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RESEARCH ARTICLE

# A review of the species of the subgenus *Callophrys* (*Ahlbergia*) (Lepidoptera: Lycaenidae) of Russia

# Ревизия видов подрода *Callophrys* (*Ahlbergia*) (Lepidoptera: Lycaenidae) России

A.V. Krupitsky, N.A. Shapoval & G.N. Shapoval

А.В. Крупицкий, Н.А. Шаповал, Г.Н. Шаповал

*Anatoly V. Krupitsky, Department of Entomology, Faculty of Biology, Lomonosov Moscow State University, 1–12 Leninskie Gory 119192, Moscow, Russia; A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninskiy Ave. 119071, Moscow, Russia. E-mail: nephrurus@yandex.ru*

*Nazar A. Shapoval, Department of Karyosystematics, Zoological Institute, Russian Academy of Sciences, 1 Universitetskaya Emb., St Petersburg 199034, Russia. E-mail: nazaret@bk.ru*

*Galina N. Shapoval, Institute of Biology and Biotechnology, Altai State University, 61 Lenina Ave., Barnaul 656049, Russia. E-mail: galinakuftina@mail.ru*

**Abstract.** The species of the subgenus *Ahlbergia* Bryk, 1947 of the genus *Callophrys* Billberg, 1820 of Russia are revised using the external characters of adults and the characters of the male and female genitalia combined with the phylogenetic analysis of the COI gene. Our analysis revealed three species present in Russia: *Callophrys* (*Ahlbergia*) *confusa* (Huang, Chen et Li, 2006), **status promotus**, *C.* (*A.*) *korea* (Johnson, 1992), **status promotus**, and *C.* (*A.*) *frivaldszkyi* (Lederer, 1855). The name *C.* (*A.*) *inopinata* (M.M. Omelko, 1995), **syn. nov.** is placed in synonymy with *C.* (*A.*) *frivaldszkyi*. An identification key for the species of the subgenus *Ahlbergia* of Russia is provided.

**Резюме.** Изучены виды подрода *Ahlbergia* Bryk, 1947 рода *Callophrys* Billberg, 1820 России. Анализ внешних признаков и признаков морфологии гениталий самцов и самок, а также молекулярно-филогенетический анализ гена COI выявили на территории России три вида: *C.* (*A.*) *confusa* (Huang, Chen et Li, 2006), **status promotus**, *C.* (*A.*) *korea* (Johnson, 1992), **status promotus** и *C.* (*A.*) *frivaldszkyi* (Lederer, 1855). Название *C.* (*A.*) *inopinata* (M.M. Omelko, 1995), **syn. nov.** синонимизировано с *C.* (*A.*) *frivaldszkyi*. Приведён ключ для определения видов подрода *Ahlbergia* России.

**Key words:** morphology, genitalia, DNA barcoding, phylogenetic analysis, Insecta, Lycaenidae, Theclinae, Eumaeini, *Callophrys*

**Ключевые слова:** морфология, гениталии, ДНК-баркодинг, филогенетический анализ, Insecta, Lycaenidae, Theclinae, Eumaeini, *Callophrys*

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## Introduction

*Ahlbergia* Bryk, 1947 is currently treated as a subgenus of the genus *Callophrys* Billberg, 1820, tribe Eumaeini, subfamily Theclinae (Robbins et al., 2022; Krupitsky et al., 2023), with most species occurring in mountains of East Asia, mainly in China (Johnson, 1992; Huang & Zhu, 2016). A consistent review of the former genus *Ahlbergia* was started by Johnson (1992), who described

most of the diversity of this genus, known to be a part of the so-called "Palaearctic elfin butterflies", apart from *Ahlbergia* uniting the subgenera *Cissatsuma* Johnson, 1992 and *Novosatsuma* Johnson, 1992. Since Johnson's study, the total number of *Ahlbergia* species has been raised to 30 (Huang & Sun, 2016; Huang, 2021; Krupitsky et al., 2023; Huang, 2023).

Our knowledge of the subgenus *Ahlbergia* is not complete yet, which is indicated by descriptions of new species and taxonomic changes published during the last decade (Huang & Zhou, 2014; Huang & Sun, 2016; Huang & Zhu, 2016; Huang, 2021, 2023). These studies considerably advanced the taxonomy of this genus but were devoted mainly to Chinese species.

The taxonomy of *Ahlbergia* inhabiting Russia is controversial. For a long time, only two species, *Callophrys* (*Ahlbergia*) *frivaldszkyi* (Lederer, 1855) and *C.* (*A.*) *ferrea* (Butler, 1866), have been reported from Russia (e.g., Korshunov, 2002). In his review of the "Palaearctic elfin butterflies", Johnson (1992) described four new taxa based on type specimens collected in Russia (in his opinion): *C.* (*A.*) *korea* (Johnson, 1992), *C.* (*A.*) *leei* (Johnson, 1992), *C.* (*A.*) *frivaldszkyi tricaudata* Johnson, 1992, and *C.* (*A.*) *frivaldszkyi aquilonaria* (Johnson, 1992). Later, M. Omelko in Omelko & Omelko (1995) described one more species from the Primorskiy Territory in the Russian Far East, *C.* (*A.*) *inopinata*. The name *C.* (*A.*) *korea* was synonymised with *C.* (*A.*) *ferrea* by Matsuda & Bae (1998), and the names *C.* (*A.*) *frivaldszkyi tricaudata*, *C.* (*A.*) *frivaldszkyi aquilonaria* and *C.* (*A.*) *leei* were usually considered subspecies or synonyms of *C.* (*A.*) *frivaldszkyi* (Matsuda & Bae, 1998; Tshikolovets et al., 2002; Tshikolovets & Streltzov, 2019). Generally, there was no consensus in treating these taxa as synonyms, subspecies, or distinct species during the last 25 years, so different authors recorded from two (Dubatolov et al., 2019; Tshikolovets & Streltzov, 2019) to five (Huang & Zhu, 2016) species in Russia.

The most recent revision of *Ahlbergia* involving the taxa known from Russia was made by Huang & Zhu (2016). They considered *C.* (*A.*) *tricaudata* a distinct species, treated *C.* (*A.*) *aquilonaria* as a synonym of *C.* (*A.*) *frivaldszkyi*, and listed *C.* (*A.*) *frivaldszkyi*, *C.* (*A.*) *ferrea*, *C.* (*A.*) *leei* (under question), *C.* (*A.*) *tricaudata*, and *C.* (*A.*) *inopinata* (as a taxon of uncertain status) for the fauna of Russia. However, the conclusions made by these authors were based mostly on materials from China and published data, so the taxa of the subgenus *Ahlbergia* of Russia still remained unrevised.

The purpose of this study is to revise *Ahlbergia* of Russia using an analysis of the morphology combined with molecular phylogenetic analysis.

## Material and methods

**Morphological analysis.** We studied the morphological characters of 136 *Ahlbergia* specimens from Russia, North Korea, South Korea, and Japan deposited in the private collection of Anatoly Krupitsky (AKM), the collection of the American Museum of Natural History, New York, USA (AMNH), the collection of the Natural History Museum of the Humbold University (Museum für Naturkunde, Zentralinstitut der Humboldt-Universitat), Berlin, Germany (MfNB), the private collection of Nazar Shapoval, St Petersburg, Russia (NSS), the collection of the Siberian Zoological Museum of the Institute of Animal Systematics, Russian Academy of Sciences, Novosibirsk, Russia (SZMN), the private collection of Vasily Tuzov, Moscow, Russia (VTM), and the collection of the Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia (ZISP). Of them, 26 specimens were dissected for analysis of the male and female genitalia. The characters used for the species delimitation in the Palaearctic elfin butterflies are selected following Johnson (1992), Huang & Zhou (2014), and Huang & Zhu (2016). The nomenclature of the genitalia and wing pattern is adapted after Johnson (1992) and Krupitsky (2018). The nervuration nomenclature follows the Comstock – Needham system adapted for butterflies (Miller, 1970). For the examination of the male genitalia, the abdomens of the specimens examined were removed and macerated in 10% KOH. After cleaning in water and dehydration in 96% EtOH, a genital capsule with valvae and a separated aedeagus were placed in a drop of glycerol, covered with a cover glass, and photographed.

The images of the specimens examined were taken with a digital camera Canon EOS 5D mark II equipped with a Sigma 150 mm f2.8 lens, using an originally developed light system and a flash Canon Speedlight 430 EX with a diffuser. The images of the genitalia were taken with a Canon

EOS 6D digital camera equipped with a Canon MP-E 65 mm f/2.8 lens, using two Micromed Dual Goose illuminators. The photos of the cornuti were taken with a Micromed 3 trinocular microscope equipped with a ToupCam 5.1 MP video eyepiece. The obtained images were edited using Adobe Photoshop CC 2014.2.2 software.

**Distribution.** Occurrence data were compiled based on the labels of the specimens examined, reliable published data, the Global Biodiversity Information Facility (GBIF, 2023), and iNaturalist (2023) research grade observations. The distribution maps were generated using SimpleMappr (https://www.simplemappr.net/) and then edited with Adobe Photoshop CC 2014.2.2 software.

**DNA extraction, amplification and sequencing.** Total genomic DNA was extracted from one leg per specimen using the QIAamp DNA Investigator Kit (Qiagen, Venlo, The Netherlands) following the manufacturer's protocol. Mitochondrial DNA barcode (a 658 bp fragment of the COI gene) was amplified using LCO1490/HCO2198 (Folmer et al., 1994) and LepF/LepR primer pairs (Hajibabaei et al., 2006). In cases where standard lepidopteran barcode primers failed to yield a sufficient product, we amplified a full-length barcode fragment using the primer pair combinations LepF/MH-MR1 + MH-MF1/LepR and LCO1490/MH-MR1 + MH-MF1/HCO2198 (Lukhtanov et al., 2009) and primers previously designed for *Ahlbergia* species (Krupitsky et al., 2023).

The PCR amplifications were performed in a 25 μL reaction volume per sample. Each reaction contained 1 μL template DNA (ca. 10–50 ng genomic DNA), 1.3 μL of both forward and reverse primers aliquoted to a standard concentration of 10 μM, 5 μL of 5× ScreenMix (Evrogen, Moscow, Russia), and 16.4 μL of ddH2O. The temperature profile was as follows: initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 1 min 30 s, with a final extension at 72 °C for 10 min.

The purified PCR products were subjected to further sequencing. Sequencing of the double-stranded product was carried out at the Research Resource Centre for Molecular and Cell Technologies (St Petersburg State University, St Petersburg, Russia) using an ABI 3500xL analyser. All sequences obtained in this study were deposited in GenBank (http://www.ncbi.nlm.nih.gov/; electronic supplementary material 1, see the section "Addenda").

**Phylogenetic analysis.** Our ingroup dataset included all taxa of *Ahlbergia* previously reported from Russia except *C.* (*A.*) *inopinata* and *C.* (*A.*) *leei*. For taxonomic purposes, specimens from Kazakhstan, South Korea, and Japan were also included in the analysis. Eight specimens were sequenced during the current study, and 15 sequences were obtained from GenBank (electronic supplementary material 1, see the section "Addenda"). The COI sequence of the hairstreak *Neolycaena* (*Rhymnaria*) *baidula* Zhdanko, 2000 (MW785936) was used as the outgroup. Thus, the final dataset for the phylogenetic analysis included 24 specimens.

The sequences were aligned with GENEIOUS v.7.1.9 (Kearse et al., 2012). Phylogenetic analysis was performed using the Bayesian inference (BI) approach. The Bayesian estimation of posterior probability was performed in MrBayes v.3.2.5 (Ronquist & Huelsenbeck, 2003), applying the GTR + G + I evolutionary model as suggested by PartitionFinder v.2.1.1 (Lanfear et al., 2012). Markov chains were sampled at intervals of 500 generations. Two runs of ten million generations with four chains (one cold and three heated) were performed. The final phylogenetic tree images were rendered in FigTree v.1.4.0 (Rambaut, 2012) and then edited using Adobe Illustrator CC 2018 and Adobe Photoshop CC 2014.2.2 software.

## Results

Order **Lepidoptera**

Family **Lycaenidae**

Subfamily **Theclinae**

Tribe **Eumaeini**

Genus ***Callophrys*** Billberg, 1820

Subgenus ***Ahlbergia*** Bryk, 1947

***Callophrys* (*Ahlbergia*) *frivaldszkyi***
(Lederer, 1855)
(Figs 1–8, 16–22, 35, 36)

*Thecla frivaldszkyi* Lederer, 1855: 100, pl. 1, fig. 1. Type locality: "Ust'-Bukhtarminsk" [Kazakhstan, East-Kazakhstan Province, Altai District, environs of New Bukhtarma, ca. 49°40′N 83°40′E].

*Satsuma inopinata* M. Omelko in Omelko & Omelko, 1995: 218, figs. 1–8, **syn. nov.** Type locality: "Gornotaezhnaya stantsiya" [Russia, Primorskiy Territory, ca. 18 km SE from Ussuriysk, Gornotaezhnoe, Mountain-Taiga Station].

*Type material examined*. *Lectotype* of *Thecla frivaldszkyi*: "Altai" [**Kazakhstan**, *East Kazakhstan Prov*., Altai Distr., New Bukhtarma env., ca. 49°40′N 83°40′E] // "Coll. Led." [collection of Lederer] // "Origin.", female (MfNB). *Paralectotype* of *Thecla frivaldszkyi*: "Frivaldsz / kyi Kind. Led. / Sibiria occ. [identalis]" [**Kazakhstan**, *East Kazakhstan Prov*., Altai Distr., New Bukhtarma env., ca. 49°40′N 83°40′E] // "Coll. Led." //"Origin.", 1 male (MfNB). *Paratyps* of *Satsuma inopinata:* "[**Russia**,] Primorskiy Terr. / Ussuriysk env. / GTS I/1981 [ca. 18 km SE from Ussuriysk, Gornotaezhnoe, Mountain-Taiga Station] / Omelko M.M." [Cyrillic script] // "Paratypus *Satsuma* / *inopinata* / M.M. Omelko, 1995", 1 male, 1 female (SZMN).

*Additional material examined*. **Russia**: *Omsk Prov.*: Tarskiy Distr., 3 km E Samsonovo Vill., 56°58′27.90″ N, 74°24′43.39″ E, 15.V.2021, S.A. Knyazev leg., 2 males, voucher Nos. 25FR (GenBank No. OL457024), 27FR (GenBank No. OL457026) (AKM); same label, 1 female, voucher No. 26FR (GenBank No. OL457025) (AKM); *Kemerovo Prov.*: Novokuznetsk, Kara-Chumysh Riv., 350 m, 4–9.V.1996, V. Sinyaev leg., 1 male (AKM); same label, 1 male, voucher No. CAL158 (AKM); *Republic of Khakassia*: Beyskiy Distr., 5 km E of Bogoslovka Vill., 52°57′56.2″N 91°24′43.6″E, 500 m, 20.V.–1.VI.2015, N.A. Shapoval leg., 9 males, 1 female (NSS); *Altai Republic*: "frivaldszkyi Kind. Altai" // "coll. Eversmann" [Altai Mts.], 1 male (ZISP); "Altai" [Altai Mts.], 2 males (ZISP); "S.E. Altai, Tchuja Valley, 4–6000 ft. [1200–1800 m a.s.l.], 18.6.[18]98, H.J. Elwes.", 1 male (ZISP); Altai Nature Reserve, southern shore of Teletskoe Lake, 51°21′41.6″N 87°50′15.4″E, 12.VI.1989, A.L. Devyatkin leg., 1 female (AKM); *Krasnoyarsk Terr.*: "25.V.[19]02 / Tyukhtyata [Vill.] / Minusinsk Distr." [Cyrillic script], 2 females (ZISP); "Bazaikha [Riv.] near Krasnoyarsk. / A. Jacobson leg., 22.V.[18]97" [Cyrillic script], 2 females (ZISP); "Mouth of Laletina [Riv.], Krasnoyarsk. / Krutovskiy [leg.]. 22.V.[19]01" [Cyrillic script], 1 male (ZISP); same label, 8.V.1901, 1 male (ZISP); "Minusinsk vic. / 23.V.1919 / A. Gerasimov leg." [Cyrillic script], 1 male (ZISP); "Lake Tiberkul" // "Sukhaya Mt." // "coll. Gerasimov" [Cyrillic script], 1 female (ZISP); Krasnoyarsk env., 60 km upstream Mana Riv., 19.VI.1966, Korshunov leg. [Cyrillic script], 1 male (ZISP); Krasnoyarsk env., Minino, 29.V.2010, Uchevatov leg., 1 male, voucher No. CAL102 (GenBank No. OQ701614) (VTM); *Irkutsk Prov.*: "Irkut" [Irkut Riv.], 9 males, 6 females (ZISP); "Kirensk [env.] Lena [Riv.] Herz [leg.] 1906", 1 male (ZISP); "Kaya [Riv.], 27.IV.[1]914, S. Rodionoff [leg.]" [Cyrillic script], 1 female (ZISP); "Glazunova Vill. / 9.V.[1]914 / S. Rodionoff [leg.]" [Cyrillic script], 1 male, 1 female (ZISP); "Irkutsk env. / V. Dorogostayskiy [leg.] / 13/V" [Cyrillic script], 2 males (ZISP); "Kashtak Vill., 7.V.1915 S. Rodionoff [leg.]" [Cyrillic script], 2 females (ZISP); "Tayshet / Yenisey Governorate / 25.V.1915" [Cyrillic script], 1 male (ZISP); "Yurty [near Tayshet], Kanskiy Uezd / Yenisey Governorate 21.V.[1]912 / Mishin & Verkhov [leg.]" [Cyrillic script], 1 male (ZISP); "Bunbuy Vill., Valdaev leg. 14.V.1916" [Cyrillic script], 1 male (ZISP); Slyudyanka env., 11.VI.1995, A.L. Devyatkin leg., 1 female (AKM); Baikal Lake, Angasolka station, 22.IV.2007, D. Fominykh leg., 2 males (AKM); Baikal Lake, Pivovarikha Vill., 8.V.2007, D. Fominykh leg., 2 males (AKM); Baikal Lake, Listvyanka env., 5.VI.2014, 1 male, voucher No. CAL162; same label, 1 female, voucher No. CAL100 (GenBank No. OQ701612) (AKM); Irkutsk Distr., Baikal Lake, Port Baikal env., 10.VI.2014, 1 male, voucher No. CAL099 (GenBank No. OQ701611) (AKM); Nizhneudinskiy Distr., Almazay env., 3.VI.2010, 1 female, voucher No. CAL101 (GenBank No. OQ701613); same label, 1 female, voucher No. CAL103 (VTM); vicinity of Bodaybo town, 1–2.VI.2016, R.V. Yakovlev leg., 1 male, voucher No. 10FR (AKM); *Republic of Buryatia*: "Tataurovo / Zabaykal'skaya Prov. / 17.V.1911" [Cyrillic script], 1 male (ZISP); "Sayan Mts. / 3.V.1918 / Koshantschikov [leg.]" [Cyrillic script], 3 females (ZISP); "[Sayan Mts.], Munku-Sardyk Mt." [Cyrillic script], 1 male (ZISP); "VI / Munku-Sardyk [Mt.] / E-Sayan [Mts.]" [Cyrillic script], 2 males, 1 female (ZISP); *Zabaykalskiy Terr.*: Ononskiy Distr., Tsasucheyskiy Bor State Natural Reserve, 19.VI.1995, 1 male (AKM); *Amur Prov.*: "Amur mer.[idionalis]" [middle stream of Amur Riv.] // "Ershov coll.", 1 male (ZISP); "Pochrofka" [Pokrovka Vill.] // "coll. Dieckmann (Graeser legit.)", 1 male (ZISP); *Jewish Autonomous Prov.*: "Raddefka" [Radde Vill.], 1 female (ZISP); *Khabarovsk Terr.*: "Nicolajefsk" [Nikolaevsk-na-Amure] // "coll. Dieckmann (Graeser legit.)", 2 males, 2 females (ZISP); "Chabarofka" [Khabarovsk] // "coll. Dieckmann (Graeser legit.)", 2 males, 1 female (ZISP); Solnechnyy Distr., Gornyy Settlm., VI.1991, 1 male, voucher No. CAL159 (VTM); same label, 1 female, voucher No. CAL160 (VTM); *Primorskiy Terr.*: "Ussuri Merid.[ionalis] / Distr. Sutschan [Partizansk] / 19.V.1922 / A. Kurentzow", 1 female (ZISP); 20 km E of Ussuriysk, Gornotaezhnoe Vill., 06.V.1993, M.M. Omelko leg., 1 female (ZISP); "Vinogradovka / Ussuri Terr. [Anuchinskiy Distr., Vinogradovka Vill.] 16.V.[1]925 / Djakonov & Filipjev leg." [Cyrillic script], 1 female (ZISP); Lazovskiy Distr., Kievka Vill., 9.VI.1969, N.N. Pugatschuk leg. [Cyrillic script], 1 male (ZISP); *Sakhalin Prov.*: Tymovskiy Distr., env. Palevo Vill., 30.VI.–1.

VII.2010, A. Zubov leg., 2 males, 1 female (AKM). **Kazakhstan**, *East Kazakhstan Prov.*,"Altay, Ust'-Kamenogorsk, 23.IV.1962" [Cyrillic script], 1 male (ZISP).

**Individual variation and comparison.** The species is rather variable. Specimens from different parts of the distribution range considerably vary in the wingspan, the size and shape of androconia, and the severity of structural coloration, especially in males, from the total absence of blue scales to the full expression of blue fields. Specimens from the eastern and southern parts of the range are usually larger and characterised by the more expressed blue coloration of the dorsal side of the wings. In the male and female genitalia, the shapes of the valva and lamella postvaginalis slightly vary. Specimens from Primorskiy Territory are usually larger and more brightly coloured. The specimens described as *C.* (*A.*) *inopinata* (Figs 7, 8) do not differ from other specimens of *C.* (*A.*) *frivaldszkyi* from this part of the range either in the external characters or in the genitalia structure and fit into the known individual variation of *C.* (*A.*) *frivaldszkyi*, so we consider *C.* (*A.*) *inopinata*, **syn. nov.** a synonym of *C.* (*A.*) *frivaldszkyi*.

Externally, *C.* (*A.*) *frivaldszkyi* differs from the other species of the genus, found in Russia, i.e. *C.* (*A.*) *confusa*, **status promotus** and *C.* (*A.*) *korea*, **status promotus** (see below), in very narrow vestigial androconia [*vs.* large lanceolate androconia], the less contrasted basal disc with distinct postbasal marks of the ventral side of the hindwing [*vs.* the more contrasted, uniformly brown basal disc], and the strong incision of the marginal band of disc at the vein *Rs* [*vs.* the marginal band of disc at the vein *Rs* is smooth or with a small incision].

In the male genitalia, *C.* (*A.*) *frivaldszkyi* differs from other species found in Russia in the valva with a broadened basal part and a nearly straight outer margin [*vs.* the lanceolate valva with a slightly curved outer margin lacking a broadened base in *C.* (*A.*) *korea*, and the compound valva with a strongly curved outer margin in *C.* (*A.*) *confusa*], and the cornuti with a small number of large spines [*vs.* a larger number of smaller spines in the cornuti of *C.* (*A.*) *confusa* and *C.* (*A.*) *korea*].

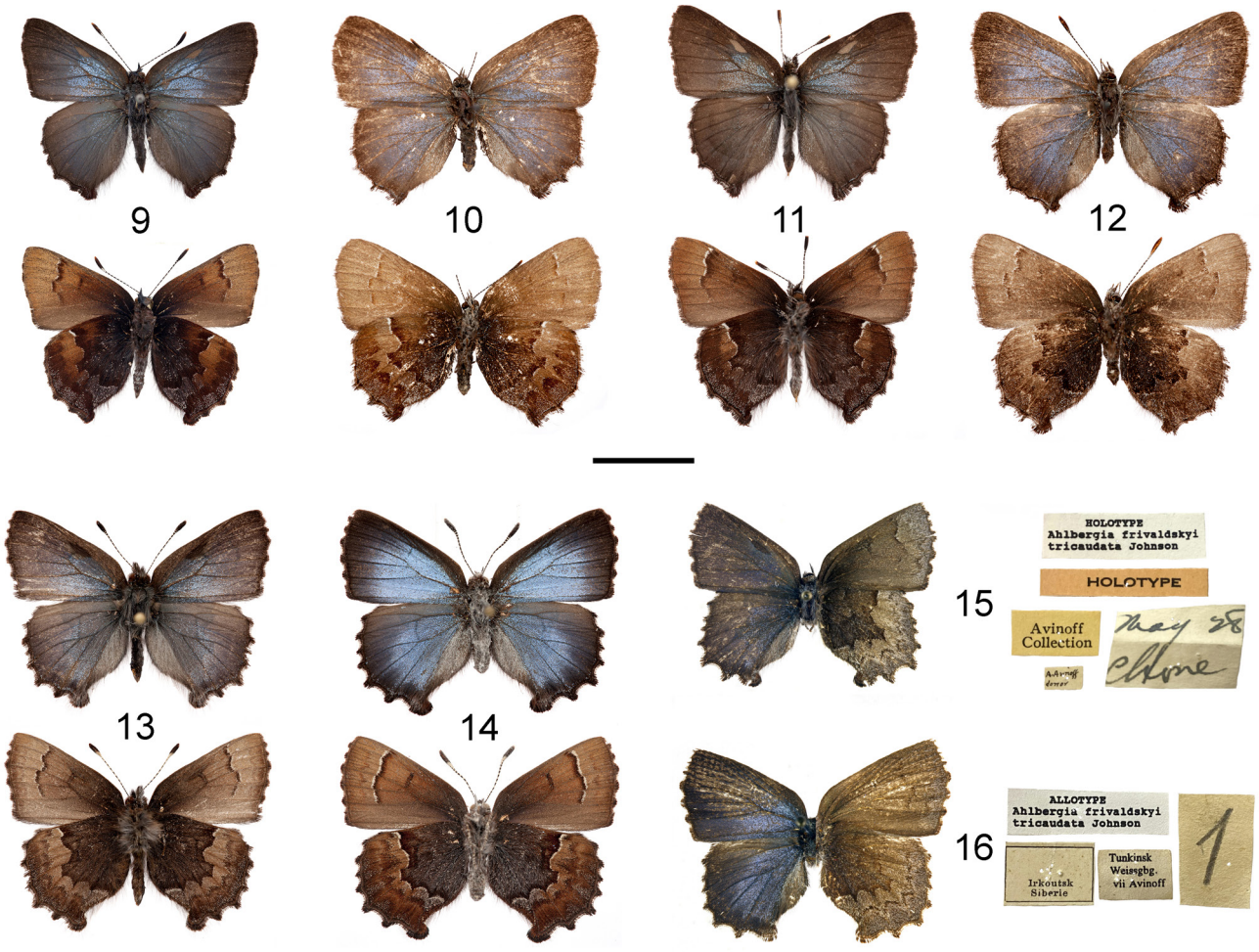
In the female genitalia, *C.* (*A.*) *frivaldszkyi* differs in the long semicircular lamella postvaginalis with convoluted lateral lobes and the short stout ductus bursae [*vs.* the short broad trapezoidal lamella postvaginalis without lateral lobes in *C.* (*A.*) *confusa*, and the very short broad lamella postvaginalis without lateral lobes in *C.* (*A.*) *korea*; the long narrow ductus bursae is present in both species].

A comparison of COI barcodes reveals 0.5% differences from *C.* (*A.*) *korea* but does not reveal differences from a single specimen of *C.* (*A.*) *confusa*. Moreover, the analysed *C.* (*A.*) *frivaldszkyi* specimens from Russia differ from specimens from Kazakhstan by 0.6%.

**Distribution.** According to the labels of the specimens examined, reliable published data (Korshunov, 2002; Tshikolovets et al., 2002; 2009a; Lukhtanov et al., 2007; Novomodny & Fonova, 2010; Ivonin et al., 2011; Tshikolovets & Streltzov, 2019), and observations from GBIF and iNaturalist, in Russia, *C.* (*A.*) *frivaldszkyi* inhabits the southern Asian part from the central Ural Mountains in the Sverdlovsk Province to Sakhalin Island. Additionally, the species was found in one location on the western slope of the Ural Mountains in the Perm' Territory. It seems to be more locally distributed in Western Siberia, although such a bias may be the result of undersampling. Based on observations from iNaturalist (2023), it is reported from the Tomsk Province for the first time. In some of the localities of the Russian Far East, *C.* (*A.*) *frivaldszkyi* lives sympatrically with *C.* (*A.*) *confusa* (Primorskiy Territory, Anuchinskiy District, Vinogradovka Village), or both with *C.* (*A.*) *confusa* and *C.* (*A.*) *korea* (Primorskiy Territory, Lazovsky District, Kievka Village). The presence of the species in Kamchatka stated in literature (e.g., Johnson, 1992; Dubatolov et al., 2019) is not confirmed by actual specimens and, most likely, was given by mistake (Gorbunov & Kosterin, 2022). The revealed morphological variation has no geographical structure, so the subspecific division of *C.* (*A.*) *frivaldszkyi* seems unfounded. Outside Russia, the species is known from Kazakhstan (Tshikolovets et al., 2016), Mongolia (Tshikolovets et al., 2009b), the Korean Peninsula, and China (Huang & Zhu, 2016).

**Nomenclatural note.** The lectotype (female; Fig. 2) of *Thecla frivaldszkyi* was designated by Matsuda & Bae (1998) from the pair of syntypes deposited in MfNB. Later, a male (paralectotype) from this pair (Fig. 1) was erroneously designated as the "lectotype" by Korb (2016). According to Article 74.1.1. of ICZN (1999), this designation is invalid.


**Figs 1–8.** *Callophrys* (*Ahlbergia*) *frivaldszkyi* (Lederer, 1855), habitus. **1**, paralectotype (male) and its labels; **2**, lectotype (female) and its labels; **3**, male, Omsk Province, voucher No. 25FR; **4**, male, Irkutsk Province, voucher No. CAL162; **5**, female, Omsk Province, voucher 26FR; **6**, female, Irkutsk Province, voucher No. CAL100; **7**, male, Primorskiy Territory, paratype of *Satsuma inopinata* M.M. Omelko, 1995 and its labels; **8**, female, Primorskiy Territory, paratype of *Satsuma inopinata* M.M. Omelko, 1995 and its labels. Scale bar: 10.0 mm.




**Figs 9–16.** *Callophrys* (*Ahlbergia*) spp., habitus. **9**, *C.* (*A.*) *ferrea* (Butler, 1866), male, Japan, Honsu Island, Yokohama, 2.IV.1911, H. Hoene leg. (MfNB); **10**, same species, female, Japan, Kyoto, voucher No. CAL164; **11**, *C.* (*A.*) *korea* (Johnson, 1992), **status promotus**, male, Primorskiy Territory, voucher No. CAL086; **12**, same species, female, Primorskiy Territory, voucher No. CAL164; **13**, *C.* (*A.*) *confusa* (Huang, Chen et Li, 2006), **status promotus**, male, Primorskiy Territory, voucher No. CAL153; **14**, same species, female, Primorskiy Territory, voucher No. CAL154; **15**, *C.* (*A.*) *tricaudata* (Johnson, 1992), holotype, male and its labels (AMNH); **16**, *C.* (*A.*) *frivaldszkyi*,"paratype" of *C.* (*A.*) *tricaudata*, female and its labels (AMNH). Scale bar: 10.0 mm.

### ***Callophrys* (*Ahlbergia*) *ferrea*** (Butler, 1866) (Figs 9, 10, 23, 37)

*Lycaena ferrea* Butler, 1866: 57. Type locality: "Hakodadi (North Japan)" [Hakodate, Hokkaido, Japan].

*Material examined*. **Japan**: *Kanto Prov.*, "Japonia / (Jocohama)[Yokohama]/H.Hoene[leg.]2.4[IV].1911", 1 male (MfNB); *Hokkaido Prefecture*, Kato-gun: Otofuke-cho, Osarushinai, 9.V.2013, T. Hirabayashi leg., 2 males, voucher No. CAL065–066 (GenBank No. OM630560–OM630561) (AKM); Otofuke-cho, Tokachigaoka, T. Hirabayashi leg., 29.V.2017, 1 male, voucher No. CAL163 (VTM); *Kyoto Prefecture*, Kyoto, 10.VI.1958, 1 female, voucher No. CAL164 (VTM).

**Distribution.** Eight males of the species *C.* (*A.*) *ferrea* or *C.* (*A.*) *korea*, **status promotus** (see below) were recently recorded from Kunashir Island (the southernmost of the Kuril Islands archipelago) as "*Callophris* [sic!] (*Ahlbergia*) *ferrea*" (Rybalkin et al., 2022). Taking into account the distribution range of *C.* (*A.*) *ferrea*, which covers Hokkaido Island adjacent to Kunashir Island, we believe these specimens belong to *C.* (*A.*) *ferrea*.

The final decision about the identity of these specimens cannot be made without an analysis of the genitalia.

***Callophrys* (*Ahlbergia*) *korea*** (Johnson, 1992), **status promotus**
(Figs 11, 12, 26–28, 38)

*Ahlbergia korea* Johnson, 1992: 23. Type locality: South Korea.

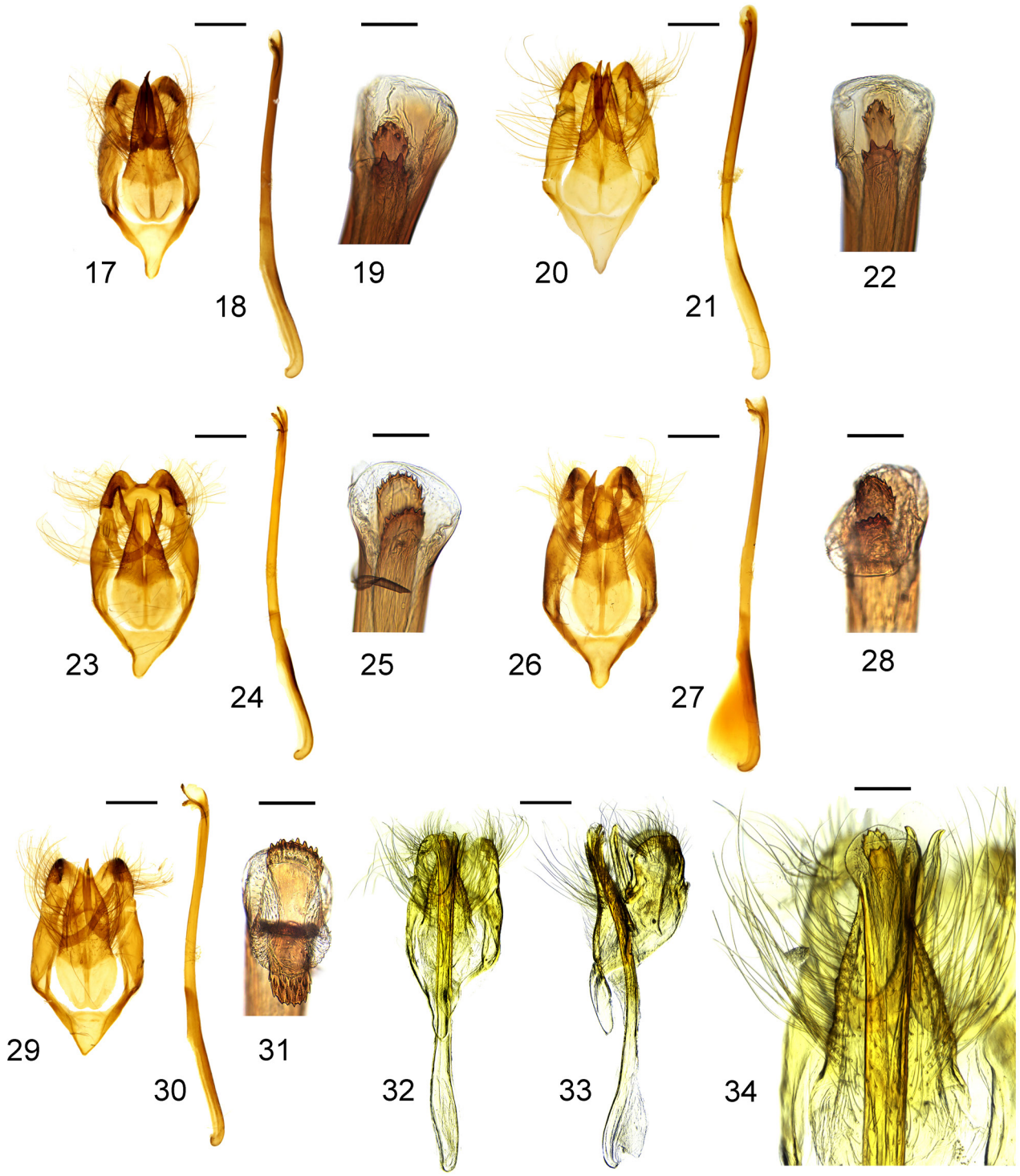
*Material examined*. **Russia**: *Amur Prov.*: "Bol'shoy Never [Never Vill.] / Amur Prov. 3.VI.[1]927 / Zakharzhevskiy [leg.] " [Cyrillic script], 1 male (ZISP); *Primorskiy Terr.*: "Vladivostok/1900/D. Grum-Grshimailo leg.", 1 male (ZISP); "Ussuri Merid.[ionalis] / Distr. Sutschan [Partizansk] / 27.V.1922 / A. Kurentzow", 1 male (ZISP); "Yakovlevka [Vill.] Spassk Uezd / Ussuri Terr. 7.V.[1]926 / Dyakonov & Filipyev", 3 males, 1 female (ZISP); "Spasskoye / Ussuri Terr. 16.V. [1]926 / Djakonov & Filipjev", 1 female (ZISP); same locality and collectors, 18.V.1926, 1 male (ZISP); Lazovskiy Distr., Kievka Vill., 9.VI.1969, N.N. Pugatschuk leg., 1 male (ZISP); N of Sikhote-Alin Mts., upper Bikin Riv., Ulunga Vill., 19–26.V.2005, D. Goshko leg., 2 males, voucher No. CAL084 (GenBank No. OQ701610), CAL086 (AKM). **Democratic People's Republic of Korea**: "Korea / Jank." [North Korea, 1897, A.M. Jankovskiy leg.], 1 female (ZISP); *South Hamgyong Prov.*, Sinpho, 28.IV.1990, S. Murzin leg., 1 female, voucher No. CAL167 (AKM). **Republic of Korea**, *Gyeonggi Prov.*: Goyang si, Myeongbongsan Mt., 250 m, 20.IV.2019, K. Tyan leg., 1 male (AKM); same label, 1 male, voucher No. CAL156 (AKM); Icheon, 1 female, voucher No. CAL157 (VTM).

**Taxonomy and comparison.** *Ahlbergia korea* was described from eight specimens collected in the Korean Peninsula and the Russian Far East (Amur Province and Primorskiy Territory). The description was based on differences in the male and female genitalia compared with *C.* (*A.*) *ferrea* from Japan. Matsuda & Bae (1998) reveled no differences either in the wing pattern and the genitalia structure between these taxa and synonymised *C.* (*A.*) *korea* with *C.* (*A.*) *ferrea*.

Despite their somewhat stylised and superfluous manner, the genitalia drawings of *C.* (*A.*) *korea* and *C.* (*A.*) *ferrea* given in the original description (Johnson, 1992: 103, figs 8–11) differ at least in the shape and size of the valva of the male genitalia and in the shape of the lamella postvaginalis. These differences correspond to the specific characters mentioned in the diagnosis of *C.* (*A.*) *korea* (Johnson, 1992: 24), namely the less robust and more sculptured valva and the convoluted ventrum of lamella postvaginalis. Contour genitalia drawings reproduced in the review by Matsuda & Bae (1998) are inaccurate and thus misleading, providing no chance to evaluate the characters of the valva, cornuti, and lamella postvaginalis of the specimens examined. Since the revision by Matsuda & Bae (1998), *C.* (*A.*) *korea* has been usually treated by various authors either as a synonym (Huang & Zhu, 2016) or a subspecies (Dubatolov et al., 2019; Tshikolovets & Streltzov, 2019) of *C.* (*A.*) *ferrea*. In fact, it seems that all subsequent authors have not compared the genitalia of these taxa. Huang & Zhu (2016) in the latest revision of *Ahlbergia* illustrated the genitalia of "*A. ferrea*" from China but did not study specimens from Japan, following the conclusion of Matsuda & Bae (1998).

As in the previous researches, our study of the specimens of *C.* (*A.*) *ferrea* and *C.* (*A.*) *korea* across the range also revealed no constant differences in habitus, but the characters of the male and female genitalia of *C.* (*A.*) *korea* generally correspond to those mentioned in the original description, distinguishing it from *C.* (*A.*) *ferrea*. Moreover, the analysed COI barcodes of *C.* (*A.*) *korea* and *C.* (*A.*) *ferrea* differ by 2.2%, suggesting genetic isolation. Taking into account the genitalic and genetic differences between these taxa, we consider the former as a distinct species, *C.* (*A.*) *korea*, **status promotus**.

As stated above, we were unable to find any consistent external differences between *C.* (*A.*) *ferrea* and *C.* (*A.*) *korea*. The latter differs both from *C.* (*A.*) *frivaldszkyi* and *C.* (*A.*) *confusa*, **status promotus** (see below) in the oblong hindwing with a less serrated margin [*vs.* the rounded hindwing with a serrated margin]. It differs from *C.* (*A.*) *frivaldszkyi* in a large androconial spot and the contrasted rusty-brown disc and limbal area of the dorsal side of hindwing [*vs.* vestigial androconia and the less contrasted basal disc with distinct postbasal marks and a brown crescent line]. It differs from *C.* (*A.*) *confusa* in the less expressed structural coloration in both sexes, especially in the male hindwing, and the less contrasted ventral surface of hindwing with a less expressed light brown postdiscal band and an uncontrasted blurred crescent line [*vs.* the




**Figs 17–34.** *Ahlbergia* spp., male genitalia. **17–19**, *C.* (*A.*) *frivaldszkyi*, Omsk Province, voucher No. 25FR; **20–22**, same species, Irkutsk Province, voucher No. CAL162; **23–25**, *C.* (*A.*) *ferrea*, Japan, Hokkaido, voucher No. CAL163; **26–28**, *C.* (*A.*) *korea*, Primorskiy Territory, voucher No. CAL086; **29–31**, *C.* (*A.*) *confusa*, Primorskiy Territory, voucher No. CAL153; **32–34**, *C.* (*A.*) *tricaudata*, holotype. Genital capsule, dorsal view (17, 20, 23, 26, 29), scale bar 0.5 mm; aedeagus, lateral view (18, 21, 24, 27, 30), scale bar 0.5 mm; vesica of aedeagus with cornuti, scale bar 0.2 mm; genital capsule with attached aedeagus, dorsal (32) and lateral (33) view, scale bar 0.5 mm; proximal parts of valvae and aedeagus, dorsal view (34), scale bar 0.2 mm.

more distinct structural coloration in both wings of both sexes and the more contrasted ventral surface of hindwing with a distinct light brown postdiscal band and a clearly defined crescent line].

The male genitalia of *C.* (*A.*) *korea* differ from those of *C.* (*A.*) *ferrea* in the longer and thinner valva with a slightly curved outer margin ("less robust and more sculptured valva" in the original description), stouter falx, and smaller cornuti bearing a smaller number of spines. *Callophrys* (*Ahlbergia*) *korea* differs from *C.* (*A.*) *frivaldszkyi* and *C.* (*A.*) *confusa* in the lanceolate valva with a slightly curved outer margin without a broadened base [*vs.* the valva with a broadened basal part and a nearly straight outer margin in *C.* (*A.*) *frivaldszkyi*, and the compound valva with a strongly curved outer margin in *C.* (*A.*) *confusa*] and the medium-sized cornuti with a large number of small spines [*vs.* the small cornuti with a small number of large spines in *C.* (*A.*) *frivaldszkyi*, and the large cornuti with a large number of small spines in *C.* (*A.*) *confusa*].

The female genitalia of *C.* (*A.*) *korea* differ from those of *C.* (*A.*) *ferrea* in the short and broad lamella postvaginalis which has the sculptured surface [*vs.* the long smooth semicircular lamella postvaginalis]. Compared with *C.* (*A.*) *frivaldszkyi*, *C.* (*A.*) *korea* differs in the short and broad lamella postvaginalis without lateral lobes and in the long, rather narrow ductus bursae [*vs.* the long semicircular lamella postvaginalis with convoluted lateral lobes and the short stout ductus bursae]. Compared to *C.* (*A.*) *confusa*, it differs in the rounded lamella postvaginalis [*vs.* the trapezoidal lamella postvaginalis].

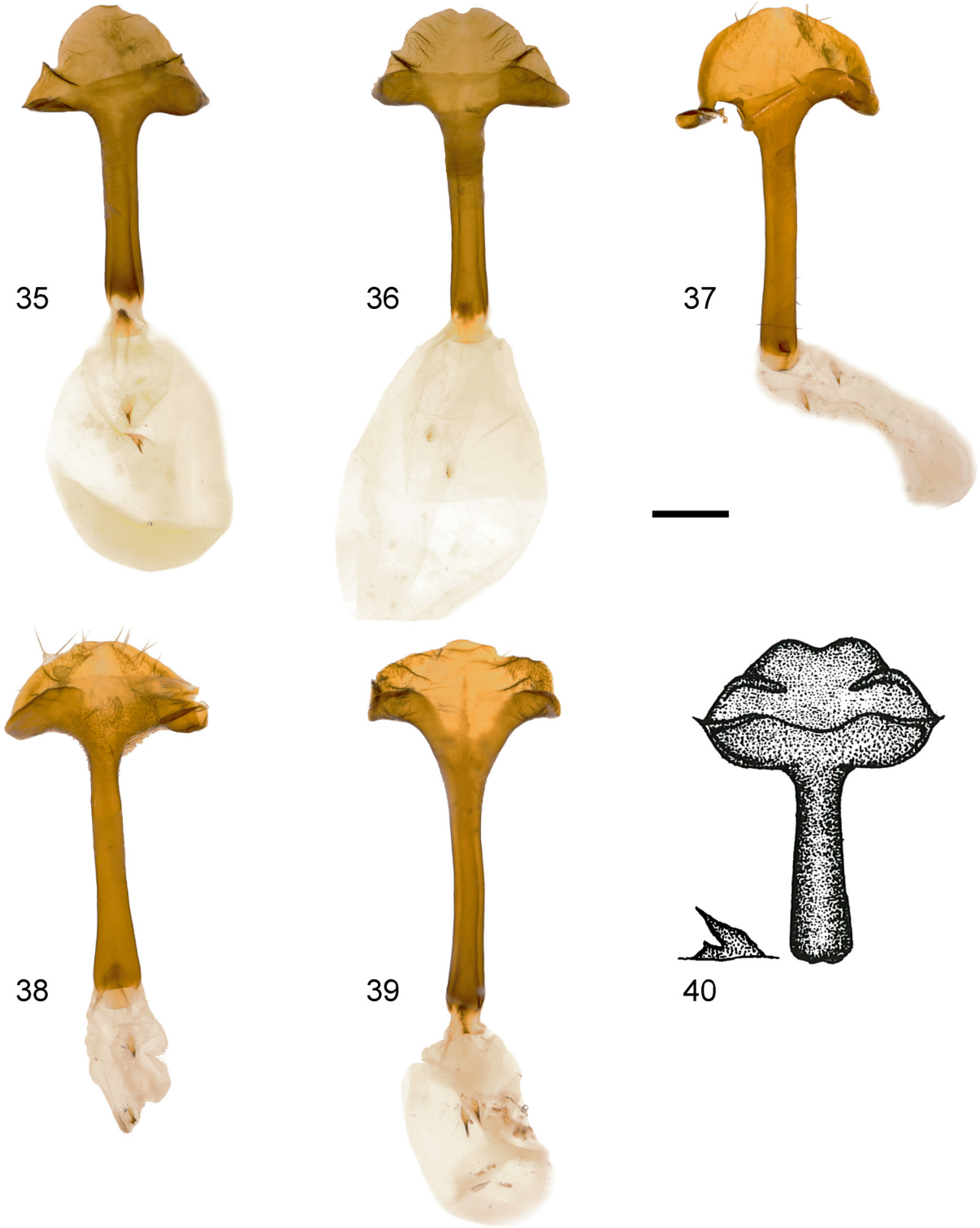
**Distribution.** According to the labels of the specimens examined, in Russia, *C.* (*A.*) *korea* is present in the Amur Province and Primorskiy Territory. In the latter (Anuchinskiy District, Vinogradovka Village), it was found sympatrically with *C.* (*A.*) *frivaldszkyi* and *C.* (*A.*) *confusa*. According to published data (Tshikolovets & Streltzov, 2019), *C.* (*A.*) *korea* was also found in the Khabarovsk Territory and the Jewish Autonomous Province. The record from the Kuril Islands (Dubatolov et al., 2019) requires examination and probably belongs to *C.* (*A.*) *ferrea*. Outside Russia, *C.* (*A.*) *korea* is present in the Liaoning Province of China (Huang & Zhu, 2016) and in the Korean Peninsula.

### ***Callophrys* (*Ahlbergia*) *confusa*** (Huang, Chen et Li, 2006), **status promotus**
(Figs 13, 14, 29–31, 39)

*Ahlbergia confusa* Huang, Chen & Li, 2006: 175. Type locality: "Zi-Jin Mt., Nanjing, Jiangsu province, China".

*Material examined*. **Russia**, *Primorsky Terr.*: "Vinogradovka / Ussuri Terr. [Anuchinsky Distr., Vinogradovka Vill.] 16.V.[1]925 / Djakonov & Filipjev leg.", 1 male, 2 females (ZISP); Yakovlevka [Vill.] Spassk Distr. / Ussuri Terr. 7.V.[1]926 / Djakonov & Filipjev [leg.]", 1 male (ZISP); same locality, 10.V.1926, 3 females (ZISP); "Suchanskiy mine [Partizansk] / Ussuri Terr. / Palshikov [leg.] 21/V.[1]931", 1 female, 1 female (ZISP); Lazovskiy Distr., Kievka Vill., 9.VI.1969, N.N. Pugatschuk leg., 2 females (ZISP); N Sikhote-Alin Mts., upper Bikin Riv., Ulunga Vill., 19–26.V.2005, D. Goshko leg., 1 male, voucher No. CAL085 (AKM); Shkotovskiy Distr., Anisimovka Vill., 2.V.2012, 1 male, voucher No. CAL153 (VTM); same label, 1 female, voucher No. CAL104 (GenBank No. OQ701615) (VTM); Khasanskiy Distr., Zanadvorovka Vill., 1.V.2013, V. Golovizin leg., 1 male, voucher No. CAL161 (VTM); same label, 2 females, vouchers No. CAL154–CAL155 (VTM).

**Taxonomy.** *Ahlbergia frivaldszkyi tricaudata* was described by Johnson (1992) on the basis of two specimens, the holotype (male) (Fig. 15) from China (without certain locality), and the paratype (female) (Fig. 16) from the Tunka Goltsy Mountains (Eastern Sayan), which originated from the collection of Andrey Avinoff and are deposited in the AMNH. As correctly noted by Huang & Zhu (2016), the paratype female obviously belongs to *C.* (*A.*) *frivaldszkyi*, the only species of the elfin butterflies inhabiting most of Siberia, including the Sayan Mountains (see below for the distribution of the latter species). Based on the original description of *C.* (*A.*) *frivaldszkyi tricaudata* supplied with black-and-white photographs of the holotype and drawings of the genitalia, Huang & Zhu (2016) considered it a distinct species. In their opinion, it includes four subspecies: the nominotypical, inhabiting Northeast China (Liaoning Province) and the Primorskiy Territory in Russia; two unnamed subspecies, one from the Beijing, Hebei, and Shanxi provinces, and another from the Shaanxi Province; and *C.* (*A.*) *tricaudata confusa* (Huang, Chen et Li, 2006) from southeastern China. The latter was initially described as a species based on four males and five females




**Figs 35–40.** *Callophrys* (*Ahlbergia*) spp., female genitalia, dorsal view. **35**, *C.* (*A.*) *frivaldszkyi*, Omsk Province, voucher No. 26FR; **36**, same species, Irkutsk Province, voucher No. CAL100; **37**, *C.* (*A.*) *ferrea*, Japan, Kyoto, voucher No. CAL164; **38**, *C.* (*A.*) *korea*, North Korea, Sinpho, voucher No. CAL167; **39**, *C.* (*A.*) *confusa*, Primorskiy Territory, voucher No. CAL154; **40**, *C.* (*A.*) *frivaldszky*, drawing of the female genitalia of the "paratype" of *C.* (*A.*) *tricaudata* from Johnson (1992). Scale bar 1.0 mm.

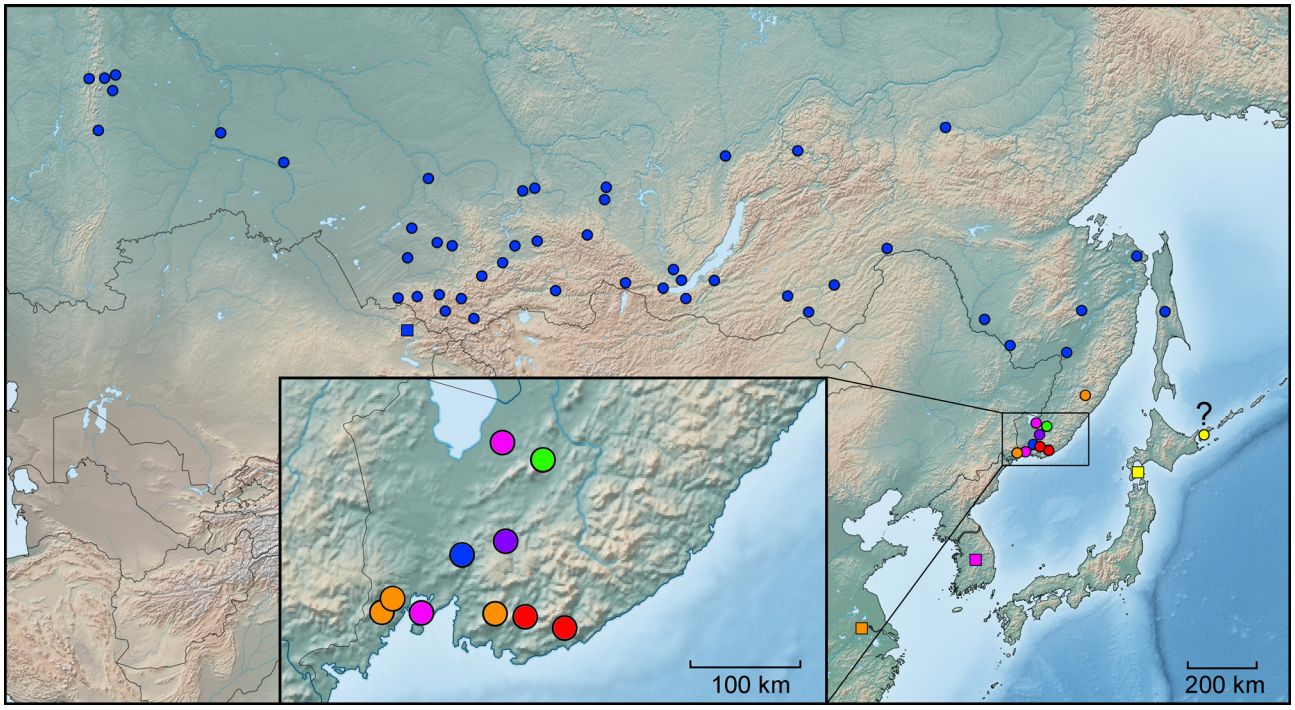



**Fig. 41.** Distribution of *Callophrys* (*Ahlbergia*) spp. found in Russia and their type localities. Blue, *C.* (*A.*) *frivaldszkyi*; orange, *C.* (*A.*) *confusa*; pink, *C.* (*A.*) *korea*; yellow, *C.* (*A.*) *ferrea*; red, shared localities of *C.* (*A.*) *frivaldszkyi*, *C.* (*A.*) *confusa* and *C.* (*A.*) *korea*; purple, shared locality of *C.* (*A.*) *frivaldszkyi* and *C.* (*A.*) *confusa*; green, shared locality of *C.* (*A.*) *confusa* and *C.* (*A.*) *korea*; squares refer to type localities; question mark refers to probable finding of *C.* (*A.*) *ferrea* in Kunashir Island. Southern part of the Primorskiy Territory is enlarged to show shared localities.

from the Jiangsu Province and, additionally, a female from the Fujian Province, but treated as a subspecies by Huang & Zhu (2016) on the basis of the male and female genitalia similar to those of the nominotypical subspecies (as they thought) of *C.* (*A.*) *tricaudata*.

We analysed colour photos of the holotype of *C.* (*A.*) *tricaudata* and its genitalia deposited in the AMNH, which were kindly provided to us by Dr David A. Grimaldi, the curator of the Lepidoptera collection of the AMNH. The comparison of the external and genitalic characters revealed that the type specimen bearing the specific name *tricaudata* and the specimens from the Primorskiy Territory and the Liaoning Province belong to different species. Differences were found in the wingspan, the shape of hindwing, coloration, the shape of valva and the structure of cornuti of aedeagus. It is important to note that the genitalia drawings of *C.* (*A.*) *tricaudata* made by Johnson (1992: 105, fig. 24C) hardly correspond to the genitalia of the holotype (Figs 32–34): the shapes of the sclerites, their proportions, and even the number of teeth of the cornuti are different.

It is impossible to properly determine the type locality of this taxon, as the label bears only the illegible handwritten inscription “May 28 / Chine” (Fig. 15). The holotype of *C.* (*A.*) *tricaudata* does not fit any other known *Ahlbergia* species, so we consider it a bona species. Its distribution needs further exploration; we cannot exclude the possibility that it originates from the mountains of Sichuan or Yunnan, known as centers of diversity for Lycaenidae.

Taking into account the similarity in coloration and the genitalia structure of *C.* (*A.*) *confusa* from the Jiangsu Province in China and the specimens from the Primorskiy Territory in Russia and the Liaoning Province in China, we treat these populations as *C.* (*A.*) *confusa*, **status promotus**. The subspecific division of the latter needs further exploration based on materials from the whole distribution range of the species, most of which is situated in China.

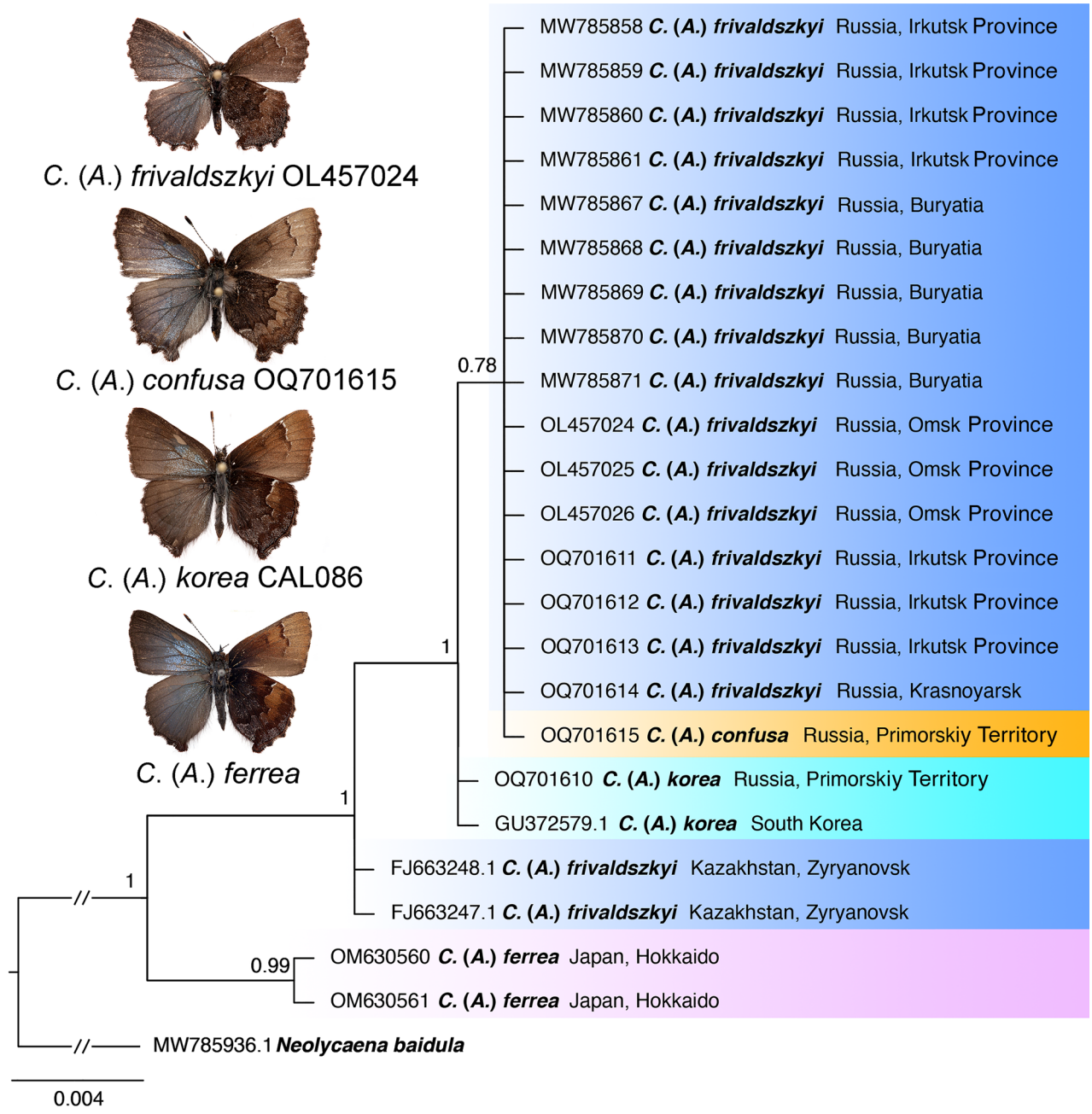



**Fig. 42.** The Bayesian phylogenetic tree of *Callophrys* (*Ahlbergia*) spp. based on analysis of the cytochrome oxidase subunit I (COI) gene fragment. Numbers at nodes indicate Bayesian posterior probabilities (PPs). Scale bar = 0.004 substitutions per position.

**Comparison.** Externally, *C.* (*A.*) *confusa* differs from somewhat similar *C.* (*A.*) *korea* in the rounded hindwing with a more serrated margin, the more distinct structural coloration in both wings of both sexes, and the more contrasted ventral surface of the hindwing with a distinct light brown postdiscal band and a clearly defined crescent line [*vs.* the less distinct structural coloration in both sexes, especially in the hindwing of male, and the less contrasted ventral surface of hindwing with a less distinct light brown postdiscal band and a uncontrasted blurred crescent line]. It differs from *C.* (*A.*) *frivaldszkyi* in a clearly defined androconial spot, the contrasted, uniformly brown

basal disc, a smooth marginal band of the disc at the vein *Rs* [*vs.* very narrow vestigial androconia, the less contrasted basal disc with distinct postbasal marks of the ventral surface of hindwing, and a strong incision of the marginal band of disc at the vein *Rs*].

In the male genitalia, *C.* (*A.*) *confusa* differs from both species in the compound valva with a strongly curved outer margin and the large cornuti bearing a large number of small spines [*vs.* the lanceolate valva with a nearly straight, slightly curved outer margin and the medium-sized cornuti with a large number of small spines in *C.* (*A.*) *korea*, and the valva with a broadened basal part and a nearly straight outer margin, and the small cornuti with a small number of large spines in *C.* (*A.*) *frivaldszkyi*].

In the female genitalia, *C.* (*A.*) *confusa* differs from both species in the trapezoidal lamella postvaginalis [*vs.* the short rounded lamella postvaginalis in *C.* (*A.*) *korea*, and the long semicircular lamella postvaginalis with convoluted lateral lobes in *C.* (*A.*) *frivaldszkyi*].

Additionally, *C.* (*A.*) *confusa* differs from the holotype of *A. tricaudata* in the rounded hindwing [*vs.* the hindwing is elongated at *Cu2*], the uniformly brown band of the disc having a smoother margin [*vs.* the disc has a band with a secondary pattern and a strong incision at *Cu2*], the curved compound valva [*vs.* the valva with a slightly curved outer margin], and the large cornuti with a large number of small spines [*vs.* the small cornuti with a small number of large spines].

**Distribution.** Primorskiy Territory of Russia, in some localities sympatrically with *C.* (*A.*) *frivaldszkyi* and *C.* (*A.*) *korea*. The distribution range outside Russia, especially on the Korean Peninsula, needs further investigation.

**Phylogenetic analysis.** The phylogenetic analysis strongly supports all the examined species of *Ahlbergia* as a monophyletic group (Fig. 42), but none of the recognised species turned out to be monophyletic except *C.* (*A.*) *korea* and *C.* (*A.*) *ferrea*. The phylogenetic tree consists of two deeply branching clades. The first clade comprises two specimens of *C.* (*A.*) *ferrea* from Japan, and the second clade unites *C.* (*A.*) *frivaldszkyi* from Siberia, the Russian Far East, and Kazakhstan, two specimens previously identified as *C.* (*A.*) *korea* from Korea and the russian Primorskiy Territory, and a specimen of *C.* (*A.*) *confusa* from the Primorskiy Territory. Surprisingly, in the latter clade, two specimens of *C.* (*A.*) *frivaldszkyi* from Kazakhstan are recovered as sister to the rest of the specimens.

Among the 23 specimens belonging to four species, the Kimura 2-parameter (K2P) distances range from 0.0% between *C.* (*A.*) *frivaldszkyi* from Russia and *C.* (*A.*) *confusa* to 2.2% between *C.* (*A.*) *ferrea* and *C.* (*A.*) *korea* (electronic supplementary material 2, see the section "Addenda").

### Key to the species of the subgenus *Callophrys* (*Ahlbergia*) of Russia

1. Basal disc of ventral side of hindwing with secondary pattern of postbasal marks and strong incision of marginal band at vein *Rs*. Androconial spot vestigial. Lamella postvaginalis with secondary convolutions . . . . . ***C.* (*A.*) *frivaldszkyi***
– Basal disc of ventral side of hindwing uniformly brown, marginal band of disc at vein *Rs* smooth or with small incision. Androconial spot distinct, ovoid. Lamella postvaginalis without secondary convolutions. . . . . 2
2. Hindwing elongated towards anal lobe, with smooth or slightly wavy margin. Outer margin of valva slightly curved. Lamella postvaginalis rounded. . . 3
– Hindwing rounded, with serrated margin. Outer margin of valva strongly curved. Lamella postvaginalis trapezoidal . . . . . ***C.* (*A.*) *confusa***
3. Valva long, protruding well beyond lobes of uncus. Lamella postvaginalis short, small, with sculptured surface. . . . . ***C.* (*A.*) *korea***
– Valva short, hardly reaching lobes of uncus. Lamella postvaginalis large, semicircular, with smooth surface. . . . ***C.* (*A.*) *ferrea*** (probably on Kuril Islands)

## Discussion

According to our study, the subgenus *Ahlbergia* is represented in Russia by three species, *C.* (*A.*) *frivaldszkyi*, *C.* (*A.*) *confusa*, and *C.* (*A.*) *korea*. The presence of the fourth species, *C.* (*A.*) *ferrea*, is very likely on the Kuril Islands, especially on Kunashir. Taking into account the distribution of most species of *Callophrys* (*Ahlbergia*) in the Shaanxi, Sichuan, and Yunnan provinces of China and the high rate of endemism of the genus in these regions, it is unlikely that species new to the Russian fauna or undescribed species will be found in Russia.

We were unable to determine in the extensive museum and private collections another species mentioned from Russia in the literature (Tuzov, 2000; Huang & Zhu, 2016), *C.* (*A.*) *leei*. None of the specimens examined, except some males of *C.* (*A.*) *frivaldszkyi*, possess its main diagnostic character, i.e., the absence of an extensive greyish blue suffusion (Johnson, 1992; Huang & Zhu, 2016). According to Korb (2016), the type locality of *C.* (*A.*) *leei* is situated in the Yinshan Mountains, Inner Mongolia Province, China. The specimens identified as *C.* (*A.*) *leei* are recorded from the Liaoning and Shaanxi provinces by Huang & Zhu (2016). The distribution and presence of this species in Russia needs further exploration; it seems that none of the previous records from Russia were based on actual specimens.

Although the species examined are well defined morphologically, the molecular phylogenetic analysis based on the COI barcode region failed to determine them, except in the case of the pair *C.* (*A.*) *korea* – *C.* (*A.*) *ferrea* which differed by 2.2%. The genetic distances between the other species were: 0% between *C.* (*A.*) *frivaldszkyi* and *C.* (*A.*) *confusa*, and 0.5% between *C.* (*A.*) *frivaldszkyi* [including *C.* (*A.*) *confusa*] and *C.* (*A.*) *korea*. This phenomenon can be explained by ongoing hybridisation leading to extensive mitochondrial introgression in the parts of the range where all the three continental species coexist (Primorskiy Territory). However, natural hybrids between these species still have not been revealed, probably due to insufficient samples from the areas where they live sympatrically. In the subfamily Theclinae, shared or very close COI mitochondrial barcodes in morphologically different species were also found in other Palaearctic *Callophrys* species (ten Hagen & Miller, 2010; Krupitsky et al., 2023), as well as in the *Tomares* Rambur, 1840 hairstreaks (Krupitsky et al., 2022). Natural hybridisation between species of *Callophrys* (sensu stricto) and *Callophrys* (*Ahlbergia*) was recently demonstrated by Shapoval et al. (2021), so it seems to be possible between species of the subgenus *Ahlbergia* too. The analysed specimens of *C.* (*A.*) *frivaldszkyi* from Russia do not have genetic differences in COI barcodes. Surprisingly, this species turned out to be polyphyletic in our analysis, as the two specimens from the southern foothills of the Altay Mountains in Kazakhstan, differing from *C.* (*A.*) *frivaldszkyi* from Russia by 0.6%, formed the sister lineage to the clade uniting the three species from continental Russia. This fact requires further exploration; it can be explained by the possible isolation of different haplotypes by *Wolbachia*, a rikketsial endosymbiont known to be affecting population genetic structure in Lepidoptera, including Lycaenidae (Bartoňová et al., 2021).

## Addenda

*Electronic supplementary material 1*. List of specimens used in this study with voucher numbers, collection localities and GenBank accession numbers. File format: XLSX.

*Electronic supplementary material 2*. Uncorrected minimal p-distances in COI marker between examined species of *Callophrys* (*Ahlbergia*). File format: XLSX.

All these materials are available from: https://doi.org/10.31610/zsr/2023.32.2.269

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## References


**Bartoňová A., Konvička M., Marešová J., Wiemers M., Ignatev N., Wahlberg N., Schmitt T. & Fric Z.** 2021. Wolbachia affects mitochondrial population structure in two systems of closely related Palaearctic blue butterflies. *Scientific Reports*, **11**: 3019. https://doi.org/10.1038/s41598-021-82433-8

**Dubatolov V.V., Lukhtanov V.A. & Streltzov A.N.** 2019. Lycaenidae. *In:* **Sinev S.Yu.** (Ed.). *Katalog cheshuekrylykh Rossii* [Catalogue of the Lepidoptera of Russia]. *Edition 2*: 204–214. St Petersburg: Zoological Institute RAS.

**Folmer O., Black M., Hoeh W., Lutz R. &Vrijenhoek R.** 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular marine Biology and Biotechnology*, **3**: 294–299.

**GBIF.** 2023. Ahlbergia frivaldszkyi (Lederer). *GBIF Backbone Taxonomy* [online]. https://www.gbif.org/species/8643155 [viewed 27 March 2023].

**Gorbunov P.Y. & Kosterin O.E.** 2022. Butterflies (Lepidoptera: Papilionoidea) of Kamchatka in nature. *Amurian zoological Journal*, **14**(3), Supplement: 1–190. https://www.doi.org/10.33910/2686-9519-2022-14-3-s

**Hajibabaei M., Smith M.A., Janzen D.H., Rodríguez J.J., Whitfield J.B. & Hebert P.D.N.** 2006. A minimalist barcode can identify a specimen whose DNA is degraded. *Molecular Ecology Notes*, **6**: 959–964. https://doi.org/10.1111/j.1471-8286.2006.01470.x

**Huang H.** 2021. New and little known butterflies from China – 4. *Atalanta*, **52**(3): 345–413.

**Huang H.** 2023. New and little known butterflies from China – 5. *Neue entomologische Nachrichten*, **82**: 93–214.

**Huang H., Chen Z. & Li M.** 2006. Ahlbergia confusa sp. n. from SE China. *Atalanta*, **37**(1/2): 175–183.

**Huang H. & Sun W.H.** 2016. Ahlbergia bijieensis spec. nov. from Guizhou, China (Lepidoptera, Lycaenidae). *Atalanta*, **47**(1/2): 151–160.

**Huang H. & Zhou L.-P.** 2014. Discovery of two new species of the "elfin" butterflies from Shaanxi province, China. *Atalanta*, **45**(1–4): 139–150.

**Huang H. & Zhu J.-Q.** 2016. Ahlbergia maoweiweii sp. n. from Shaanxi, China with revisional notes on similar species (Lepidoptera: Lycaenidae). *Zootaxa*, **4114**: 409–433. https://www.doi.org/10.11646/zootaxa.4114.4.3

**ICZN.** 1999. *International Code of Zoological Nomenclature. Fourth edition adapted by the International Union of Biological Sciences.* London: The International Trust for Zoological Nomenclature. xxix + 306 p.

**iNaturalist.** 2023. Hvostatka Frival'dskogo (Ahlbergia frivaldszkyi) [online] https://www.inaturalist.org/observations?taxon_id=830598 [viewed 27 March 2023]

**Ivonin V.V., Kosterin O.E. & Nikolaev S.L.** 2011. Butterflies (Lepidoptera, Diurna) of Novosibirskaya Oblast, Russia. 2. Lycaenidae. *Euroasian entomological Journal*, **10**(2): 217–242. (In Russian)

**Johnson K.** 1992. The Palaearctic "Elfin" Butterflies (Lycaenidae, Theclinae). *Neue entomologische Nachrichten*, **29**: 1–141.

**Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Meintjes P. & Drummond A.** 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, **28**: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

**Korb S.K.** 2016. The lectotype designation of Thecla frivaldszkyi Lederer, 1855 with remarks to the distribution and systematics of the blue butterflies of the genus Ahlbergia Bryk, 1947 (Lepidoptera, Lycaenidae). *Amurian zoological Journal*, **10**(3–4): 171–176. (In Russian). https://doi.org/10.33910/1999-4079-2018-10-3-4-171-176

**Korshunov Yu.P.** 2002. *Butterflies of North Asia*. Moscow: KMK Press. 242 p. (In Russian).

**Krupitsky A.V.** 2018. A new "elfin" butterfly species of Cissatsuma Johnson, 1992 (Lepidoptera, Lycaenidae) from northwestern Sichuan, China. *Zootaxa*, **4524**: 482–488. https://doi.org/10.11646/zootaxa.4524.4.5

**Krupitsky A.V., Shapoval N.A., Schepetov D.M., Ekimova I.A. & Lukhtanov V.A.** 2022. Phylogeny, species delimitation and biogeography of the endemic Palaearctic tribe Tomarini (Lepidoptera: Lycaenidae). *Zoological Journal of the Linnean Society*, **196**: 630–646. https://doi.org/10.1093/zoollinnean/zlab055

**Krupitsky A., Shapoval N. & Shapoval G.** 2023. DNA barcoding of the Palaearctic elfin butterflies (Lepidoptera, Lycaenidae) with a description of four new species from Vietnam. *Insects*, **14**: 352. https://doi.org/10.3390/insects14040352

**Lanfear R., Calcott B., Ho S.Y.W. & Guindon S.** 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**: 1695–1701. https://doi.org/10.1093/molbev/mss020

**Lukhtanov V.A., Sourakov A., Zakharov E.V. & Hebert P.D.N.** 2009. DNA barcoding Central Asian butterflies: increasing geographical dimension does not significantly reduce the success of spe-

cies identification. *Molecular Ecolology Resources*, **9**: 1302–1313. https://doi.org/10.1111/j.1755-0998.2009.02577.x

**Lukhtanov V.A., Vishnevskaya M.A., Volynkin A.V., Yakovlev R.V.** 2007. Butterflies (Lepidoptera, Rhopalocera) of the West Altai. *Entomologicheskoe Obozrenie*, **86**(2): 347–369. (In Russian; English translation: *Entomological Review*, **87**: 524–544. https://doi.org/10.1134/S001387380705003X).

**Matsuda S. & Bae Y.S.** 1998. Systematic study on the "Elfin" butterflies, Callophrys frivaldszkyi and C. ferrea (Lepidoptera, Lycaenidae), from the Far East. *Transactions of the Lepidopterological Society of Japan*, **49**(1): 53–64.

**Miller L.D.** 1970. Nomenclature of wing weins and cells. *Journal of Research on the Lepidoptera*, **8**(2): 37–48. https://doi.org/10.5962/p.333547

**Novomodnyi E.V. & Fonova E.A.** 2010. Butterflies (Insecta, Lepidoptera: Hesperioidea, Papilionoidea) from the Ayano-Maiskii District Khabarovskii Krai Province. *Amurian zoological Journal*, **2**(4): 322–337. (in Russian). https://doi.org/10.33910/1999-4079-2010-2-4-322-337

**Omelko M.M. & Omelko M.A.** 1995. Novye dannye po sistematike i biologii khvostatok roda Satsuma Murr. (Lepidoptera, Lycaenidae) Primor'ya [New data on systematics and biology of the elfin-butterfly genus Satsuma Murr. (Lepidoptera, Lycaenidae) from the Primorskiy Territory]. *In*: *Biologicheskie issledovaniya na Gornotaezhnoy stantsii* [Biological investigation on the Mountain-Taiga Station], **2**: 218–233. Ussuriysk. (in Russian).

**Rambaut A.** 2012. FigTree. *Molecular evolution, phylogenetics and epidemiology* [online]. http://tree.bio.ed.ac.uk/software/figtree [viewed 25 March 2023].

**Robbins R.K., Cong Q., Zhang J., Shen J., Busby R.C., Faynel C., Duarte M., Martins A.R.P., Prieto C., Lamas G. & Grishin N.** 2022. Genomics-based higher classification of the species-rich hairstreaks (Lepidoptera: Lycaenidae: Eumaeini). *Systematic Entomology*, **47**: 445–469. https://doi.org/10.1111/syen.12541

**Ronquist F. & Huelsenbeck J.P.** 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**(12): 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

**Rybalkin S.A., Benedek B. & Dubatolov V.V.** 2022. New for the fauna of Kunashir Island moths and butterflies (Lepidoptera: Carposinidae, Zygaenidae, Tortricidae, Geometridae, Notodontidae, Erebidae, Nolidae, Noctuidae, Lycaenidae). *Far Eastern Entomologist*, **457**: 13–32. https://doi.org/10.25221/fee.457.3

**Shapoval N.A., Yakovlev R.V., Kuftina G.N., Lukhtanov V.A., Knyazev S.A., Romanovich A.E. & Krupitsky A.V.** 2021. Identification of natural hybrids between Ahlbergia frivaldszkyi (Lederer, 1853) and Callophrys rubi (Linnaeus, 1758) (Lepidoptera, Lycaenidae) using mitochondrial and nuclear markers. *Insects*, **12**: 1124. https://doi.org/10.3390/insects12121124

**ten Hagen W. & Miller M.A.** 2010. Molekulargenetische Untersuchungen der paläarktischen Arten des Genus Callophrys Billberg, 1820 mit Hilfe von mtDNA-COI-Barcodes und taxonomische Überlegungen (Lepidoptera: Lycaenidae). *Nachrichten des entomologischen Vereins Apollo*, **30**: 177–197.

**Tshikolovets V., Bidzilya O. & Golovushkin M.** 2002. *The butterflies of Transbaikal Siberia*. Brno – Kiev: Konvoj Ltd. 320 p.

**Tshikolovets V., Kosterin O., Gorbunov P. & Yakovlev R.** 2016. *The Butterflies of Kazakhstan (Lepidoptera, Rhopalocera)*. Pardubice: Tshikolovets Publications.379 p.

**Tshikolovets V. & Streltzov A.** 2019. *The butterflies of Russian Far East (Khabarovskiy and Primorskiy Kray, Jewish Autonomous and Amur Regions), Sakhalin and Kuril Islands*. Pardubice: Tshikolovets Publications. 472 p.

**Tshikolovets V., Yakovlev R. & Balint Z.** 2009. *The butterflies of Mongolia*. Kyiv – Pardubice: Tshikolovets Publications. 320 p.

**Tshikolovets V., Yakovlev R. & Kosterin O.** 2009. *The Butterflies of Altai, Sayans and Tuva (South Siberia)*. Kyiv – Pardubice: Tshikolovets Publications. 374 p.

**Tuzov V.K.** 2000. Genus Ahlbergia. *In*: **Tuzov V.K.** (Ed.). *Guide to the butterflies of Russia and adjacent territories (Lepidoptera, Rhopalocera)*, **2**: 118–120. Sofi a– Moscow: Pensoft.

**Valencia-Montoya W.A., Quental T.B., Tonini J.F.R., Talavera G., Crall J.D., Lamas G., Busby R.C., Carvalho A.P.S., Morais A.B., Oliveira Mega N., Romanowski H.P., Liénard M.A., Salzman S., Whitaker M.R.L., Kawahara A.Y., Lohman D.J., Robbins R.K. & Pierce N.E.** 2021. Evolutionary trade-offs between male secondary sexual traits revealed by a phylogeny of the hyperdiverse tribe Eumaeini (Lepidoptera: Lycaenidae). *Proceedings of the Royal Society B: Biological Sciences*, **288**(1950): 20202512. https://doi.org/10.1098/rspb.2020.2512

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