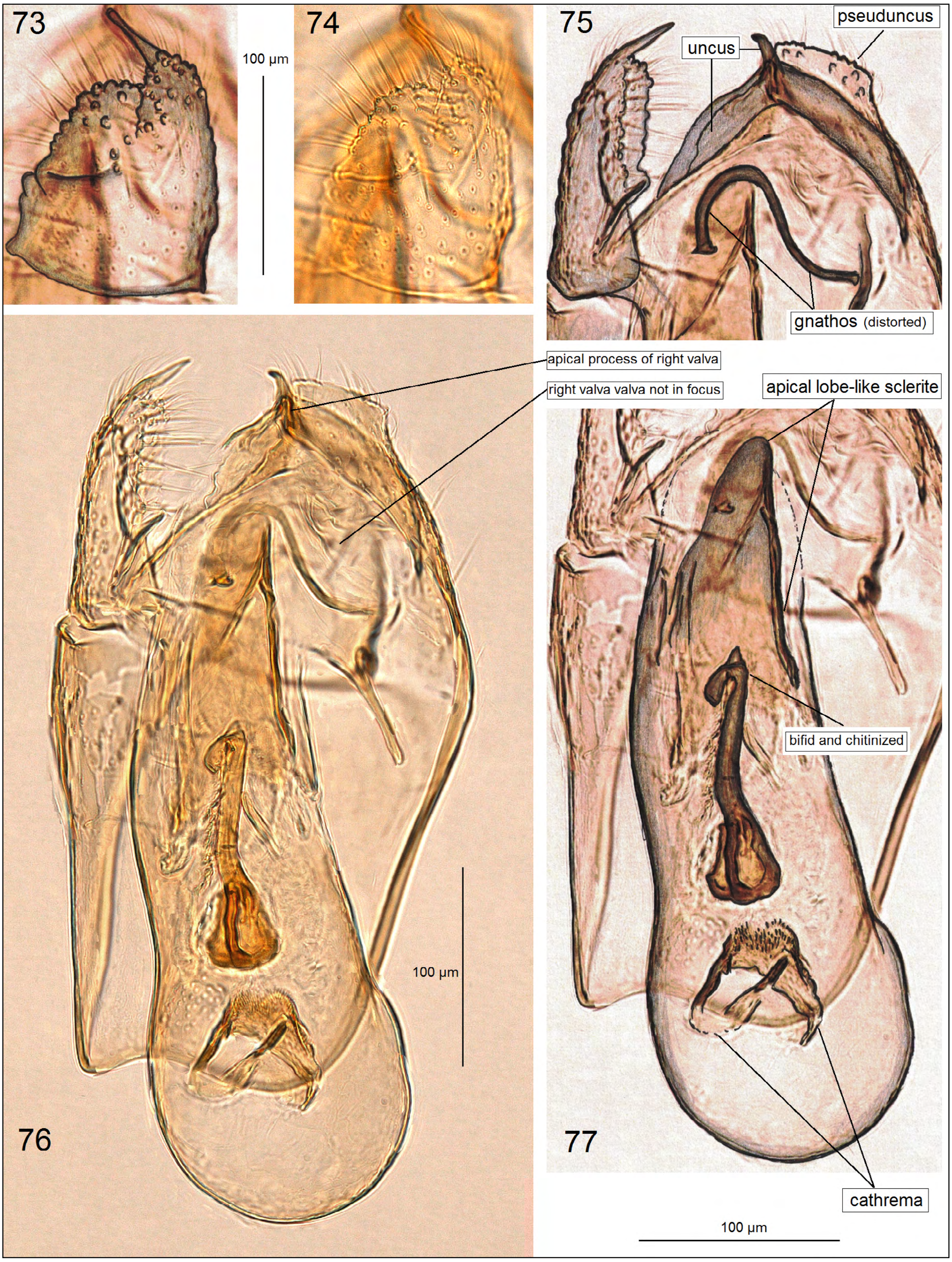
Figs 56–61. SEM photography of the abdomen of Nepticulidae discovered in Armenia. 56 – *Ectoedemia* (*Zimmermannia*) *longicaudella* Klimesch, Antarut, 12.viii.2022, ventral aspect of male abdomen; 57 – same, long and slender lamellar scales of the anal tufts; 58 – *Stigmella roborella* (Johansson), Antarut, 2.viii.2022, ventral aspect of female abdomen; 59 – *Stigmella* sp., Armenia, viii.2022, ventral aspect of female abdomen; 60 – same, lamellar scales of abdomen; 61 – same, lamellar and piliform scales of ovipositor



Figs 62–67. First documentation of *Stigmella klimeshi* Puplesis, 1978 discovered in Armenia. 62, 63 – genitalia slide no. DV059, Garni, 1310 m (MfN); 64–67 – genitalia slide no. DV051, E of Garni, 1360 m (MfN)



Figs 68–72. First documentation of *Stigmella kuznetzovi* Puplesis, 1994 discovered in Armenia. 68, 70, 71 – genitalia slide no. DV052, Garni, 1360 m (MfN); 69, 72 – genitalia slide no. DV096, Garni, 1370 m (MfN)



Figs 73–77. First documentation of *Glaucolepis melanoptera* (van Nieukerken & Puplesis, 1991) based on the material from Armenia, Jrvezh Forest Park, 1520 m, genitalia slide no. DV117, (MfN). 73, 74 – valva; 75 – pseuduncus, uncus, and gnathos; 76, 77 – phallus inside of the genital capsule

543 bp long COI sequences from Armenia are characterised by two novel mitotypes (Fig. 78), expanding not only the existing number of *S. aceris* mitotypes but also their geographical distribution. The majority of them are represented by only one sequence each (mitotype diversity Hd ± SD = 0.91 ± 0.035) and differ from each other by a few mutational steps (nucleotide diversity π ± SD = 0.007 ± 0.0007). The most common mitotype, detected in northern (Finland, Norway), eastern (Belarus, Bulgaria, European Russia), and central (Austria) parts of Europe, consists of seven sequences, constituting 24% of all analysed *S. aceris* sequences. Specimens from Armenia appear to be most closely related to a specimen collected in Ukraine (NEPTA890-13); their CO1-5' sequences differ by only 1–2 hypothesised mutational steps (intraspecific evolutionary divergence ranged from 0.19 ± 0.21% to 0.39 ± 0.30%) (Fig. 78). Thus, our analysis of DNA sequences fully confirms that the Armenian specimens represent the same species as those found in Europe.

The phylogenetic relationships between *S. aceris* and its morphologically similar *Stigmella* species from the *S. ultima* group need further investigation, as no COI sequences of *S. acerna* Puplesis, 1988, *S. bicolor* Puplesis, 1988, *S. orientalis* Kemperman & Wilkinson, 1985, and *S. semiaurea* Puplesis, 1988 are available.

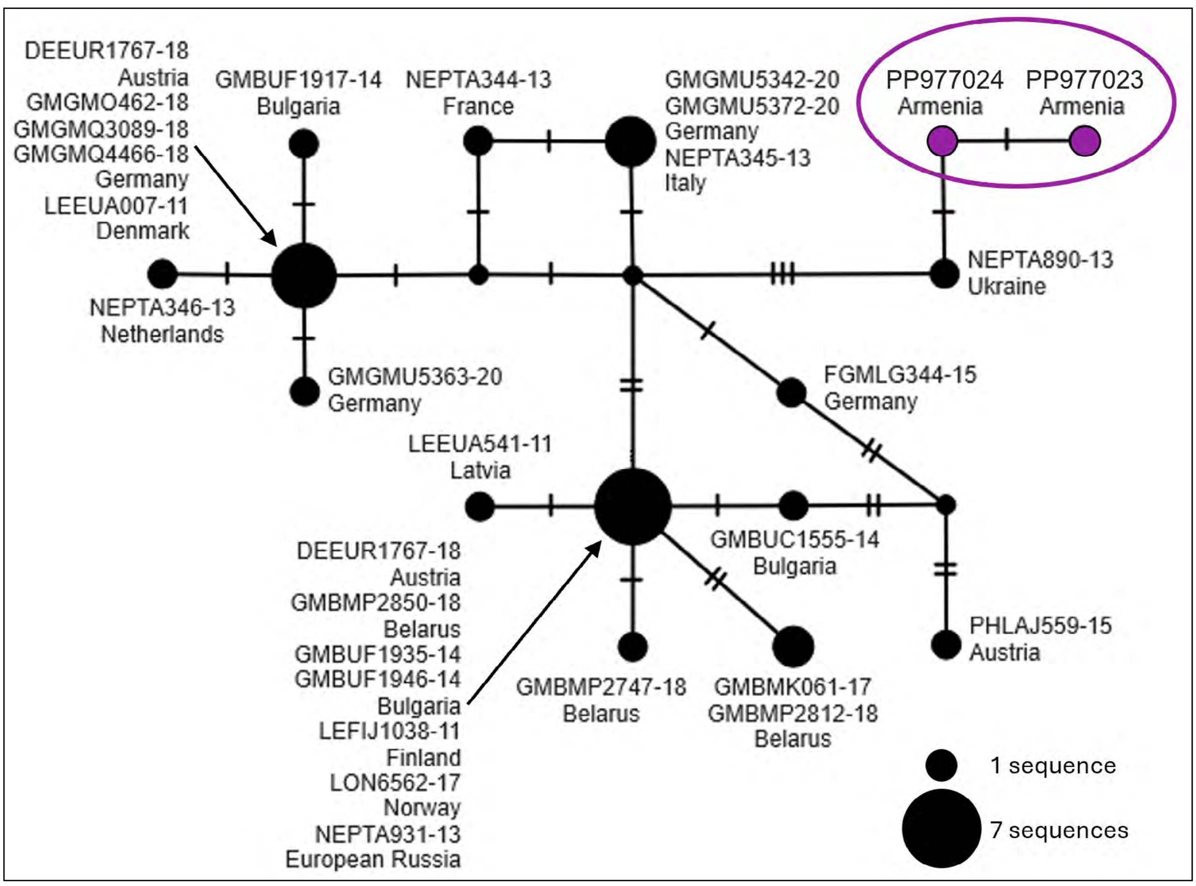


Fig. 78. The mitotype network of the 543 bp long COI *Stigmella aceris* specimens constructed by the Median Joining Network algorithm. Each circle represents a unique mitotype, their size is proportional to mitotype frequency. Mitotypes not sampled in the study but predicted to be are represented by small unnamed circles. Dashes on the lines connecting mitotypes indicate hypothesised mutational steps

Molecular support for *Stigmella inopinoides* Dobrynina, a recently described species from Armenia

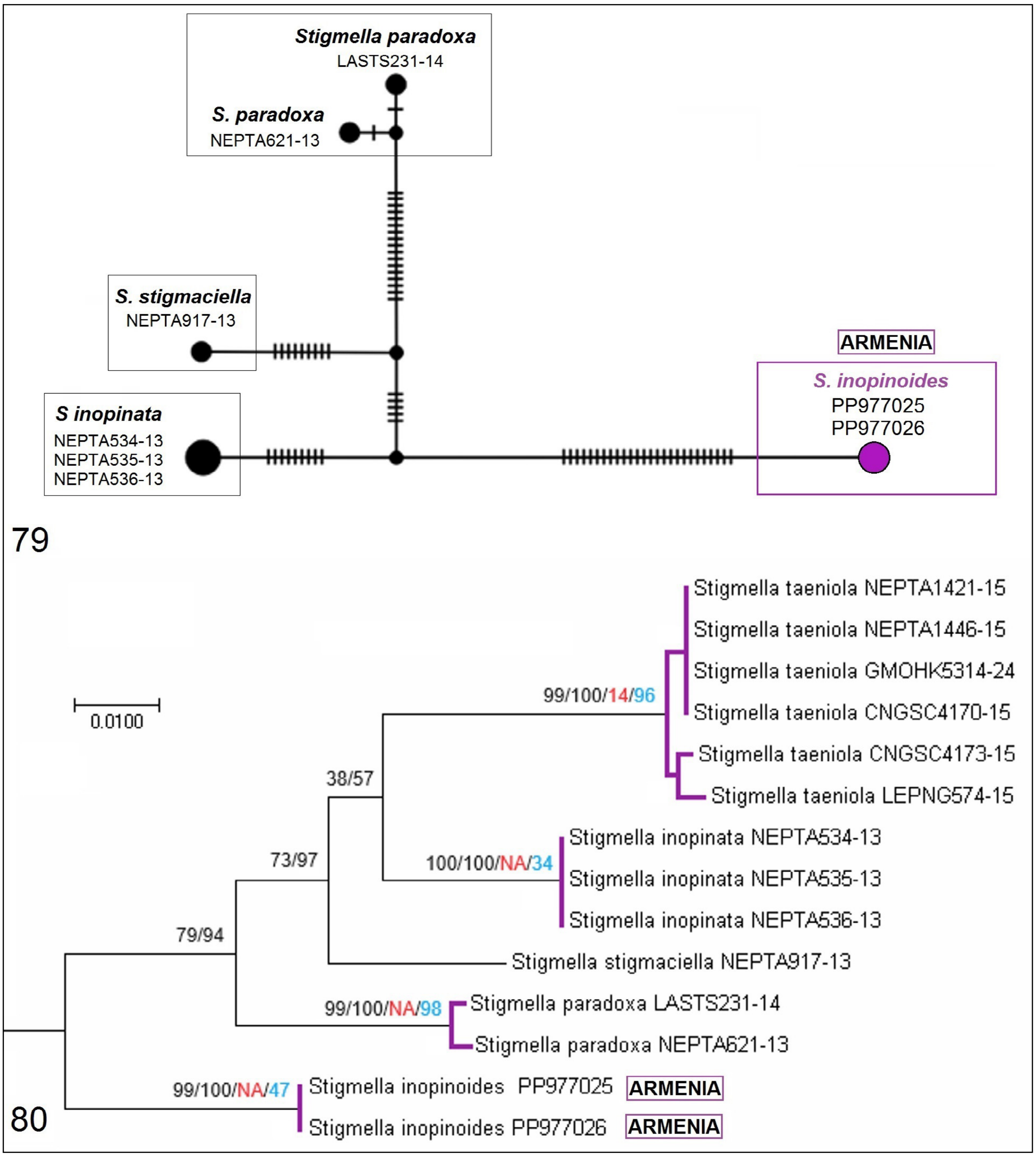
Externally and in the male genitalia, *Stigmella inopinoides* Dobrynina, 2024, a recently described species from Armenia, resembles the European species *S. inopinata* Laštůvka & Laštůvka, 1990. Previously, based on specimens collected by Friedrich Kasy in Armenia, the latter species was also reported from that country (Laštůvka & Laštůvka, 1990). However, in Stonis et al. (2024b), *S. inopinata* from Armenia was considered to be a case of misidentification. To support or cancel the description of *S. inopinoides* by molecular characters, we sequenced a couple of specimens from our Armenian material. As a result, we got the sufficiently resolved phylogenetic tree of *S. inopinoides* and its morphologically closest relatives, *S. inopinata*, *S. paradoxa* (Frey, 1858), *S. stigmaciella* Wilkinson & Scoble, 1979, and *S. taeniola* (Braun, 1925) (Figs 79, 80). Among them, *S. inopinata*, *S. paradoxa*, *S. stigmaciella*, and *S. taeniola* reliably formed a monophyletic clade (ML bootstrap value = 79%, Bayesian posterior probability = 94%), separate from *S. inopinoides*. Despite the fact that some of the probabilities of ASAP and bPTP delimitation algorithms were small enough or not applicable, both methods confirmed the genetic distinctness of all analysed species, which were represented by more than one specimen.

The interspecific evolutionary divergence between *S. inopinata* and *S. inopinoides* equalled 9.55 ± 2.74%, while in comparison with *S. inopinata* and other analysed species, it ranged between 4.96 ± 1.36% and 7.90 ± 2.23%, thus implying the presence of a bigger barcoding gap between *S. inopinata* and *S. inopinoides* than *S. inopinata* and the rest of the species. Consequently, the results of our molecular analysis provided additional evidence to morphological studies (see Stonis et al., 2024b) and confirmed *S. inopinoides* as an independent species separate from the morphologically closest European *S. inopinata*.

Molecular justification of *Glaucolepis melanoptera* (van Nieukerken & Puplesis), a species discovered in Armenia

Based on the results of our previous fieldwork in Armenia (Stonis et al., 2024b), *Glaucolepis melanoptera* (van Nieukerken & Puplesis, 1991) appears to be a common species in that country, exhibiting variation in external characteristics. Previously, this species was recorded in the fauna of Armenia based on a single aberrant non-type specimen (van Nieukerken & Puplesis, 1991), which raised concerns and prompted molecular studies of newly collected specimens from Armenia.

The topology of the phylogenetic tree, which includes five 657 bp long COI *Glaucolepis* Braun species (*G. bleonella* (Chrétien, 1904), *G. headleyella* (Stainton, 1854), *G. lituanica* (van Nieukerken & Ivinskis, 2012), *G. melanoptera* (van Nieukerken & Puplesis, 1991), and *G. raikhonae* Puplesis, 1985), was relatively well supported and all analysed species with more than one specimen appeared to be monophyletic (Fig. 81). *G. melanoptera* was situated as the sister taxon to *G. raikhonae* (ML bootstrap value was 82%, Bayesian posterior probability – 99%), thus considering the latter species phylogenetically close to *G. melanoptera* and confirming their morphological similarity. According to the ASAP and bPTP species delimitation algorithms, three analysed specimens, identified as *G. melanoptera* from Armenia and characterised by the same mitotype, were not assigned to the rest of *G. melanoptera* mitotypes. This can be explained by higher intraspecific divergence within this species (PP977020 differs from other mitotypes by 6.12 ± 1.13% – 7.31 ± 1.48%, while within other mitotypes the variability was at most 2.95 ± 0.77%), which possibly led to the formation of cryptic species. More clarity could be provided with additional genetic analysis and the incorporation of more specimens.



Figs 79, 80. Molecular support for *Stigmella inopinoides* Dobrynina. 79 – the mitotype network of the 657 bp long COI *Stigmella inopinoides* Dobrynina and *S. inopinata* sequences constructed by the TCS Network algorithm. *S. paradoxa* and *S. stigmaciella* were included as the most related species. Each circle represents a unique mitotype, their size is proportional to mitotype frequency. The unnamed small circles represent mitotypes not sampled in the study but predicted to be. Dashes on the lines connecting mitotypes indicate hypothesised mutational steps; 80 – the phylogenetic relationships of five species of the *Stigmella paradoxa* group based on the 657 bp long COI sequences and GTR+G+I evolution model. Numbers represent the bootstrap values obtained for maximum likelihood probability (10,000 bootstrap replicates) (black) / Bayesian posterior probability (12,000,000 generations) (black) / ASAP probability (red) / bPTP support value (blue) in %. Magenta clusters of the tree were supported as separate species by both ASAP and bPTP delimitation algorithms. *Pseudopostega cucullata* (Opostegidae) was included as an outgroup

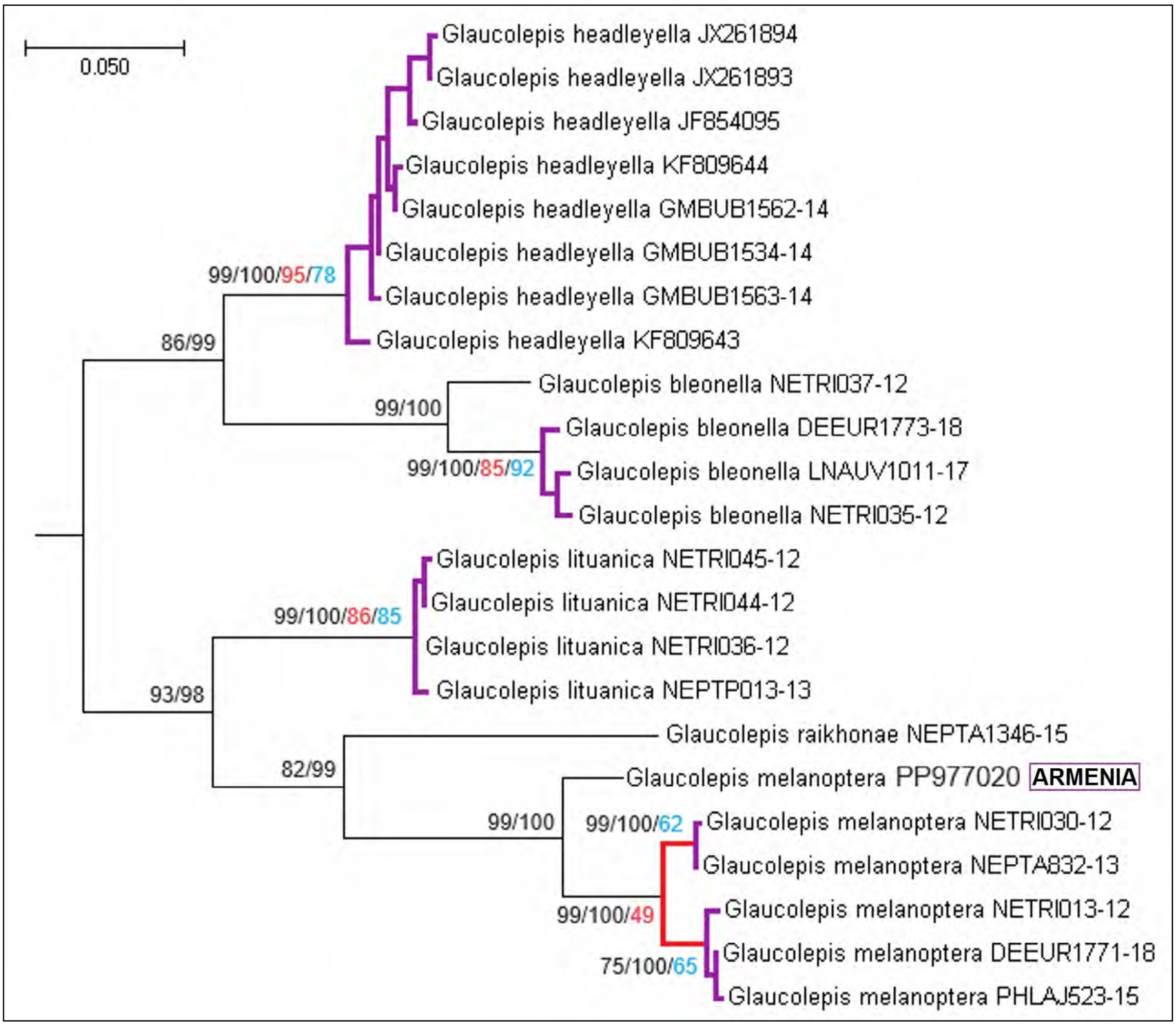


Fig. 81. The phylogenetic relationships of five *Glaucolepis* Braun species based on the 657 bp long COI sequences and using GTR+G+I evolution model. Numbers represent the bootstrap values obtained for maximum likelihood probability (10,000 bootstrap replicates) (black) / Bayesian posterior probability (5,000,000 generations) (black) / ASAP probability (red) / bPTP support value (blue) in %. Magenta clusters of the tree were supported as separate species by both ASAP and bPTP delimitation algorithms, red – only by ASAP. *Pseudopostega cucullata* was included as an outgroup

Molecular support for *Etainia caucasi* Remeikis, a recently described species from Armenia

Based on the results of our previous fieldwork in Armenia, *Etainia caucasi* was described by Andrius Remeikis (Stonis et al., 2024b). Despite the fact that *E. caucasi* differs from the closely related species *E. louisella* (Sircom, 1849), *E. sericopeza* (Zeller, 1839) and *E. decentella* (Herrich-Schäffer, 1855) in the morphology of male and female genitalia, we needed to sequence at least one specimen of the new species to support its description.

According to the maximum likelihood and the Bayesian inference algorithms, the phylogenetic analysis of the COI mitotypes of *E. caucasi* and its morphologically closest species demonstrated mostly well supported clades (Fig. 82). The application of the ASAP and bPTP species delimitation algorithms confirmed the distinctness of all analysed species, which were represented by more than one specimen. The mean

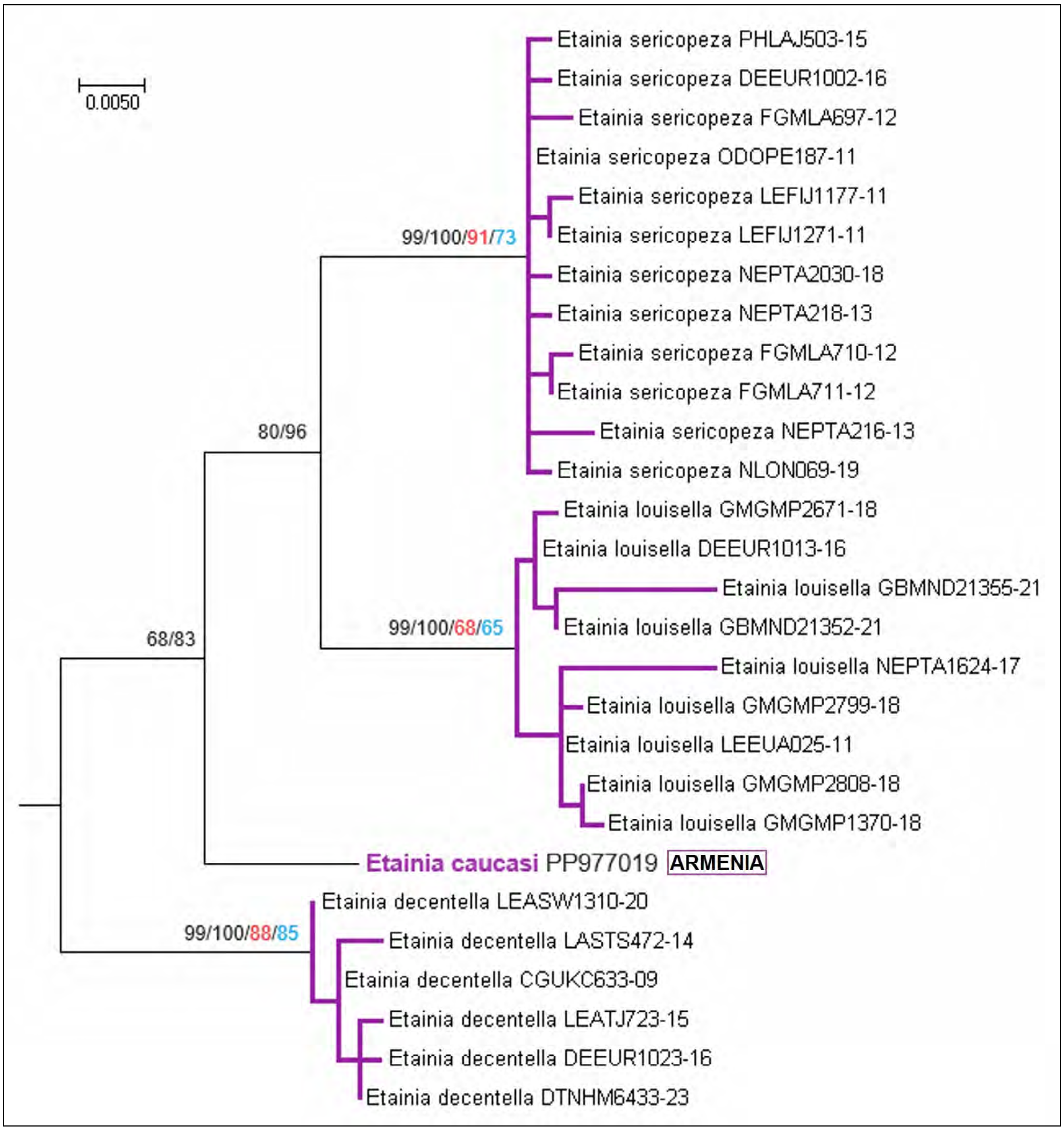


Fig. 82. The phylogenetic relationships of four *Etainia* Beirne species based on the 657 bp long COI sequences and using GTR+G+I evolution model. Numbers represent the bootstrap values obtained for maximum likelihood probability (10,000 bootstrap replicates) (black) / Bayesian posterior probability (10,000,000 generations) (black) / ASAP probability (red) / bPTP support value (blue) in %. Magenta clusters of the tree were supported as separate species by both ASAP and bPTP delimitation algorithms. *Pseudopostega cucullata* was included as an outgroup

interspecific evolutionary divergence between the *E. caucasi* and other included species was ranged from 3.80% (*E. caucasi*–*E. sericopeza*) to 4.41% (*E. caucasi*–*E. decentella*), while the mean intraspecific distances among the mitotypes of species were only 0.36% for *E. decentella*, 0.40% for *E. sericopeza* and 0.94% for *E. louisella*, thus implying the presence of a barcoding gap between them and *E. caucasi*. Our next molecular analysis, which included some other *Etainia* species from Europe, East Asia, and North America, not only justified the description of *E. caucasi* but also provided some interesting insights (Fig. 83).

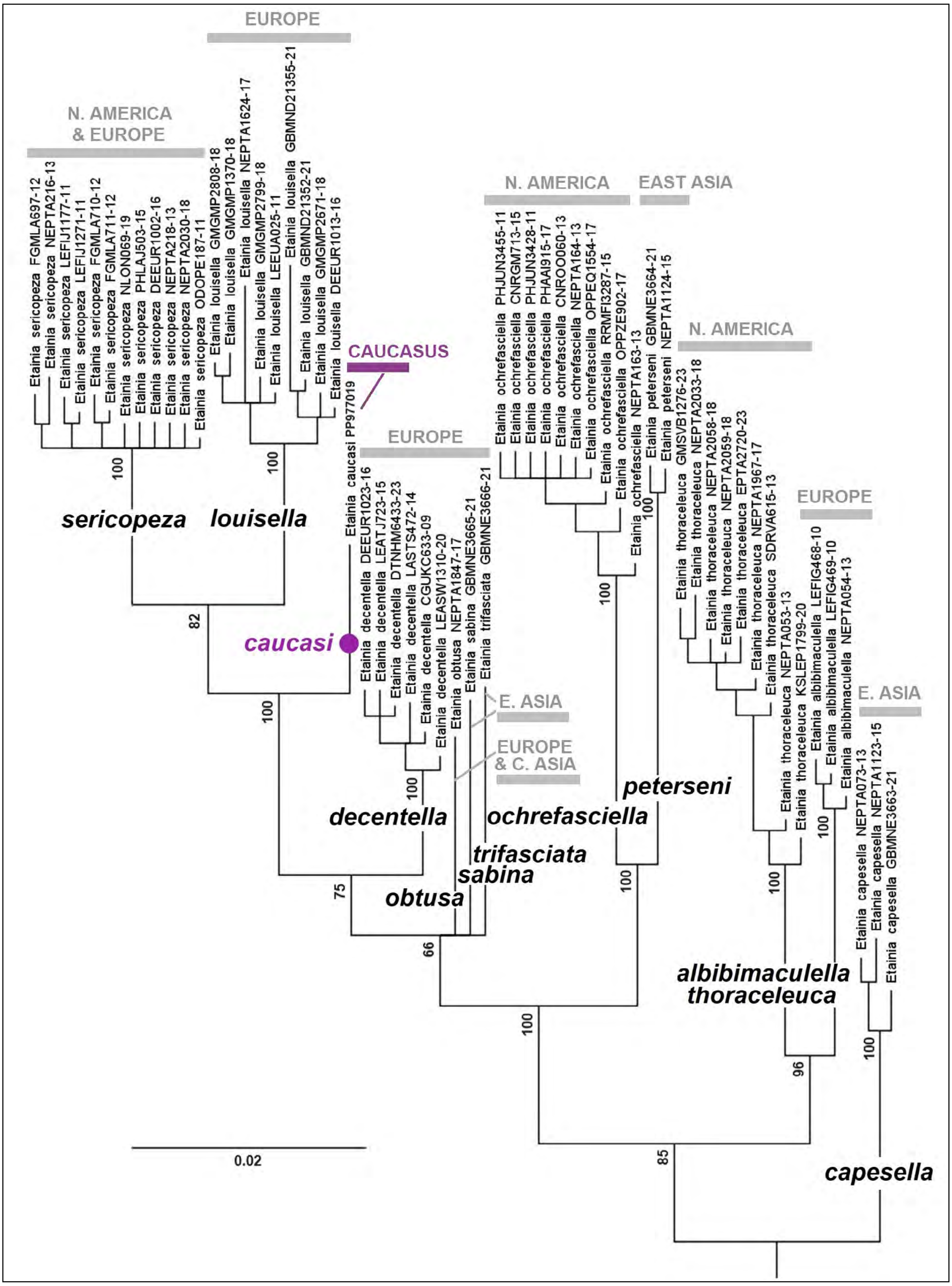


Fig. 83. The Bayesian phylogenetic tree of *Etainia* Beirne species based on the 657 bp long COI sequences. The GTR+G+I evolution model and 10,000,000 generations were applied. *Pseudopostega cucullata* was included as an outgroup

In conclusion, our molecular analyses support previous morphological studies of Caucasian *E. caucasi* (see Stonis et al., 2024b) and confirm it as an autonomous taxon, separate from other morphologically similar *Etainia* species.

DISCUSSION

Nepticulidae moths can be referred to as 'micro wonders' or 'tiny marvels' due to their minuscule size, distinct and intricate wing patterns, and specialised ecological role as leaf-mining herbivores that create distinctive leaf mines. Despite their small stature (the smallest moths in the world, see Stonis et al., 2021), these phylogenetically old moths provide valuable insights into evolutionary history, biodiversity, and ecological interactions in ecosystems worldwide. Their beauty, combined with their diminutive size, makes them truly remarkable creatures. The delicate patterns and vibrant colors on their wings, often accompanied by iridescence or subtle metallic sheens, add to their allure and highlight their remarkable aesthetic appeal and biological uniqueness.

In 2022, we embarked on the first targeted fieldwork in Armenia to investigate the diversity of these tiny yet enigmatic organisms. Currently, the 32 species identified (including eight recently described as new taxa) represent approximately 40–45% of the expected total species diversity in Armenia (Stonis et al., 2024b), highlighting the vast potential for new discoveries in this under-explored field: some 40 or more species could still be found with further study.

Our previous genetic analyses also revealed intriguing findings: some specimens showed no obvious morphological or ecological differences from the known European species like *Simplimorpha promissa* (Orlovskytė et al., 2023) and *Ectoedemia longicaudella* (Stonis et al., 2024b). However, detailed examination of molecular characters unveiled significant genetic differences, suggesting the presence of cryptic taxa, potential allopatric subspecies, or even entirely new species adapted to local environments in the Caucasus. These discoveries once again underscore the critical role of molecular techniques in uncovering hidden biodiversity. Molecular methods have been rapidly developing and are widely applied for the delimitation of cryptic species, including insects (e.g., Anderson et al., 2013; Orlovskytė et al., 2016; Saldaitis et al., 2021; Nazari et al., 2023; Budrys et al., 2024). By further exploring these molecular signatures, we aim to understand the extent of cryptic diversity in the Caucasus region. Our recent findings (see Stonis et al., 2024b) possibly indicate that the Caucasus is a hotspot for cryptic diversity within Nepticulidae moths. Each newly identified cryptic species not only contributes to our knowledge of biodiversity but also enhances our understanding of evolutionary adaptations and the complex relationships between organisms and their environments; cryptic taxa play a valuable role in improving understanding of evolution, in particular of morphological stasis (Monro & Mayo, 2022).

As a phylogenetically basal and one of the oldest groups of Lepidoptera that originated around 130 million years ago (Doorenweerd et al., 2016), Nepticulidae can offer insights into the historical genesis of the global biota and the evolutionary processes or biogeographical patterns that have shaped biodiversity over millions of years. Moreover, the highly specialised nature of pygmy moths adds another layer of interest. The larvae of these moths feed within plant tissues, and their interactions with host plants can shed light on coevolutionary dynamics and plant-insect relationships. This specialisation also means that nepticulid species can act as pests when in large numbers, impacting agriculture and natural ecosystems.

Altogether, the potential for uncovering new species, including those with cryptic characteristics, the specific role of Nepticulidae in ecosystems, and their phylogenetic importance underscore the need for comprehensive studies and more fieldwork. Moreover, fieldwork, especially in lesser-studied and scenic countries like Armenia, located in the biodiverse and geographically unique Caucasus region, is indeed fascinating and exciting. Armenia harbors a wealth of biodiversity, and our collecting experience has already proven that the diverse habitats of Armenia provide rather ideal environments for Nepticulidae moths.

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ĮŽVALGOS IR NAUJI DUOMENYS APIE NEPTICULIDAE ĮVAIROVĘ PAGAL ANKSTESNIŲ LAUKO DARBŲ ARMĖNIJOJE REZULTATUS

Santrauka

Straipsnyje pateiktas papildytas Armėnijoje aptiktų mažųjų gaubtagalvių (Nepticulidae) rūšių sąrašas ir pirmą kartą iliustruojamos šioje šalyje mitybinių augalų lapuose rastos Nepticulidae minos. Remiantis originalia, Armėnijoje surinkta medžiaga, straipsnyje pirmąkart pateikiama detali iki šiol menkai žinomų rūšių taksonominė dokumentacija su ištirtų *Stigmella klimeschi* Puplesis, *S. kuznetzovi* Puplesis ir *Glaucolepis melanoptera* (van Nieukerken & Puplesis) patinų genitalinių struktūrų fotografijomis. Taip pat molekuliniais tyrimais patvirtintas *Stigmella aceris* (Frey) ir *Glaucolepis melanoptera* aptikimo Armėnijoje faktas ir pagrįstas dviejų anksčiau aprašytų naujų rūšių (*Stigmella inopinoides* Dobrynina ir *Etainia caucasi* Remeikis) teisėtas paskelbimas.

Raktažodžiai: Kaukazo fauna, lapų minos, mažieji gaubtagalviai, mitotipai, Nepticulidae