

The native parasitoids exploiting the invasive leafminer *Coptodisca lucifluella* (Lepidoptera: Heliozelidae) in Southern Russia and Abkhazia

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Academic editor: R. Yakovlev | Received 1 July 2025 | Accepted 12 July 2025 | Published 9 August 2025

<http://zoobank.org/7EE4BB3D-4334-4BD3-B7CF-3F3D54425994>

Citation: Kosheleva OV, Zhuravleva EN, Karpun NN, Kirichenko NI (2025) The native parasitoids exploiting the invasive leafminer *Coptodisca lucifluella* (Lepidoptera: Heliozelidae) in Southern Russia and Abkhazia. Acta Biologica Sibirica 11: 863–887. <https://doi.org/10.5281/zenodo.16760824>

Abstract

The leafmining moth *Coptodisca lucifluella* (Lepidoptera: Heliozelidae) is the North American species, which recently invaded Europe. Here, we provide first data on the parasitoid assemblage associated with this leafminer in Southern Russia and Abkhazia. In 2024, altogether 28 parasitoid specimens were reared from the late-instar larvae and pupae of *C. lucifluella* and identified to seven parasitic wasp species. Among them, six species were from Eulophidae: *Pnigalio soemius* (Walker), *Cirrospilus variegatus* (Masi), *C. viticola* (Rondani), *Chrysocharis pentheus* (Walker), *Closterocerus* sp. (presumably new species to science), *Minotetrastichus frontalis* (Nees) and one from Eupelmidae: presumably *Eupelmus kiefferi* De Stefani. All these parasitoids are native to the studied area and have been documented on

C. lucifluella for the first time. In Russia and Abkhazia, the parasitism rates reached 13% and 31%, respectively. Four species contributed the most to the leafminer mortality: *M. frontalis* (11 out of 13%) in Sochi (Russia), *C. pentheus* (12 out of 31%), *C. viticola* (8%), and *C. variegatus* (8%) in Gagra (Abkhazia). For the recorded parasitoids, the distribution and hosts are mentioned, and the original photographs of parasitoid adults are provided. Additionally, an exhaustive checklist of parasitoids associated with *C. lucifluella* in its modern range was compiled, accounting 32 species. Altogether, our findings suggest that during the invasion, *C. lucifluella* escaped from its aborigine enemies but became a target for the parasitoids naturally present in Southern Russia and Abkhazia.

Keywords

North American heliozelid, parasitoids, new trophic associations, invaded range, Sochi, Western Caucasus

Introduction

The North American leafmining moth *Coptodisca lucifluella* (Clemens, 1860) (Lepidoptera: Heliozelidae) has attracted significant attention following its recent spread in Europe (Takács et al. 2020; Mustăţea and Chireceanu 2023; Lepiforum 2025).

For the first time in Europe, *C. lucifluella* was documented in Italy in 2010 (Bernardo et al. 2012, 2015). Shortly after, it was detected sequentially in Hungary (Takács et al. 2017, 2020; Szabóky and Takács 2018), Ukraine (Pályi et al. 2019), Bulgaria, Czech Republic (Tomov 2020; Laštůvka and Laštůvka 2020), Austria, Slovakia, France (Huemer 2021; Tokár et al. 2021; Rennwald 2022), Romania, Germany, Slovenia, Switzerland, Serbia (Chireceanu et al. 2022; Fuchs et al. 2022; Kirichenko et al. 2023; Lepiforum 2025), and Croatia (Kirichenko et al. 2025). In 2023 and 2024, the moth was recorded for the first time in Russia (on the south of the European part) and in Abkhazia, raising concerns about its potential impact to walnut trees and further spread to neighboring countries where its host plants are cultivated (Kirichenko et al. 2024).

The larvae of this species make small mines in the leaves of economically important plants from the genera *Carya*, *Juglans*, and *Pterocarya* (Juglandaceae) (Lepiforum 2025), sometimes resulting in considerable damage to the foliage (Kirichenko et al. 2024). The moth can produce several generations per year. For instance, up to four generations were recorded in Italy, with each successive generation contributing to more pronounced damage to its host plants (Bernardo et al. 2012, 2015; Takács et al. 2020).

Despite range expansion of *C. lucifluella* in Europe, limited data are available on interactions of native parasitoids with the alien micromoth. Invasive species may experience reduced pressure from natural enemies in new environments, a phenomenon known as enemy release (Prior and Hellmann 2014; Heger et al. 2024). Such escape from natural enemies can facilitate the successful establishment and spread of invasive species (Heger et al. 2024). However, as they continue spreading in new regions, local enemies (i.e., those native to invaded area), including parasi-

toids, may eventually shift to the novel hosts from local insects (Gröbner and Lewis 2008; Kirichenko et al. 2013; Muru et al. 2020).

The expansion of *C. lucifluella* into new geographic areas raises questions about how local parasitoid complexes may respond to this novel host. Bearing in mind that in Southern Russia and Abkhazia, *C. lucifluella* was revealed already at noticeable densities (see Kirichenko et al. 2024), we hypothesized that the moth escaped from its aborigine enemies and with the time, local parasitoids will form trophic association with the new host. To investigate this hypothesis, we investigated parasitism rates and identified parasitoid species attacking *C. lucifluella* in Southern Russia and Abkhazia.

Materials and methods

Study region

The study was performed in June–July 2024 in 13 localities: 3 in Southern Russia (Sochi: Adler and Khosta districts, and the Federal territory Sirius) and 9 in Abkhazia (Gagra, Pitsunda, Sukhum, Gulripsh, Bagmaran, Dranda Adzyubzha, Kyndyg, and Tkuarchal) (Fig. 1).

In all localities, the ornamental plantings in streets, parks, gardens and trees in agroecosystems were examined. Following tree species from the family Juglandaceae were surveyed: the common walnut *Juglans regia* (widely naturalized in Europe), Caucasian wingnut *Pterocarya fraxinifolia* (native to Caucasus region), Persian walnut *Juglans regia* (native to Eurasia), and the eastern American black walnut *Juglans nigra*, pecan *Carya illinoensis*, and mockernut hickory *C. tomentosa* (syn. *C. alba*) (the latter three species are of North American origin).

The subtropical zone of Russia extends along the Black Sea coast of the Caucasus, reaching altitudes of up to 200 meters above sea level. This region spans from Tuapse in the north to the Psou River in the south, which is served as the border with Abkhazia (Gulia et al. 2014). Abkhazia, predominantly mountainous, shares its borders with Russian territories along the crest of the Main Watershed Range of the Greater Caucasus and adjoins Georgia to the east. The high mountain ranges of the Main Caucasus Range, characterized by their towering peaks and gentle slopes, act as a barrier against the intrusion of cold continental winds (Gulia et al. 2014).

The Black Sea moderates temperatures by retaining heat, significantly influencing the climate of the humid subtropical regions in both Russia and Abkhazia. The climate in these areas is characterized by warm winters, hot and humid summers, long cool springs, and dry warm autumns (Fedina 1968). While the Black Sea coast predominantly experiences a humid subtropical climate, the foothills and highlands exhibit distinct mountain climatic characteristics due to altitudinal zonation. The Russian subtropics benefit from 2200 to 2400 hours of sunshine per year, while Abkhazia has up to 2500 such hours. Average annual precipitation is about 1534 mm in

the Russian subtropics and around 1500 mm in Abkhazia, with June and July being the driest months and December and January the wettest (Fedina 1968).

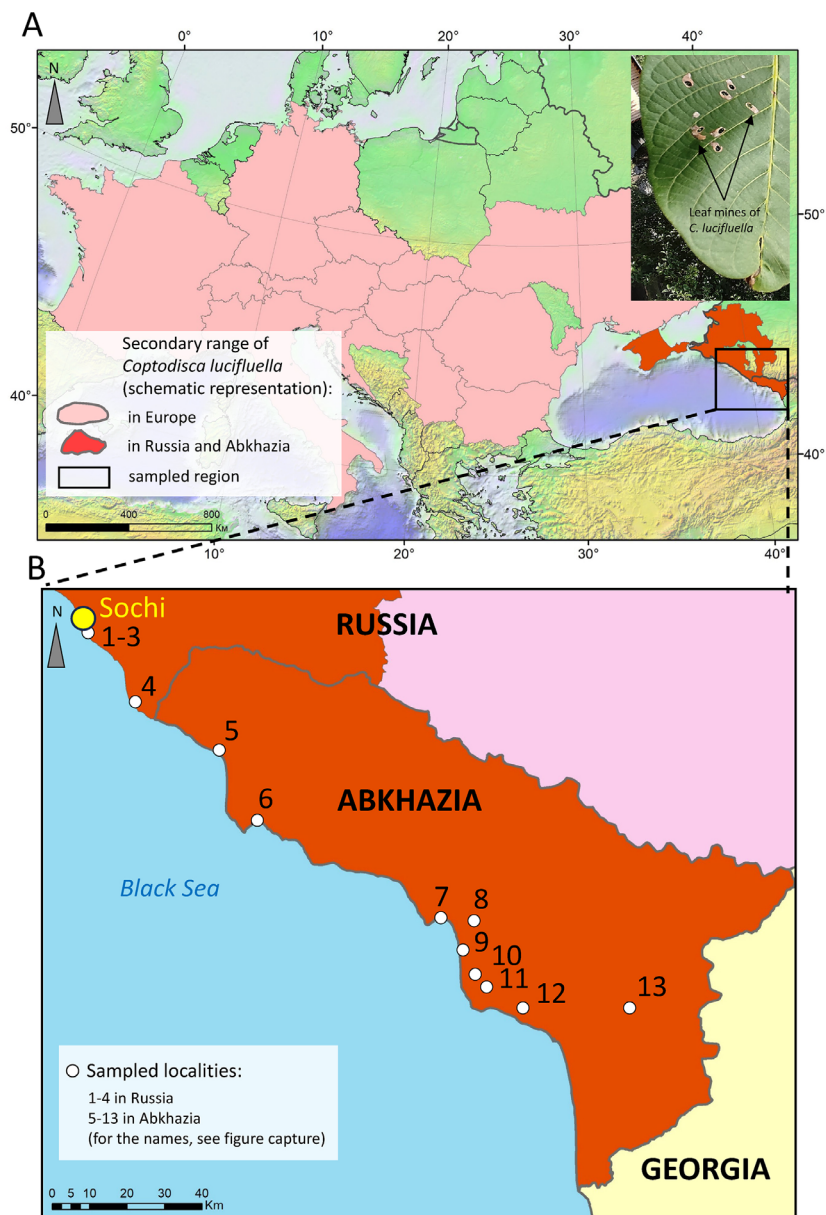


Figure 1. Current secondary range of *Coptodisca lucifluella* in Europe (A) and sampling localities in Southern Russia and Abkhazia in 2024 (B). Names of sampled localities (No. 1–13): in Russia (1 – Sochi, Gnilushka river embankment; 2 – Sirius, park “Yuzhnye Kultury”; 3 – Sochi, park of M.V. Frunze sanatorium; 4 – Sochi, park of “Zolotoy Kolos” sanatorium) and Abkhazia (5 – Gagra, park “Prince of Oldenburg”; 6 – Pitsunda; 7 – Sukhum, the Sukhum botanical garden; 8 – Bagmaran vilage (below shorten to vil.); 9 – Gulripsh; 10 – Dranda vil.; 11 – Adzyubzha vil.; 12 – Kyndyg vil.; 13 – Tkuarchal).

Field sampling

From 1 to 5 tree individuals of each species were examined in the above-mentioned localities. On trees, from 20 to 40 leaves on four low branches were checked around tree crown for the presence of characteristic leaf mines (see description in Kirichenko et al. 2024) and the shields in which larvae pupate (Fig. 2). Sampling period was adjusted to the time when the moth was about to complete the first generation. At this time, the late-instar larvae were found in the leaf mines or the larvae were vacating leaf mines (by cutting the shields from leaf epidermis) for pupating externally, on leaves along the main rib, next to petiole or on branches. By 10 leaves of *Juglans* spp. and by 10 leaf compounds of *Carya* spp. with leaf mines or shield were collected and transported to the insectarium of the Subtropical Scientific Centre of the Russian Academy of Science (Sochi) for rearing.

Parasitoids rearing, identifying, and parasitism assessment

The segments of leaves with leaf mines were cut out from the leaves to accommodate the size of Petri dishes. The segments were placed in the dishes lined with filter paper according to sampled locality and host plant; a segment of moisturized cotton was attached on the dish lid from inside. From 5 to 40 leaf mines or by 10–20 shield found on the leaves were placed in dishes. Altogether, 20 Petri dishes were filled in with sampled leaf mines and shields of *C. lucifluella*. The dishes were kept in constant conditions (temperature 25°C, 55% humidity) in shade. Moisture in dishes was maintained by adding moderate volume of water on the cotton attached to the dishes' lids. The dishes were checked every 2nd or 3rd day and the number of parasitoids and *C. lucifluella* adults emerged was counted. The parasitoids were preserved in 95% ethanol in 1.5 ml vials with hermetic lids, and the moth adults were collected to 1.5 ml Eppendorf tubes on cotton.

The parasitoids were identified based on their morphological characteristics using the taxonomic and faunistic publications by Masi (1907), Bouček (1959), Hansson (1985, 1987, 1990, 1994, 1995), Graham (1987), Kurashev (1991), Zhu et al. (2002), Gibson and Fusu (2016). Additionally, sampled parasitoids were compared with specimens from the Hymenoptera collection Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZISP) (identification by Dr. Bouček and Dr. Hansson). Parasitoids specimens collected in Southern Russia and Abkhazia are stored in dry collection at ZISP.

Parasitism was estimated taking into account the contribution of different parasitoid species. The number of emerged parasitoids of each species in each locality was counted and divided to the total number of leaf mines and leaf shields involved to rearing in each locality, so that allowing to estimate parasitism level (expressed in %). For gregarious parasitoid species, the data on their parasitism was divided per 2 as most often by 2 such parasitoids emerged from certain host. Bearing in mind that the data on parasitism were obtained from different host plants, no statistical

comparison was done. By the same reason, the resultant data were graphed separately for each locality.

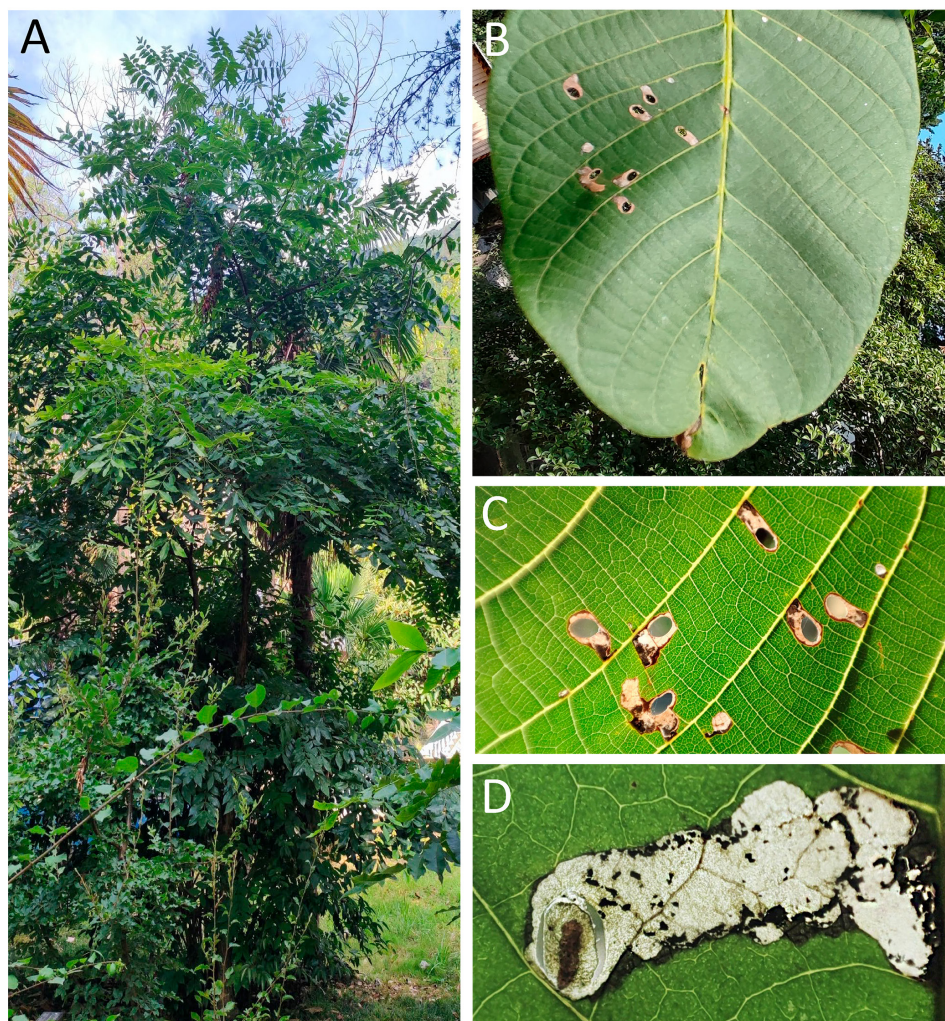


Figure 2. The tree of *Carya illinoensis* (A), and the leaf of *Juglans regia* with the mines *Coptodisca lucifluella* (B–C) and the mine with larva cutting out the shield (D), Sochi, July 2024. Photo N. Kirichenko and N. Karpun.

Compiling the checklist of parasitoids

The checklist of *C. lucifluella*'s parasitoids was compiled based on the data provided for North America (native range), Mexico (unclear range type), Europe, Southern Russia and Abkhazia (invaded range). In the checklist, following information is given: species of parasitoids, type of parasitism, host range, distribution, regions

where certain parasitoid was reared from *C. lucifluella*. Altogether these data were extracted from various literature sources (Bouček and Askew 1968; Turnbow and Franklin 1981; Hansson 1985, 1987, 1990, 1994, 1995; Heyerdahl and Dutcher 1985; Graham 1987, 1991; Bouček 1988; Gibson 1995; Zuparko 1995; Trjapitzin 2009; Gebiola et al. 2012; Gualtieri et al. 2015; Ávila-Rodríguez et al. 2015; Gibson and Fusu 2016; Yu et al. 2016; Belokobylskij et al. 2019; Perry and Heraty 2021; UCD Community 2025).

Photographing and mapping

Photographs of adult parasitoids were taken with a Canon EOS 70D digital camera mounted on an Olympus SZX10 microscope. Wings and antennae slide-mounts in Canada balsam were photographed with a ZEISS SteREO Discovery.V12 modular stereo microscope and an AxioCam MRC3 camera. Sampled localities in Southern Russia and Abkhazia were mapped using ESRI ArcGIS Pro 3.1 software (ESRI 2024).

Results

1. Parasitoids and parasitism of *C. lucifluella* in Southern Russia and Abkhazia

Overall, 28 parasitoid specimens were obtained from *C. lucifluella*'s mines and shields, i.e., 16 from Southern Russia and 12 from Abkhazia. They were all identified to 7 species of hymenopteran parasitoids: *Pnigalio soemius* (Walker), *Cirrospilus variegatus* (Masi), *C. viticola* (Rondani), *Chrysocharis pentheus* (Walker), *Closterocerus* sp., *Minotetrastichus frontalis* (Nees) (Eulophidae) and presumably *Eupelmus kiefferi* De Stefani (Eupelmidae).

The mentioned above parasitoids were grown from 7 out of 13 studied localities, i.e., from 3 localities in Southern Russia and from 4 localities in Abkhazia (Fig. 3).

They all were reared from *C. lucifluella* leaf mines and shields found on five host plants: *Pterocarya fraxinifolia*, *Juglans regia*, *J. nigra*, *Carya illinoensis*, *C. tomentosa*. In Sochi, the highest parasitism (13%) was observed in the locality No. 4 (park of "Zolotoy Kolos" sanatorium) on *C. tomentosa*, with the predominance of *Minotetrastichus frontalis*, the mortality from which reached 11 out of 13% (Fig. 3). In other two localities in Sochi, the parasitism varied from 3.5 to 5%. In Abkhazia, the highest parasitism (31%) was documented in the locality No. 5 (Gagra, park "Prince of Oldenburg"), with the noticeable contribution to the host mortality from the parasitic wasps *Chrysocharis pentheus* (12 out of 31%), *Cirrospilus viticola* (8%), and *C. variegatus* (8%) (Fig. 3).

Below, the species essays of parasitoids recorded on *C. lucifluella* in Southern Russia and Abkhazia are provided.

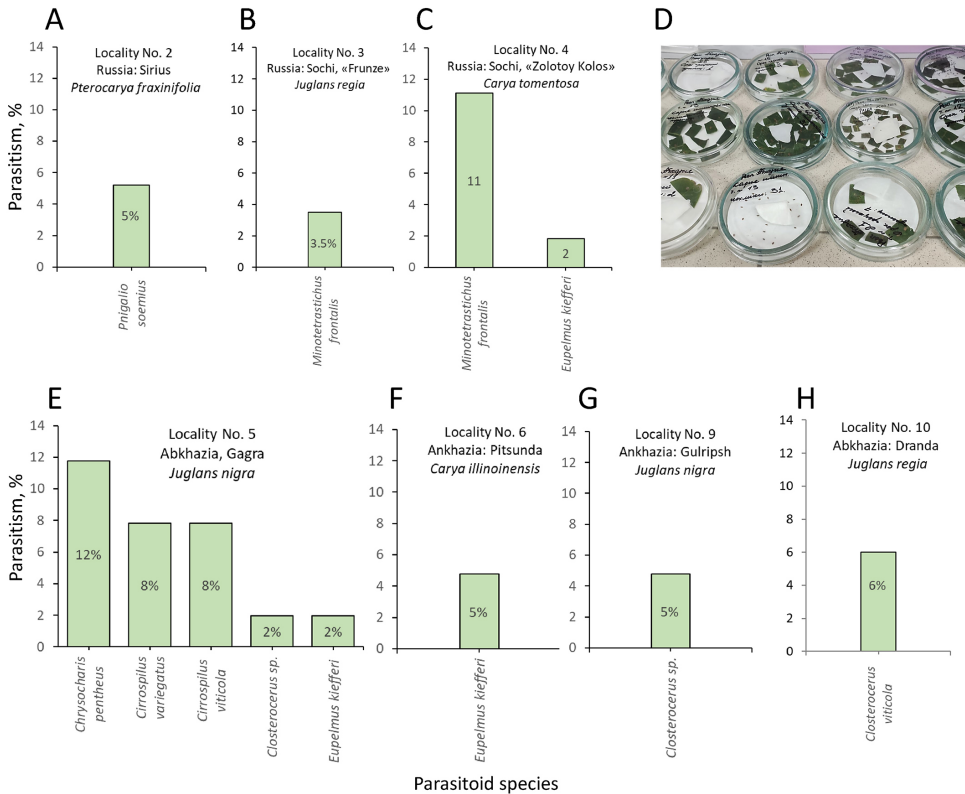


Figure 3. Parasitism of *Coptodisca lucifluella* in Southern Russia and Abkhazia in 2024. The localities, from where parasitoids emerged from larvae and pupae of *C. lucifluella* in Russia: (A–C) – the locality No. 2 – Sirius, the park “Yuzhnye Kultury”; 3 – Sochi, the park of M.V. Frunze sanatorium; No. 4 – Sochi, the park of “Zolotoy Kolos” sanatorium, and in Abkhazia: (E–H) – No. 5 – Gagra, the park “Prince of Oldenburg”; No. 6 – Pitsunda; No. 9 – Gulripsh; No. 10 – Dranda vil. (the locality numbers correspond to those given in Fig. 1); (D) – indoor rearing of parasitoids.

Order Hymenoptera Linnaeus, 1758

Superfamily Chalcidoidea Latreille, 1817

Family Eulophidae Westwood, 1829

Subfamily Eulophinae Westwood, 1829

***Phigalia soemius* (Walker, 1839)**

Fig. 4A

Material examined. 2 females Russia: Sochi, Adler, park “Yuzhnye Kultury”, *Carya illinoensis*, 25.VI.2024 (mines coll.), 14.VII.2024 (parasitoid em.), N. Karpun., E. Zhuravleva, N. Kirichenko coll.

Distribution. Russia: Leningrad, Moscow, Vladimir, Voronezh and Ulyanovsk Provinces, Krasnodar and Stavropol Territories, Crimea, Novosibirsk, Amur Province, Khabarovsk and Primorsky Territories. Europe, Georgia, Turkey, Syria, Iraq, Israel, Iran, Pakistan, China, Korean Peninsula, southeast Asia (Belokobylskij et al. 2019; Yefremova et al. 2024; UCD Community 2025).

Hosts. Ectoparasitoid on leafminers of Lepidoptera (Gracillariidae, Lyonetiidae, Nepticulidae, Yponomeutidae, Heliozelidae), Coleoptera (Curculionidae), and Diptera (Agromyzidae, Cecidomyiidae) (Bouček and Askew 1968; Gualtieri et al. 2015; UCD Community 2025). According to Bernardo et al. (2006) this eulophid develops as idiobiont, synovigenic, solitary, biparental parasitoid that practices host-feeding and host-stinging.

Remark. First record as a parasitoid of *C. lucifluella* (present study).

Comments. *P. soemius* is a highly variable species and currently considered as two cryptic species that are morphologically indistinguishable (e.g. Bernardo et al. 2008; Gebiola et al. 2012). The reared specimens have completely pale-yellow legs, including the hind coxae, except for the fore coxa and fore femur, which are brownish dorsally with pale apices.

***Cirrospilus variegatus* (Masi, 1907)**

Fig. 5

Cirrospilus (*Zagrammosoma*) *variegatus* (Masi): Bouček 1959: 173, 185; Bouček and Askew 1968: 39.

Cirrospilus variegatus (Masi): Bouček 1988: 616; Kurashev, 1991: 27; Zhu et al. 2002: 42.

Material examined. 4 females, Abkhazia: Gagra, park “Prince of Oldenburg”, *Juglans nigra*, 15.VII.2024 (mines coll.), 25.VII.2024 (parasitoid em.), (N 27), N. Karpun, E. Zhuravleva, N. Kirichenko coll.

Distribution. Russia: Ulyanovsk Province, Krasnodar, Stavropol Territories, Dagestan, Crimea. Europe, North Africa, Abkhazia (first record), Armenia, Azerbaijan, Turkey, Yemen, United Arab Emirates, Yemen, Iran, Pakistan, Turkmenistan, Uzbekistan, China, India, Southeast Asia, Afrotropics, South America, Australia, New Zealand (Belokobylskij et al. 2019; UCD Community 2025).

Hosts. Ectoparasitoid on leafmining larvae of Lepidoptera (Gracillariidae, Lyonetiidae, Nepticulidae, Heliozelidae, Leucopteridae); on *Bactrocera oleae* (Rossi, 1790) and *Liriomyza trifolii* (Burgess, 1880) (Bouček and Askew 1968) and *Liriomyza saliva* Blanchard, 1938 (Diptera) (Hesami et al. 2006).

Remark. First record as a parasitoid of *C. lucifluella* (present study).

Comments. The Abkhazian specimens are quite similar to the original description by Masi (1907), but have a slightly shorter clava (1.88 times as long as broad) (vs. 2.00) and scape (4.50 times as long as broad) (Fig. 5D, E) (vs. 5.40), and fore wing with a broad, bare region behind the apex of parastigma (Fig. 5F) (vs. forewing

densely pubescent, except the speculum). In addition, the colour of the body of the recently collected specimens, lemon yellow with dark brown stripes, compared to the dark yellowish gray (head), yellow-green (prothorax and mesothorax) and pale green (metathorax and gaster) with brown stripes in Masi's description, and the orange yellow colour with brown stripes in the specimens from Moldova [5 females, Kishinev, ex. *Nepticula* sp., on *Pyrus*, 5.VII.1959, V.I. Talitskiy coll, det. Z. Bouček (ZISP) (Fig. 5C)].

***Cirrospilus viticola* (Rondani, 1877)**

Fig. 4E

Cirrospilus subviolaceus Thomson, 1878. Synonymized by Bouček 1974: 278.

Material examined. 3 female. Abkhazia: Gagra, park “Prince of Oldenburg”, *Juglans nigra*, 15.VII.2024 (mines coll.), 25.VII.2024 (parasitoid em.), (N 27) N. Karpun, E. Zhuravleva, N. Kirichenko; 1 female *Juglans regia* (№ 21), 15.VII.2024 (mines coll.), 06.VIII.2024 (parasitoid em.) N. Karpun, E. Zhuravleva, N. Kirichenko coll.

Distribution. Russia: Leningrad, Ulyanovsk, Volgograd Provinces, Krasnodar, Stavropol Territories, Crimea, Primorsky Territory, Kuril Islands. Europe, Abkhazia (first record), Azerbaijan, Turkey, Iran, Turkmenistan (Belokobylskij et al. 2019; UCD Community 2025).

Hosts. Ectoparasitoid on leafminers of *Rhynchaenus* spp. (Coleoptera: Curculionidae and Lepidoptera (Gracillariidae, Nepticulidae, Tischeriidae, Heliozelidae and Leucopteridae); secondary parasitoid of *Apanteles circumscriptus* Nees (Hymenoptera: Braconidae) on *Lithocolletis* (Gelechiidae) (Bouček and Askew 1968; UCD Community 2025).

Remark. First record as a parasitoid of *C. lucifluella* (present study).

Subfamily Entedoninae (Foerster, 1856)

***Chrysocharis pentheus* (Walker, 1839)**

Fig. 4D

Material examined. 1 female. Russia: Sochi, Khosta District, park of M.V. Frunze sanatorium, *Juglans regia*, 24.VI.2024 (mines coll.), 1.VII.2024 (parasitoid em.), N. Karpun, E. Zhuravleva, N. Kirichenko coll. 1 female, Abkhazia: Gagra, park “Prince of Oldenburg”, *Juglans nigra* (N 27), 15.VII.2024 (mines coll.), 25.VII.2024 (parasitoid em.), N. Karpun, E. Zhuravleva, N. Kirichenko coll.; 2 females, same label, 15.VII.2024 (mines coll.), 31.VII.2024 (parasitoid em.); 1 female, same label, 15.VII.2024 (mines coll.), 07.VIII.2024 (parasitoid em.)

Distribution. Russia: Leningrad, Ulyanovsk Provinces, Krasnodar and Stavropol Territories, Irkutsk, Amur Provinces, Primorsky Territory. Europe, Abkhazia (first record), Turkey, China, Korean Peninsula, Japan, North America, Malaysia (Belokobylskij et al. 2019; UCD Community 2025).

Hosts. Endoparasitoid on leafminers of Diptera (Agromyzidae), Lepidoptera (Nepticulidae, Lyonetiidae, Gracilariidae, Elachistidae, Heliozelidae, Bucculatricidae, Coleophoridae), and Coleoptera (Curculionidae, Chrysomelidae) (Hansson 1985, 1987; UCD Community 2025).

Remark. First record as a parasitoid of *C. lucifluella* (present study).

Closterocerus sp.

Fig. 4C

Material examined. 1 female. Abkhazia: Gagra, park “Prince of Oldenburg”, *Juglans nigra* 10.VII.2024 (mines coll.), 20.VII.2024 (parasitoid em.) (N 15), N. Karpun, E. Zhuravleva, N. Kirichenko coll.

Hosts. A wide range of hosts, mainly leaf-mining and gall-forming insects and eggs of Symphyta (Argidae, Diprionidae) (as per Hansson 1994).

Distribution. All zoogeographical regions (Hansson 1994).

Comments. This specimen is similar in general appearance to *Closterocerus trifasciatus* Westwood, 1833, but differs in having an antenna with a not compressed scape (vs. strongly compressed), the pronotal collar without a distinct carina (vs. with a carina, sometimes weak), the forewing not fuscous (vs. usually with 1–3 dark cross bands or with a fuscous spot below the stigmal vein), and the second segment of the clava pale yellowish (vs. antenna completely dark). Presumably, the female specimen from Abkhazia could represent a new species to science. Further sampling would be needed to clarify the species status.

Subfamily Tetrastichinae Förster, 1856

Minotetrastichus frontalis (Nees, 1834)

Fig. 4B

Material examined. 6 females, 5 males. Russia: Sochi, Khosta District, park of “Zolotoy Kolos” sanatorium, *Carya tomentosa*, 27.VII.2024 (mines coll.), 4.VII.2024 (parasitoid em.); 1 female, park of M.V. Frunze sanatorium, *Juglans regia*, 9.VII.2024, N. Karpun, E. Zhuravleva, E. Shoshina, N. Kirichenko coll.

Distribution. Russia: Nizhny Novgorod, Moscow and Ulyanovsk Provinces, Stavropol and Krasnodar Territories, Crimea, Ural, Altai Territories, Novosibirsk, Amur Provinces, Khabarovsk, Primorsky Territories. Europe, Georgia, Turkey, Pakistan, United Arab Emirates, North America (Belokobylskij et al. 2019; UCD Community 2025).

Hosts. Gregarious ectoparasitoid on leafminers of Lepidoptera (Gracillariidae, Coleophoridae), Coleoptera (Curculionidae), and Hymenoptera (Cynipidae, Tenthredinidae); sometimes a facultative secondary or tertiary parasitoid of Braconidae and Chalcidoidea (Hymenoptera) (Graham 1987; UCD Community 2025).

Remark. First record as a parasitoid of *C. lucifluella* (present study).

Family Eupelmidae Walker, 1833

Eupelmus kiefferi De Stefani, 1898

Fig. 4F

Material examined. 1 male, Russia: Sochi, Khosta District, park of “Zolotoy Kolos” sanatorium, *Carya tomentosa*, 17.VII.2024 (mines coll.), 30.VII.2024 (parasitoid em.) (No. 2) N. Karpun, E. Zhuravleva, E. Shoshina, N. Kirichenko coll.; 1 male, Abkhazia, Pitsunda, *Carya illinoensis*, 10.VII.2024 (mines coll.), 21.VII.2024 (parasitoid em.) (No. 13), N. Karpun, E. Zhuravleva, N. Kirichenko coll.

Distribution. Russia: Moscow and Rostov Provinces, Krasnodar Territory, Crimea, Primorsky Territory. Europe, North Africa, Abkhazia (first record), Turkey, Syria, Jordan, Lebanon, Saudi Arabia, Kazakhstan, China, Korean Peninsula, Japan (Gibson and Fusu 2016; Belokobylskij et al. 2019).

Hosts. Primary parasitoid of insects from the families Curculionidae (Coleoptera), Cecidomyiidae (Diptera), Aphididae and Coccidae (Hemiptera), Cynipidae, Diprionidae and Tenthredinidae (Hymenoptera), Gelechiidae, Gracillariidae, Lasiocampidae and Tortricidae (Lepidoptera) (Gibson and Fusu 2016).

Remark. First record as a parasitoid of *C. lucifluella* (present study).

Comments. The specimens collected in Sochi and Abkhazia correspond in most characteristics to the description by Gibson and Fusu (2016), differ only in the colour of the legs, the knees are dark and the tarsomeres of the meso- and metatarsus are white except for the two apical tarsomeres dark brown.

II. Check list of parasitoids associated with *C. lucifluella*

An exhaustive checklist of parasitoids associated with *C. lucifluella* in its modern range accounts 32 species (Table 1). In North America (native range), the hymenopterian parasitoids complex includes *Mirax minuta* Ashmead, 1893 (Braconidae), *Parablastothrix* sp. (Encyrtidae), *Eupelmus* sp. (Eupelmidae), *Burkseus vittatus* (Walker, 1838), *Cirrospilus pictus* (Nees, 1834), *Cirrospilus* sp.1 and *Cirrospilus* sp.2 (as *Winnemana* sp.1 and *Winnemana* sp.2), *Pnigalio longulus* (Zetterstedt, 1838), *P. minio* (Walker, 1847), *Zagrammosoma americana* Girault, 1916, *Z. multilineatus* (Ashmead, 1888), *Chrysocharis laomedon* (Walker, 1839), *Ch. nitetis* (Walker, 1839), *Chrysonotomyia* sp., *Closterocerus trifasciatus* Westwood, 1833, two unknown genera from subfamily Tetrastichinae and one unknown genus from subfamily Entedoninae (Eulophidae) (Heyerdahl and Dutcher 1985).

In Mexico, where *C. lucifluella* was first reported in 2012 and where its origin remains unclear, the hymenopterian parasitoids from eight genera *Protopanteles* (Ichneumonidea: Braconidae), *Apostrocetus*, *Elachertus*, *Closterocerus*, *Chrysocharis*, *Pnigalio*, *Quadrastichus*, and *Baryscapus* (Chalcidoidea: Eulophidae) were recorded (Ávila-Rodríguez et al. 2015).

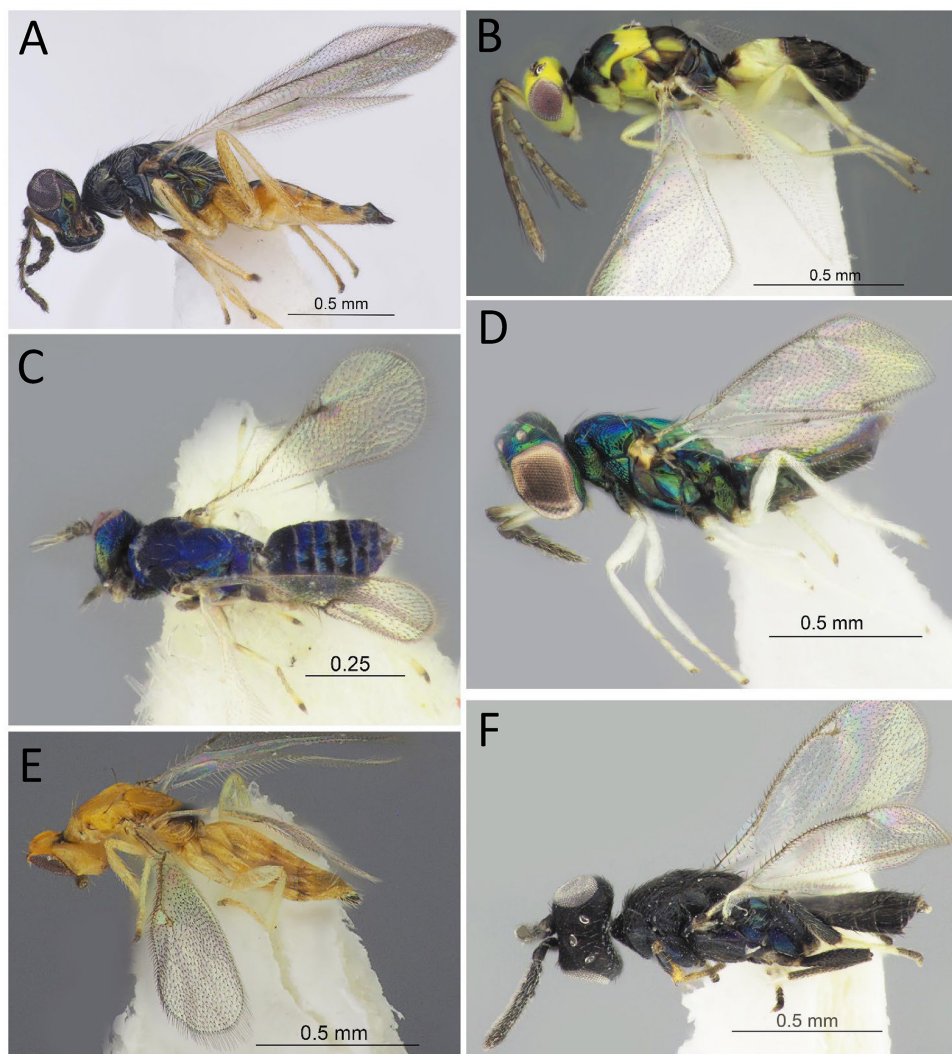


Figure 4. Parasitoids from the superfamily Chalcidoidea, lateral view: (A) *Pnigalio soemius*; (B) *Minotetrastichus frontalis*; (C) *Closterocerus* sp.; (D) *Chrysocharis pentheus*; (E) *Cirrospilus viticola* (Eulophidae); (F) *Eupelmus kiefferi* (Eupelmidae). (A, C–E) females; (B, F) males. Photos: O.V. Kosheleva.

In Europe (invaded range), *Chrysocharis* spp., *Neochrysocharis* sp. and *Pnigalio soemius* were documented (Gualtieri et al. 2015). Same authors also reared the North American *Cirrospilus coptodiscae* (Girault, 1916), which seems to host-tracked *C. lucifluella*. Furthermore, *Cirrospilus* sp. (which was erroneously mentioned as *Closterocerus*) was reared from *Coptodisca juglandiella* (Chambers, 1874) in Hungary (Takács et al. 2020).

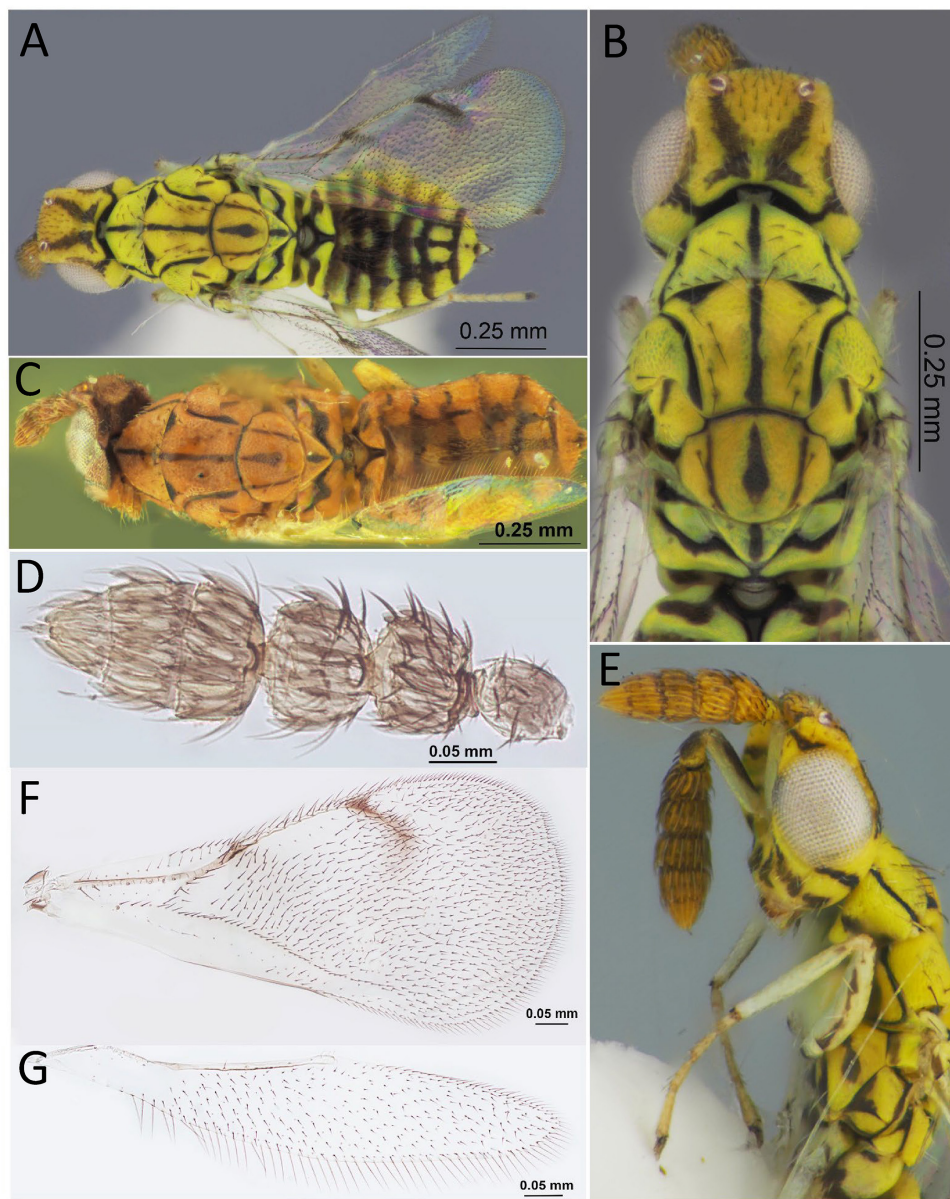


Figure 5. Parasitoid *Cirrospilus variegatus* (Masi), female: (A, C) – dorsal habitus; (B, E) – head with mesosoma (B – dorsal, E – lateral); (D) – pedicel with flagellum; (F) – forewing; (G) – hind wing; (A, B, D–G) – Abkhazia; (C) – Moldova (Kishinev). Photos: O. Kosheleva.

Our observations expanded the checklist of *C. lucifluella* parasitoids by seven species: *Pnigalio soemius*, *Cirrospilus variegatus*, *C. viticola*, *Chrysocharis pentheus*, *Closterocerus* sp., *Minotetrastichus frontalis* (Eulophidae), and presumable *Eupelmus kiefferi* (Eupelmidae) (Table 1).

Table 1. The checklist of hymenopteran parasitoids associated with *Coptodisca lucifluella**

No	Species of parasitoids	Type of parasitism	Host range of parasitoids	Distribution	Regions where parasitoid was recorded on <i>C. lucifluella</i>
BRACONIDAE: Miracinae					
1	<i>Mirax minuta</i> Ashmead, 1893	Primary, solitary endoparasitoid of larvae (19)	<i>C. lucifluella</i> (Lepidoptera: Heliozelidae), <i>Cameraria caryaeifoliella</i> (Clemens) (Gracillariidae) (19)	Nearctic realm (19)	USA (Georgia) (8)
Microgastrinae					
2	<i>Protapanteles</i> sp.	Primary endoparasitoid of larvae (19)	Lepidoptera (19)	All zoogeographical regions (19)	Mexico (Comarca Lagunera) (18)
ENCYRTIDAE: Encyrtinae					
3	<i>Parablastothrix</i> sp.	Primary, solitary endoparasitoid of larvae (8, 12)	Lepidoptera: Nepticulidae, Gracillariidae, Lyonetiidae, Heliozelidae, and Bucculatricidae (13)	Holarctic region (13)	USA (Georgia) (8)
EULOPHIDAE: Eulophinae					
4	<i>Burkseus vittatus</i> (Walker, 1838) (= <i>vittatus</i>)	Primary, occasionally secondary, solitary or gregarious ectoparasitoid of leaf-mining larvae, occasionally eggs (1)	Lepidoptera, Diptera, and Hymenoptera; parasitoid hosts Braconidae, Ichneumonidae and Eulophidae (Hymenoptera) (22)	Holarctic region (22)	USA (Georgia) (8)
5	<i>Cirrospilus coptodiscae</i> (Girault, 1916)	Primary or secondary, ectoparasitoid of larvae (22)	<i>Coptodisca splendoriferella</i> (Clemens) (Lepidoptera: Heliozelidae) (22)	Nearctic realm (22)	Italy (17)
6	<i>Cirrospilus pictus</i> (Nees, 1834)	Primary or secondary, solitary or gregarious ectoparasitoid of larvae, rarely pupae (1)	Lepidoptera, Coleoptera and Hymenoptera; parasitoid hosts Braconidae, Eulophidae and Ichneumonidae (Hymenoptera) (22)	Holarctic region (22)	USA (Georgia) (8)
7	<i>Cirrospilus variegatus</i> (Masi, 1907)	Primary ectoparasitoid of larvae (1)	Lepidoptera and Diptera (22)	Palearctic, Oriental, Australian and Neotropical regions (22)	Abkhazia (present study)

No	Species of parasitoids	Type of parasitism	Host range of parasitoids	Distribution	Regions where parasitoid was recorded on <i>C. lucifluella</i>
8	<i>Cirrospilus viticola</i> (Rondani, 1877)	Primary, rarely secondary ectoparasitoid of larvae (1)	Coleoptera, Lepidoptera; parasitoid hosts <i>Apanteles circumscriptus</i> Nees (Hymenoptera: Braconidae) (22)	Palearctic realm (22)	Abkhazia (present study)
9	<i>Cirrospilus</i> sp.	Primary or secondary ectoparasitoid of larvae, some are egg-parasites (1, 5)	<i>Phyllonorycter</i> spp. (Lepidoptera: Gracillariidae) (1)	All zoogeographical regions (5)	USA (Georgia) (8), Mexico (Comarca Lagunera) (18)
10	<i>Elachertus</i> sp.	Ectoparasitoid of larvae (1)	Lepidoptera (1)	All zoogeographical regions (1)	Mexico (Comarca Lagunera) (18)
11	<i>Pnigalio longulus</i> (Zetterstedt, 1838)	Primary ectoparasitoid of larvae (1)	Lepidoptera, Coleoptera, Diptera, Hymenoptera; parasitoid hosts Braconidae and Eulophidae (20)	Holarctic region (22)	USA (Georgia) (8)
12	<i>Pnigalio minio</i> (Walker, 1847)	Primary parasitoid of larvae (22)	Lepidoptera, Coleoptera, Diptera, Hymenoptera (22)	Nearctic realm (22)	USA (Georgia) (8)
13	<i>Pnigalio soemius</i> (Walker, 1839)	Primary solitary ectoparasitoid of larvae (1)	Lepidoptera, Coleoptera, Diptera, Hymenoptera (18)	Palearctic realm and Oriental region (20)	Italy (17) Abkhazia (present study)
14	<i>Pnigalio</i> sp.	Primary or secondary ectoparasitoid of larvae (1)	Lepidoptera, Coleoptera (Curculionidae), Hymenoptera (Tenthredinidae), Diptera (Agromyzidae, Cecidomyiidae); parasitoid hosts Braconidae and Eulophidae (1)	All zoogeographical regions (1)	Mexico (Comarca Lagunera) (18)
15	<i>Zagrammosoma americana</i> Girault, 1916	Primary parasitoid of larvae (8, 22)	Lepidoptera, Coleoptera, Diptera (9, 21, 22). Doubtfully Hemiptera (21)	Nearctic realm (22)	USA (Georgia) (8)
16	<i>Zagrammosoma multilineatus</i> (Ashmead, 1888)	Primary parasitoid of larvae (8, 22)	Lepidoptera, Coleoptera, Diptera, Hymenoptera (21)	Nearctic realm and Neotropical region (22)	USA (Georgia) (8)
			Entedoninae		
17	<i>Chrysocharis laomedon</i> (Walker, 1839)	Primary, rarely secondary solitary endoparasitoid of larvae (1, 2)	<i>Phyllonorycter</i> spp. (Lepidoptera: Gracillariidae) (3)	Holarctic region (3)	USA (Georgia) (8)

No	Species of parasitoids	Type of parasitism	Host range of parasitoids	Distribution	Regions where parasitoid was recorded on <i>C. lucifluella</i>
18	<i>Chrysocharis nitetis</i> (Walker, 1839)	Primary, solitary endoparasitoid of larvae (1, 2)	Hymenoptera (Tenthredinidae), Coleoptera (Curculionidae), Lepidoptera (1, 3)	Holarctic region (3)	USA (Georgia) (8)
19	<i>Chrysocharis pentheus</i> (Walker, 1839)	Primary endoparasitoid of larvae (1, 3)	Diptera (Agromyzidae), Lepidoptera (Nepticulidae), Coleoptera (Curculionidae) (4, 22)	Holarctic and Oriental regions (22)	Abkhazia (present study)
20	<i>Chrysocharis</i> sp.	Primary, rarely secondary endoparasitoid of larvae and pupae (1)	Lepidoptera, Coleoptera (Curculionidae), Diptera, Hymenoptera; parasitoid hosts Braconidae and Eulophidae, Encyrtidae, and Eulophidae (1)	Holarctic, Neotropical, Ethiopian and Oriental regions (2)	Mexico (Comarca Lagunera) (18), Abkhazia (present study)
21	<i>Chrysonotomyia</i> sp.	Primary parasitoids of eggs or young larvae (2)	Diptera, Lepidoptera (2)	All zoogeographical regions (2)	USA (Georgia) (8)
22	<i>Closterocerus trifasciatus</i> Westwood, 183	Primary, rarely secondary solitary or gregarious endoparasitoid of larvae (1, 6)	Lepidoptera, Coleoptera, Diptera, Hymenoptera (6)	Holarctic region (6)	USA (Georgia) (8)
23	<i>Closterocerus</i> sp.	Primary, rarely secondary solitary or gregarious koinobiont endoparasitoids in eggs or larvae (1, 6)	Lepidoptera, Coleoptera, Diptera, Hymenoptera (1)	All zoogeographical regions (6)	Mexico (Comarca Lagunera) (18)
24	<i>Closterocerus</i> sp.1	Primary, rarely secondary solitary or gregarious koinobiont endoparasitoids in eggs or larvae (1, 6)	Lepidoptera, Coleoptera, Diptera, Hymenoptera (1)	All zoogeographical regions (6)	Abkhazia (present study)
25	<i>Neochrysocharis</i> sp.	Primary, rarely secondary, solitary or gregarious endoparasitoids in immature stages (5)	Diptera, Lepidoptera, Coleoptera (Chrysomelidae), Hymenoptera (Diprionidae, Tenthredinidae); parasitoid hosts Ichneumonoidea (5)	Holarctic, Ethiopian, Oriental, and Australian regions (5)	Italy (17)

No	Species of parasitoids	Type of parasitism	Host range of parasitoids	Distribution	Regions where parasitoid was recorded on <i>C. lucifluella</i>
Tetrastichinae					
26	<i>Minotetrastichus frontalis</i> (Nees, 1834)	Primary, secondary or tertiary gregarious ectoparasitoid on leafmining or gall-inducing insects (10)	Lepidoptera, Coleoptera, Hymenoptera (10)	Holarctic region (10)	Abkhazia (present study)
27	Genus 1	Primary parasitoids of late instar larvae and cocoons (8)	<i>C. lucifluella</i> (Lepidoptera: Heliozelidae) (8)	USA (Georgia) (8)	USA (Georgia) (8)
28	Genus 2	Primary parasitoids of larvae (8)	<i>C. lucifluella</i> (Lepidoptera: Heliozelidae) (8)	USA (Georgia) (8)	USA (Georgia) (8)
29	<i>Aprostocetus</i> sp.	Primary or secondary solitary or gregarious ecto- or endoparasitoids of larvae (2, 10)	Diptera (Cecidomyiidae), Hymenoptera (Cynipoidea), occasionally Coleoptera, Coccoidea and Lepidoptera; rarely Aranei (Araneidae), Acarina (Eriophyidae) (10)	All zoogeographical regions (10)	Mexico (Comarca Lagunera) (18)
30	<i>Baryscapus</i> sp.	Primary, sometimes secondary, gregarious, occasionally solitary endoparasitoids of larvae or pupae (11)	Lepidoptera, some Hymenoptera, Coleoptera, Diptera (Tephritidae), Neuroptera and Coccoidea; parasitoid hosts Ichneumonidae, Braconidae, Chalcidoidea (11)	All zoogeographical regions (11)	Mexico (Comarca Lagunera) (18)
31	<i>Quadrastichus</i> sp.	Primary endoparasitoids of larvae or pupae, rarely eggs (11)	Diptera (Cecidomyiidae), Coleoptera (Curculionidae, Buprestidae); and Acarina (Eriophyidae) (11)	All zoogeographical regions (11)	Mexico (Comarca Lagunera) (18)
EUELMIDAE: Eupelminae					
32	<i>Eupelmus kiefferi</i> De Stefani, 1898 (preliminary identification, see the species essay)	<i>Eupelmus</i> spp. are primarily idiobiont ectoparasitoids or predators of the larvae and prepupae (14)	Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera (15)	Palearctic realm (15)	Abkhazia, Russia: Krasnodar Territory (present study)

Note: *The references to the literature sources from where biological and distribution data were retrieved are indicated in the table by following numbers: 1 (Bouček and Askew 1968); 2 (Bouček 1988); 3 (Hans-

son 1985); 4 (Hansson 1987); 5 (Hansson 1990); 6 (Hansson 1994); 7 (Hansson 1995); 8 (Heyerdahl and Dutcher 1985); 9 (Turnbow and Franklin 1981); 10 (Graham 1987); 11 (Graham 1991); 12 (Zuparko 1995); 13 (Trjapitzin 2009); 14 (Gibson 1995); 15 (Gibson and Fusu 2016); 16 (Gebiola et al. 2012); 17 (Gualtieri et al. 2015); 18 (Ávila-Rodríguez et al. 2015); 19 (Yu et al. 2016); 20 (Belokobylskij et al. 2019); 21 (Perry and Heraty 2021); 22 (UCD Community 2025).

Discussion

Our study provided first data about parasitoid complex of *Coptodisca lucifluella* in Southern Russia and Abkhazia, the invasive leafminer that was recorded in these regions in 2023–2024 already at noticeable densities. Suggestively, this species arrived to Russia not directly from North America, but rather from early-invaded European countries (Kirichenko et al. 2024).

The key finding of our present study is that *C. lucifluella* appears to have invaded Southern Russia and Abkhazia without its specific aborigine parasitoids, i.e., those originating from its native range in North America. Whether or not its aborigine parasitoids came with *C. lucifluella* to the European countries, where the moth was recorded before its revelation in Russia and Abkhazia, remains unclear. The only exception is *Cirrospilus coptodiscae* (Girault, 1916), a parasitoid native to North America, which was reared from *C. lucifluella* in Europe and is believed to follow its host (Gualtieri et al. 2015).

In the compiled checklist of *C. lucifluella*'s parasitoids, there are two species, *Minotetrastichus frontalis* and *Chrysocharis pentheus*, which are shared between invaded and native ranges of the moth (Belokobylskij et al. 2019). However, we doubt that they arrived to Southern Russia and Abkhazia with this invasive moth, as they are widely distributed in these regions and are common parasitoids of a variety of leafmining insects (not only Lepidoptera, but other Coleoptera, Hymenoptera, and Diptera) (Belokobylskij et al. 2019; UCD Community 2025). Furthermore, they are not known as parasitoids of *C. lucifluella* in its native range (Table 1). We could not find any information about such trophic associations in North America despite of exhaustive literature search, except that *M. frontalis* was documented to develop on *Coptodisca splendoriferella* (Clemens) in North America (LaSalle, 1994).

Thus, the fact that in Southern Russia and Abkhazia we did not reveal any parasitoids, which are associated with *C. lucifluella* in North America, suggests that the moth has escaped its native enemies during invasion to these regions. Such examples are not rare for invasive insects, including leafminers (Klug et al. 2008; Kirichenko et al. 2019; Kosheleva et al. 2022).

Indeed, all parasitoids documented in our study are native to the invaded Southern Russia and Abkhazia. This supports the hypothesis, which we tested in our study that local parasitoids may have begun shifting to this new host. This is also in agreement with our early assumption that the moth was present in Southern Russia and Abkhazia for quite some time (at least for a decade) before its revela-

tion in 2023–2024 (Kirichenko et al. 2024), as native parasitoids commonly begin exploiting the new host species with a delay, i.e. some years after its establishment and spread in new regions.

After the invasive species establishes in a new environment, parasitoid populations may start utilizing the novel host (Vercher et al. 2005; Kirichenko et al. 2019). If the invader lacks resistance mechanisms, parasitoids may soon shift to it, incorporating the invasive species into their trophic net (Vercher et al. 2005; Kirichenko et al. 2019). In our present study we showed that, in fact, the local parasitoids can lead lead mortality up to 1/3 of *C. lucifluella*'s population in some localities in Abkhazia, which corresponds to our preliminary observations in 2023 (Kirichenko et al. 2024). In 2024, four parasitic wasps, i.e., *Chrysocharis pentheus*, *Minotetrastichus frontalis*, *Cirrospilus viticola*, and *C. variegatus* were notable contributors to the mortality of *C. lucifluella* in Southern Russia and Abkhazia.

Further studies covering larger invaded territory (i.e., invaded countries in Europe) and additional study in Southern Russia and Abkhazia would be needed to gain better knowledge about the assemblage of native parasitoids exploiting the new host, *C. lucifluella*, and their role in controlling its populations.

Conclusions

Our study provides valuable insights into the formation of novel trophic associations between the alien leafminer and native parasitoids in the invaded area. Furthermore, it highlights that while invasive insects may initially benefit from enemy release, some of them eventually become targets to native parasitoids. These findings underscore the importance of monitoring such ecological shifts to anticipate the future trajectory of invasive species and control of their populations.

Acknowledgements

We thank Elena Shoshina (Federal Research Centre the Subtropical Scientific Centre of the Russian Academy of Sciences, Sochi) for assisting in field collection and laboratory rearing, Irina Mikhailova (Sukachev Institute of Forest SB RAS, Krasnoyarsk) for help with mapping. The study was performed with the support of the Russian Science Foundation (RSF), grant No. 22-16-00075-P (parasitoids rearing and identification) and partially as the implementation of the state task of FRC SSC of RAS FGRW-2025-0002, state registration number 125021202045-8 (phytosanitary monitoring of plantings and field sampling).

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