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Abstract. The present paper summarises data on the northern localities of *Parnassius mnemosyne* (L.) (Papilionidae), which are mostly situated in the Russian Federation, and gives a thorough description of the species' northern range location. It is shown that the northernmost populations exist within the karst landscapes in the north of White Sea-Kuloi Plateau (between $65^{\circ}35'$ and $66^{\circ}03'$ N) in the lower valleys of the rivers Soyana and Kuloi and in the north of Timan Highland ($66^{\circ}10'$ N) along the shore of Kosminskoe Lake (the Pechora river basin). The northern limits of the Clouded Apollo's range appear to be strongly determined by the distribution of its larval host plants (primarily *Corydalis solida* (L.) Clairv., Papaveraceae) and the role of climate and relief seems to be of minor importance.

Introduction

The Clouded Apollo butterfly *Parnassius mnemosyne* (Linnaeus, 1758) (Papilionidae) is an endangered species in Europe (Van Swaay & Warren 1999; Van Swaay et al. 2010). Its decline has been attributed to the cessation of traditional management, grazing and mowing of semi-natural grasslands and coppicing in woodlands (Luoto et al. 2001; Väisänen & Somerma 1985). The distribution of the species in European countries is known with a high certainty, but it remains less thoroughly known in the Russian Federation (Kudrna et al. 2011; Weiss 1999) due to the less intensive recording in northern Russia. In the meantime, a few individuals from Northern Russia have been described as separate subspecies or other morphological forms (e.g., Eisner & Sedych 1964; Kreuzberg 1989; and others). Some predictive models have been published on the distribution of *P. mnemosyne* which reveal its possible change under biotic (larval host plants) interactions, climate conditions (Araújo & Luoto 2007; Settele et al. 2008), and habitats (Heikkinen et al. 2007), based on West European data.

The habitat preferences of the Clouded Apollo in European countries and the southern regions of European Russia are well studied, but the northern part of Russia has not yet been surveyed (Gorbach & Kabanen 2010; Lyvovsky & Morgun 2007; Weideman 1986; etc.). As populations of this species inhabit heterogeneous environments, their structure generally conforms to the metapopulation model in which a landscape is divided into suitable patches and unsuitable matrix (Gorbach & Kabanen 2010; Luoto et

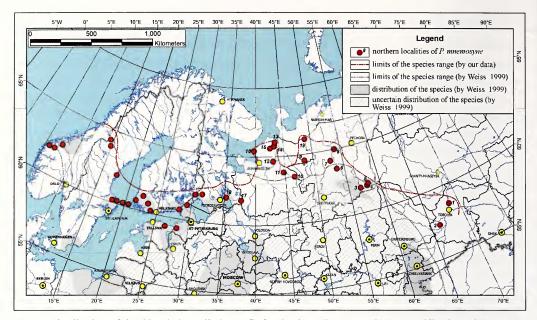


Fig. 1. Distribution of the Clouded Apollo butterfly in Northern Europe and Western Siberia and the northern boundary of the species range. The Russian localities – according to data from Table 1 (locality numbers on the map correspond to numbers in the Table); the Western European localities – according to Settele et al. (2008) and Somerma & Yakovlev (1998).

al. 2001). For example, in Fennoscandia the Clouded Apollo inhabits a dense network of semi-natural grasslands (with mating sites and nectar sources) and deciduous forest patches (with larval food plants) (Heikkinen et al. 2007). Migration routes of individuals can extend onto the meadows and shrubs of open spaces in forests (Gorbach & Kabanen 2010; Konvička et al. 2006; Meier et al. 2005; Valimaki & Itamies 2003).

The Clouded Apollo butterfly is a specific K-strategist; females can mate only once and lay about 50 eggs dispersed over a large area (Meglecz et al. 1997; Weideman 1986). *P. mnemosyne* is an oligophagous species and its larvae develop on various plant species of the genus *Corydalis* DC. (Papaveraceae). In the north of Russia, *Corydalis solida* (L.) Clairv. and *C. capnoides* (L.) Pers. have been recorded (Korshunov 2002; Tatarinov & Dolgin 1999). Reports from other countries include *Corydalis solida* for Finland (Luoto et al. 2001; Somerma 1997), *C. intermedia* (L.) Mérat and *C. pumila* (Host) Rchb. for Sweden (Franzén & Imby 2008), and *C. intermedia* for Norway (Aagaard & Hanssen 1989). Knowledge of the host-plant species is important to explain the local and landscape distribution of the Clouded Apollo butterfly (Heikkinen et al. 2005; Luoto et al. 2001). Spatial structure of *P. mnemosyne* metapopulations is determined by the distribution of the *Corydalis* populations (Gorbach & Kabanen 2010).

This paper maps the northern boundary of the *P. mnemosyne*'s range, summarising the information about the peripheral northern localities of this species and discussing the relative influence of climatic factors and host-plant availability upon the limits of the species range.

Materials and methods

The survey of marginal northern *P. mnemosyne* populations was conducted in Arkhangelsk oblast (Russian Federation). A. M. Rykov studied the populations in the Pinega State Nature Reserve annually during 1978–2011. Field studies on the Soyana, Kuloi, Pinega and Yula Rivers were conducted between 2002 and 2007. In 2003, collector L. P. Shoshin (Arkhangelsk) sampled a few specimens of the Clouded Apollo in the Ivovik Stream Valley, located at the Winter Coast of the White Sea. Data on other northern *P. mnemosyne* localities were obtained from different research papers. The arrangement of the localities was digitised and mapped. The species range data in this map were added from Weiss' (1999) book.

The distribution of *Corydalis* plants was obtained from a digitised version of "Atlas Flora Europaeae" (AFE) (Lahti & Lampinen 1999) and from "Flora Sibiriae" (Malyschev & Pechkova 1994). Additional data originated from regional botanic publications (Liden 2001; Puchnina et al. 2000; Schmidt 2005). All botanical data were transferred to the AFE grid map (squares of ca. 50 km \times 50 km, the Universal Transverse Mercator (UTM) projection and the Military Grid Reference System (MGRS)) (Jalas & Suominen 1972–1996). Meteorological data were obtained from the website of the World Data Center for Meteorology, Asheville, North Carolina.

Northern localities of the Clouded Apollo butterfly

As shown in Fig. 1, the northern boundary of the range stretches from the Norwegian coast in the West to the Irtysh river headstream in the East, about 4000 km in length. Some northern localities of this species in Fennoscandia are highly populated (Aagaard & Hanssen 1989; Luoto et al. 2001; Opheim 1983; Somerma 1997; Väisänen & Somerma 1985). There is little data on regional expansions (Marttila et al. 2001; Meier et al. 2005). Information about marginal northern localities of *P. mnemosyne* in Russia is compiled in Tab. 1.

Tyumen oblast. In 1987–1988 *P. mnemosyne* populations were discovered in the Irtysh (near the city of Tobolsk) and Iska (Korshunov 2002; Kreuzberg 1989) river valleys. The populations inhabit hay-harvested and grazed floodplain meadows, maintained in river valleys since the 19th century.

Komi Republic. The most northern localities of *P. mnemosyne* were discovered in the valleys of the Pechora river basin at the foothills of the Northern Urals and Timan Highland (Tatarinov & Dolgin 1999, 2001). The cited authors have conducted field studies there since the 1990s. The highest density of populations was detected in the Pechoro-Ilychsky Nature Reserve (Tatarinov & Dolgin 1999). The habitats of the populations were natural humid mixed-herb meadows in river valleys, which are characterised by heterogeneity of species composition and density of vegetation. The dominant species were *Filipendula ulmaria* (L.) Maxim. (Rosaceae), *Crepis sibirica* L. (Asteraceae), *Thalictrum* sp., *Trollius europaeus* L. and *Aconitum septentrionale* Koelle (Ranunculaceae), *Valeriana wolgensis* Kazak. (Valerianaceae), *Geranium sylvaticum* L. (Geraniaceae).

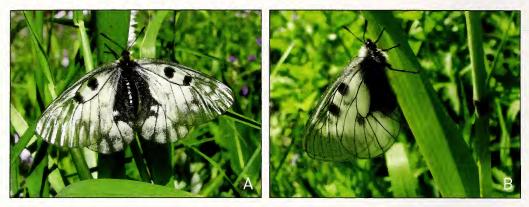


Fig. 2. The Clouded Apollo butterfly specimens from peripheral northern populations inhabited meadows in Moseev Ravine in the White Sea-Kuloi Plateau, Arkhangelsk oblast, Northern European Russia. A: upper-side; B: underside.

Arkhangelsk oblast. The populations are located within the frontiers of the northern part of the Timan Highland (Tatarinov & Dolgin 1999), at the White Sea-Kuloi Plateau (Belomorsko-Kuloiskoe Plato) and in the Pinega river basin. These are probably the largest populations of P. mnemosyne among the northern ones. In the Southeast of the White Sea-Kuloi Plateau, in the Pinega State Nature Reserve, observations of P. mnemosyne populations have been made since 1978. The populations were discovered in three large karst ravines (Moseev, Vizgunov and Severny), belonging to the Sotka river basin (tributary of the Kuloi river) (Figs 2a, b). The butterfly inhabited small patches of natural humid mixed-herb meadows at the ravine bottoms (Fig. 3). The dominant species of these meadows are Aconitum septentrionale Koelle and Thalictrum sp. (Ranunculaceae), Anthriscus sylvestris (L.) Hoffm. (Apiaceae), Geranium sylvaticum L. (Geraniaceae), Filipendula ulmaria (L.) Maxim. (Rosaceae), Cirsium oleraceum (L.) Scop. (Asteraceae), Chamerion angustifolium (L.) Holub (Onagraceae), Paeonia anomala L. (Paeoniaceae) and Elymus caninus (L.) L. (Poaceae). Here, the ravines are surrounded by Siberian spruce (Picea abies ssp. obovata (Ledeb.) Domin, Pinaceae) forests, with small inclusions of Siberian larch (Larix sibirica Ledeb., Pinaceae). These meadows were formed in karst ravines about 2500-3500 years ago and existed hereafter owing to harsh local microclimates, which prevented forest expansion (Titova et al. 2011). The total area of the Clouded Apollo habitats is ~4 ha within Vizgunov ravine, ~ 10 ha within Moseev ravine and ~ 15 ha within Severny ravine. The flight period of adult P. mnemosyne continues from mid-June to the beginning of August (13.vi-6.viii), and adult density varies highly from year to year (Bolotov 2004; Rykov 2009). Imagines were observed annually in 1978-2011 in two of the three patches, but in Vizgunov ravine they have not been recorded since 2000.

The *P. mnemosyne* population inhabiting the karst areas of the Soyana river valley was observed in the Northeast of the White Sea-Kuloi Plateau during 2002-2007. Zonal vegetation is represented by spruce and larch forests. The butterflies inhabit a river valley about 50 km long, as well as humid mixed-grass meadows, which are typical of the river valley bottom and which form small patches about 1-3 ha in size,



Figs 3–4. Habitats of the Clouded Apollo butterfly in the White Sea-Kuloi Plateau, Arkhangelsk oblast, Northern European Russia. **3**. Meadow in the Moseev Ravine. **4**. Meadow in the Soyana river valley.

divided by thin forests and shrubs (Fig. 4). The meadows form natural floodplains, and they were used for hay production until the end of the 20th century. The dominant plant species were similar to those of meadows in large karst ravines.

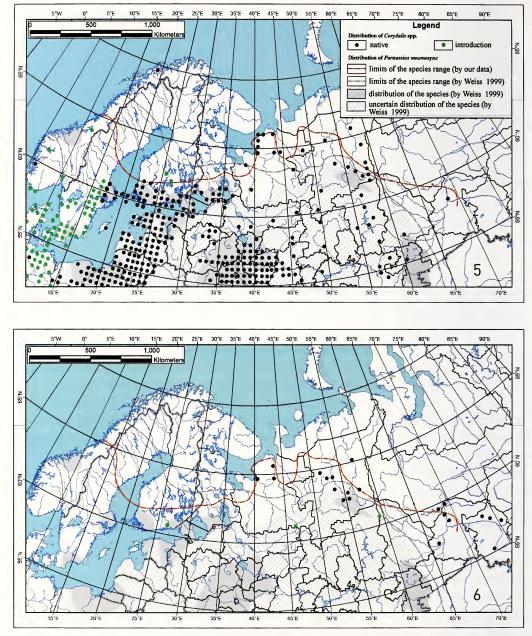
A population of *P. mnemosyne* was found in the Ivovik Stream valley (the northwest of the White Sea-Kuloi Plateau) in 2003. The stream has a deeply scarred valley, restricted to places of Vendian (Ediacara) rocky outcrop on the Winter Coast of the White Sea. The butterflies inhabit small patches of natural humid mixed-herb meadows. This population is isolated from all other localities by continuous stretches of spruce forests. **Nenetsky autonomous district.** Only a few specimens of *P. mnemosyne* were discovered on the Kosminskoe Lake shore meadows (northern part of Timan Highlands) (Tatarinov 2006).

Karelia Republic. The distribution of the species is localised around Onega Lake and the eastern part of Ladoga Lake areas (Gorbach & Kabanen 2010; Gorbach & Reznichenko 2009; Kaisila 1947; Somerma & Yakovlev 1998). Localities of *P. mnemosyne* also exist on upland meadows on the islands of Bolyshoy Klimenetskiy and Kizhi in Onega Lake, and at the flood-land meadows along the Koloda river shores in the southeastern part of Russian Karelia (Humala 1998). The meadows were used as hayfields until the beginning of the 21th century. The dominant species of the meadows are *Heracleum sphondylium* ssp. *sibiricum* (L.) Simonk. (Apiaceae), *Rumex acetosa* ssp. *thyrsiflorus* (Fingerh.) Hayek (Polygonaceae), *Centaurea scabiosa* L., *Tanacetum vulgare* L. and *Taraxacum officinale* F.H. Wigg. (Asteraceae), *Barbarea vulgaris* W.T. Aiton (Brassicaceae), *Poa pratensis* L. and *Phleum pratense* L. (Poaceae). In some localities, high abundance of adults was observed (Gorbach & Kabanen 2010).

Northern boundary of the species range: the outcome of biotic interactions and climate conditions

It was mentioned before that *P. mnemosyne* is not usually found farther north than $63-64^{\circ}$ N (Kudrna et al. 2011; Lyvovsky & Morgun 2007; Settele et al. 2008; Weiss

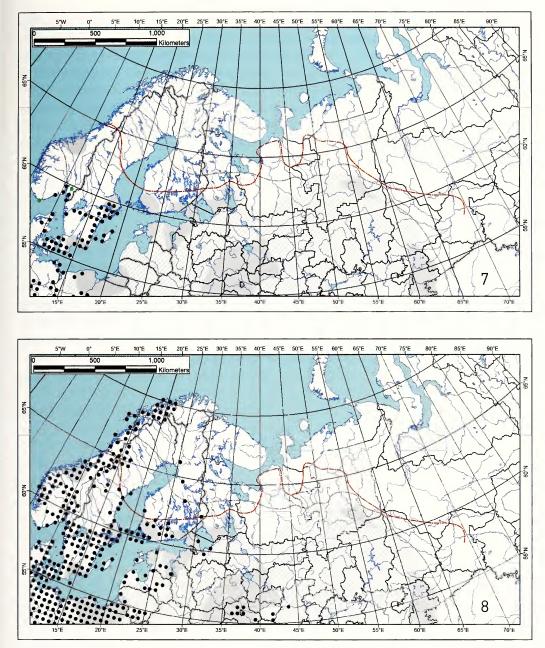
BOLOTOV et al .: Northern range boundary of Parnassius mnemosyne



Figs 5–6. Distribution of the four species of *Corydalis* spp. and the northern boundary of the Clouded Apollo butterfly range. 5. *C. solida* (L.) Clairv. 6. *C. capnoides* (L.) Pers.

1999). New data allow us to specify the northern limits of the species distribution. The world's northernmost populations have been registered at the north of the White Sea-Kuloi Plateau (between $65^{\circ}35'$ and $66^{\circ}03'$ N) in the Soyana and Kuloi lower river valleys and in the north of Timan Highland ($66^{\circ}10'$ N) at the Kosminskoe Lake shore (the Pechora river basin).

Nota lepid. 36 (1): 19-33



Figs 7–8. Distribution of the four species of *Corydalis* spp. and the northern boundary of the Clouded Apollo butterfly range. 7. *C. pumila* (Host) Rchb. 8. *C. intermedia* (L.) Mérat.

Sedimentary Paleozoic bedrock and modern areas of active karst processes form both of these territories (Gofarov et al. 2006; Shvartsman & Bolotov 2008). The karstic rocks are represented by Carboniferous limestone in the Timan Highland and Permian gypsums and anhydrites in the White Sea-Kuloi Plateau. The plateau region is known as a refuge for different animal and plant species, some of which are northern postgla-

cial and some are southern Atlantic relicts. Dryads Dryas octopetala L. and D. o. ssp. punctata (Juz.) Hultén (Rosaceae), osiers Salix myrsinites L. and S. reticulata L. (Salicaceae) (Puchnina et al. 2000; Simacheva 1986), pond damselflies Coenagrion glaciale (Selys, 1872) and C. hylas (Trybom, 1899) (Coenagrionidae) (Bernard & Daraż 2010), carabid beetles Pterostichus brevicornis (Kirby, 1837) and Bembidion yukonum Fall, 1926 (Carabidae) (Mokhnatkin et al. 2010), collembolans Desoria tshernovi (Martynova, 1974) and D. inupikella Fjellberg, 1978 (Isotomidae) (Babenko 2008) may be considered to be postglacial relict species. In Europe, these postglacial relicts are representatives of a cold-stenothermal fauna that probably colonised the subcontinent during the late Pleistocene and early Holocene in the period of the maximum distribution of birch and pine (Bernard & Daraż 2010; Elina et al. 2005). Other Atlantic relicts, besides P. mnemosyne, include its larval host plants Corydalis solida and C. capnoides, as well as the plants Stellaria nemorum L. (Caryophyllaceae), Cypripedium parviflorum Salisb. (Orchidaceae), Paeonia anomala L. (Paeoniaceae) (Puchnina et al. 2000; Simacheva 1986), the blue butterflies Cupido alcetas (Hoffmannsegg, 1803), C. minimus (Fuessly, 1775) and Aricia nicias (Meigen, 1829) (Lycaenidae) (Bolotov 2004), and the carabid beetles Calosoma investigator (Illiger, 1798), Lebia cruxminor (Linnaeus, 1758) and Badister lacertosus Sturm, 1815 (Carabidae) (Mokhnatkin et al. 2010). They probably migrated to Northern Europe during the Atlantic period of the Holocene. According to the studies of molecular markers, expansion of P. mnemosyne northern lineages took place during the postglacial warming period 5000-7000 years ago (Gratton et al. 2008).

During the present period, populations of both groups of relict species remain isolated in the same regions of the European taiga, particularly in karst landscapes (Shvartsman & Bolotov 2008). The coexistence of such different relict species is possible due to the high heterogeneity of karst landscapes. Sites with highly contrasting temperatures exist in such areas: very cold sites near caves with long-term ice alternating with well-heated patches in slopes of south exposure and wide karst ravines. These sites can easily be located near each other. For example, upland herb meadows grow at the bottom of Moseev ravine (inhabited by the Clouded Apollo and other southern relicts), whereas small patches of mountain dryads tundra with *Salix myrsinites* and *S. reticulata* occur on the nearby gypsums and anhydrites outcrops.

The altitude range of the northern localities of *P. mnemosyne* is very broad (Tab. 1). Here populations exist under different climatic conditions (Tab. 2). Therefore, climate and relief cannot be considered as major limiting factors for the expansion of the Clouded Apollo northward. Dot maps of the distribution area of different *Corydalis* species (Figs 5-8) reveal that the northern boundary of *P. mnemosyne*'s range almost fully correlates with the distribution of only one larval food species – *Corydalis solida*. *Corydalis intermedia* is widespread in Western Fennoscandia, but *P. mnemosyne* is found only in a few localities. However, Fennoscandian populations of *P. mnemosyne* mostly prefer *Corydalis solida*, which is represented usually by introduced individuals (Liden 2001). These differ from native populations in flower and bract constitution details. This plant species is widely cultivated in parks and gardens and escapes from cultivation frequently. Many naturalised populations of *Corydalis solida* exist in the

south of Norway (primarily along the seacoast), southern Sweden and central Finland (AFE Secretariat, A. Sennikov, pers. comm.).

Studies of regional differences in the Clouded Apollo larval food preference may be enlightening. For example, in the European part of Russia (Penza oblast), *P. mnemosyne* larvae were registered feeding only on *Corydalis solida*, although *C. cava* (L.) Schweigg. & Körte and *C. cava* ssp. *marschalliana* (Willd.) Hayek occur in the same biotopes (Polumordvinov & Shibaev 2007). Also, models using larval host plants as a predictor of variability of the studied species predicted the presence of the Clouded Apollo when *Corydalis solida* was present and the absence of the Clouded Apollo when *C. solida* was also absent; this was true even when other *Corydalis* species were present (Araújo & Luoto 2007).

Given that the distribution of *P. mnemosyne* in the north mostly correlates with the presence of *Corydalis* populations, and populations of the butterfly inhabit natural meadows, it is difficult to forecast significant future changes in the northern boundary of the species range. Geographically, the majority of peripheral northern localities of this species is concentrated in sparsely populated areas in the Russian Federation, in predominantly non-disturbed taiga landscapes with difficult access, which do not seem to be threatened by human activities. Many Russian populations inhabit the state nature reserve territories: "Kizgi Scerries" Reserve (Karelia Republic), Pinega and Soyansky Reserves (Arkhangelsk oblast), Pechoro-Ilychsky and "Belaja Kedva" Reserves (Komi Republic).

P. mnemosyne occupies habitats with optimal ecological conditions in different biomes, therefore this species has a zonal replacement of habitat preferences (Bei-Bienko 1966; Chernov 2008). In the north, it behaves like a typical mesophilous species, which prefers open intrazonal habitats with medium humidity and solar heat (in different types of open meadows). Southern populations prefer mostly humid and less warm habitats. In Central Europe, including southern regions of European Russia, the Clouded Apollo is a woodland species and inhabits forest steppes, sparse deciduous forests and forest clearings where the larval host plants grow (Konvička & Kuras 1999; Konvička et al. 2006; Meglecz et al. 1997; Polumordvinov & Shibaev 2007; Weidemann 1986). In the south of Europe, its populations avoid lowlands, where the environment is too hot and dry, and reside primarily in the humid and cool habitats of mountain-subalpine belts (Descimon & Napolitano 1993; Lyvovsky & Morgun 2007; Napolitano et al. 1988; Napolitano & Descimon 1994). Hence, the distribution of the Clouded Apollo in the North is limited principally by the distribution of its larval food plants. However, it should be stated that the latitudinal change of landscape-habitat occupancy also depends on regional climatic conditions (temperature and humidity). The results of this paper agree with the importance of biotic interactions for modelling individual species distribution at the macroecological scale under climate change (Araújo & Luoto 2007).

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Tab. 1. Peripheral ne
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No.* Coordinates	linates	Altitude, Locality m.a.s.l.	Locality	Administrative region Geographic region	Geographic region	Information source
58°3'	58° 37' 44″ N 68° 34' 00″ E	40	Irtysh river valley (near Nadzy village); other locality nearby: Ingair railway station (58°37'N, 68°46'E)	Tyumen oblast	Western Siberian Plain, Irtysh River basin	Korshunov 2002
57°2	57°23'07" N 66° 14'50" E	60	Iska river valley, Irtysh river basin (near Shapkul village)	///	//	//
61°4	61°49′14″ N 56°51′02″ E	140	Pechora river valley (near Yaksha village)	Komi Republic	Northern Ural	Tatarinov & Dolgin 1999, 2001; A. G. Tatarinov & O. I. Kulakova, pers. comm.
61°5	61° 52' 32" N 57° 56' 31" E	200	Garevka river valley, Pechora river basin, Pechora-Ilychsky State Nature Reserve	//	//	//
62°(62°01′43″ N 58°10′28″ E	170	Yany-Pupu-Nier mountain range, Pechora-Ilychsky State Nature Reserve	//	//	//
63°3	63°33'07" N 53°29'33" E	120	Ukhta river valley (near city of Ukhta), Izhma river basin	//	Foothills of Timan Highland	//
64°]	64° 13' 07" N 52° 53' 44" E	110	Belaya Kedva river valley, Pechora river basin	//	Timan Highland	//
64°:	64°55'34" N 53°46'37" E	30	Izhma river valley (near Izhma village)	//	//	//
64°.	64°32'59" N 48°26'57" E	140	Mezen river valley (near Vozhgora village)	Arkhangelsk oblast	//	//
63°:	63°25′57″ N 46°30′19″ E	80	Pinega river valley (near Nyukhcha village)	//	Northern Dvina-Mezen Our observations	Our observations
63°.	63°48′34″ N 44°44′24″ E	50	Yula river valley, Pinega river basin	//	//	//
64°.	64°38'29″ N 43°03'39″ E	60	Moseev karst ravine, Pinega State Nature Reserve; two other localities nearby: Vizgunov karst ravine (64°39'N; 43°02'E) and Seventy karst ravine (64°32'N;	//	White Sea-Kuloi Plateau	//

No.*	No.* Coordinates	Altitude, Locality m.a.s.l.	Locality	Administrative region Geographic region	Geographic region	Information source
13	66° 02′ 43″ N 43° 28′ 13″ E	20	Mouth of the Kuloi river (near Dolgoschelye village)	//	//	//
14	65° 44' 32" N 43° 15' 12" E	20	Lower course of the Soyana river, Kuloi river basin	//	//	//
15	65°36′33″ N 42°32′31″ E	30	Soyana river valley, Kuloi river basin; many other localities along the river valley were also recorded here (see Rykov 2009)	//	//	//
16	65°27'00" N 39°42'34" E	40	Ivovik stream valley	//	Winter Coast Mountains, shore of the White Sea	//
17	17 61°47′30″ N 37°43′03″ E	110	Koloda river valley (near Ust- Reka village)	Karelia Republic	Onega lake area	Humala 1998
18	62°05′00″ N 35°13′00″ E	40	Kizhi Island; other locality nearby: Bolshoy Klimenetsky Island (61°58'N, 35°15'E)	//	//	Gorbach & Kabanen 2010; Humala 1998
19	66° 10' 00" N 48° 57' 00" E	110	Kosminskoe Lake, Pechora river Nenetsky autonomous Timan Highland basin	Nenetsky autonomous district	Timan Highland	Tatarinov 2006

Table 1 continued.

ria 1 1 3, 1 3, 1 6, 10, 10, 10, 110, 11, 14 10, 11, 14 11, 14	Weather station	July mean temperature, °C	January mean temperature, °C	Summarised daily means above 10°C	Length of the period with summarised daily means above 10°C [days]
per la construction de la constr	Tobolsk	18.8	-16.9	2090	127
per la construction de la constr	Troitzko-Pechorskoje	16.6	-16.6	1499	91
hern	Izgma	15.7	-18.4	958	61
hern	Koinas	16.3	-15.5	1327	86
hern	Sura	16.7	-14.2	1342	86
hern	Pinega	15.5	-15.0	1216	85
	Mezen	14.8	-13.2	1036	75
Winter Coast 16 Mountains, shore of the White Sea	Zimnegorskij	14.7	-9.8	746	50
Southern Karelia 17, 18	Petrozavodsk	16.8	-8.0	1773	118
Northern Estonia —	Tallin-Toravere	18.3	-3.6	2137	117
Southern Finland —	Helsinki-Vantaa	17.7	-3.4	2001	131
Central Sweden	Ostersund-Froson	14.5	-4.8	1327	94
Southern Norway —	Trondheim-Vernes	17.4	-2.9	1936	128

Tab. 2. Climatic conditions of northern localities of the Clouded Apollo butterfly.

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Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

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