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Relict occurrence of East Palaearctic dragonflies in northern European Russia, with first records of *Coenagrion glaciale* in Europe (Odonata: Coenagrionidae)

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Abstract

The East Palaearctic *Coenagrion glaciale* and *C. hylas* are characterized by a current disjunct distribution. New data from northern European Russia significantly modify the earlier known pattern of their distribution. The first European records of *C. glaciale* and a new record of *C. hylas* west of the Urals are reported from the environs of Pinega village (Arkhangelsk oblast, Pinega region). Distribution ranges of these two species are analysed in light of their palaeogeography. These postglacial relicts in Europe are representatives of a cold-stenothermal fauna that probably colonized the continent during the late Pleistocene and early Holocene in the period of the maximum spread of birch and pine. During the Atlantic period they withdrew far to the East remaining probably only as isolates in the Urals and in Europe. However, the new records suggest that the European remains of the early Holocene distribution may be more numerous and extensive than previously believed and are concentrated especially in the almost unexplored northeast. The survival of *C. glaciale* and *C. hylas* in the presumptive isolate of their distribution range in the Pinega region is probably a consequence of a specific combination of severe climate and habitat and microclimatic conditions, largely influenced by karst. The habitat conditions at 'Pinega' localities are analysed in the context of the species' requirements. Additionally, biogeographically important findings of the North and Central Asian *Aeshna serrata* are recorded. This species was previously assumed to occur in Europe only as an isolate around the Baltic Sea, but the new records suggest that it has a much more extensive but fragmented distribution in the European north and northeast.

Introduction

The distribution of Palaearctic dragonflies is relatively well known in comparison with that of other biogeographical regions. However, there are still unsolved or only partly solved biogeographical problems, especially when dealing with some Asian and East European areas and their fauna. Recognition of the current patterns of distribution in the context of species palaeogeography is an area of interest that still poses many questions and can offer fascinating answers. One such issue is the postglacial westward penetration by the East Palaearctic odonate fauna and its consequences for current species distributions. Beginning with the discovery of *Coenagrion hylas* in Central Europe in the 1950s (Bilek 1954), this issue has frequently been the subject of new findings and interpretations (e.g. Haritonov 1974, 1976; Heidemann 1974; Kiauta & Kiauta 1991; Lohmann 1992; Kosterin 2005; Yanybaeva et al. 2006; Brockhaus 2007).

The aim of this paper is to explore this issue with two East Palaearctic coenagrionids, *C. glaciale* and *C. hylas* in the light of new data from northern European Russia. Their distribution areas are largely confined to central and eastern areas of Asian Russia and to a lesser degree to adjacent East and Central Asian countries. Up to 2008 the only occurrence of *C. hylas* known outside of Asia was a small isolate in Central Europe (Kiauta & Kiauta 1991; Lohmann 1992; Kosterin 2005). However, the details of these species' distributions are largely unknown. The almost unexplored north of Russia in particular has been a terra incognita in this respect. This incomplete state of knowledge on the one hand and the discoveries from the Ural Mountains and their Asian foothills (Haritonov 1974, 1976; Yanybaeva et al. 2006) on the other hand have raised some questions concerning the actual patterns of distribution of these and other East Palaearctic Odonata species, as well as the postglacial westward expansion and eastward withdrawal of the East Palaearctic odonate fauna. Aiming to answer some of these questions, we visited an area in northern European Russia in 2009 and made the first European records of *C. glaciale*, together with biogeographically important findings of *C. hylas* and *Aeshna serrata*.

In this paper, we ask the following questions:

- Was the postglacial westward long-distance expansion of East Palaearctic Odonata restricted to only very few species or was it more common?
- Was this expansion mainly restricted to Asian parts of the Palaearctic or did it cross the Ural Mountains?
- Was the north of Europe the last refugium and the 'way of withdrawal' of cold-stenothermal East-Palaearctic fauna in the warmer Holocene phases?
- Have range isolates of some East Palaearctic species survived in the north and, if so, in which climatic and habitat conditions?

Study area and methods

Description of the study area

The study area in the region of Pinega village (64°30-58'N, 43°13-30'E) was situated in the northern part of the Arkhangelsk Oblast and in the southeastern corner of the karst plain of the White Sea-Kuloi Plateau (Belomorsko-Kuloiskoe Plato). It was located between the abruptly descending margin of the more elevated parts of the plateau and the valleys of the Pinega (in its middle course) and Kuloi Rivers.

The karst rock of the study area mainly consisted of gypsum and dolomite of the Upper Kuloi suite of the Lower Permian. It was exposed on the surface or was covered with Quaternary sediments of diverse thickness, both of glacial and postglacial origin, such as loess-like loam, sandstone, sand, gravel and peat (Shavrina & Malkov 2008). The landscapes of the study area were mosaic, karst and postglacial, or were a combination of these. The relief was relatively flat or gently undulating, but shallow depressions and deeper karst hollows of diverse size, often occupied by pools and small lakes, were locally abundant. There was also a large lake complex in the northern part of the study area. The water bodies were numerous and highly diverse in their trophic status, parameters of mineralization, acidity/alkalinity and vegetation. Besides lakes, which were rather poor in nutrients and influenced by karst water, there were various water bodies in the river valleys, small acidic lakes bordered by *Sphagnum* and complexes of manifold bogs and fens. The area was mostly overgrown with the northern taiga. In the northern part, pine forest (*Pinus sylvestris*) prevailed, while the central and southern parts were dominated by spruce forest (*Picea obovata*) or spruce and pine forest with an admixture of birch (*Betula pubescens*), locally on peat.

Generally, the study area belongs to the Atlantic-Arctic climatic province of the temperate zone and is characterized by a moderate continental humid climate. The winter is long and cold, the summer short, moderately warm and cloudy, and the spring and autumn are fairly long with frequent temperature changes. Mean annual air temperature, calculated from 1978 to 2008, is 0.4°C, mean January temperature is -14.7°C and mean July temperature is +15.6°C. Mean precipitation is 569 mm. The data from the last decade compared with those from the previous two decades showed a 1.0°C increase in the mean annual air temperature and 2°C in the mean July temperature (Fedchenko et al. 2008).

Localities with *Coenagrion glaciale*, *C. hylas* and/or *Aeshna serrata*

Plant species are listed according to their frequency.

Loc. 1: 1 km N of Maletino (64°36'17"N, 43°20'24"E); small (< 1 ha) lake surrounded by pine and spruce forest, the open water table girdled by a narrow (1-4 m) transition mire zone consisting of mosses (*Sphagnum* sp. and *Warnstorfia fluitans*) and helophytes, such as diverse *Carex* spp. (*C. rostrata, C. limosa, C. lasiocarpa, C. canescens*) and *Menyanthes trifoliata, Potentilla palustris, Equisetum fluviatile* (Fig. 1). 3 and 7 July 2009.

Loc. 2: 1.1 km N of Maletino (64°36'17"N, 43°20'18"E); small (0.2 ha) lake situated in the same complex of bogs and water bodies as loc. 1; partly surrounded by peaty pine forest, partly by pine, spruce and birch forest and partly by an open peat bog; the open water girdled by a narrow transition mire zone, i.e. by a 1-1.5 m wide belt of mosses (*Sphagnum* sp.) and helophytes such as diverse *Carex* spp. (*C. limosa, C. lasiocarpa, C. canescens, C. diandra, C. rostrata*) and *Menaynthes trifoliata, Potentilla palustris, Equisetum fluviatile*; some *Nuphar lutea* and *Nymphaea tetragona* on the water surface. 3 and 7 July 2009.

Loc. 3: 0.9 km W of the Khaimusovo settlement (64°38'33"N, 43°21'27"W), 0.75 km SE of the main road to Pinega; a meso-oligotrophic complex of a small lake and diverse bogs, transition mires and alkaline fens, partly permanently flooded with shallow water; also with water-filled depressions ('Schlenken') and open-water 'channels' (Fig. 2); acidic waters, poor in nutrients and dissolved solids, and non-acidic waters, more minerotrophic and mesotrophic, occurred; a local inflow of mineralized, alkaline water from the surrounding karst (at least via a small trickle) was clearly recognizable in the species composition of vegetation;

Figure 1: Habitat of *Coenagrion glaciale* — lake near Maletino (loc. 1), Arkhangelsk oblast, European Russia, 3 July 2009. Photo by BD.

moss layer dominated by *Sphagnum* sp., helophytes dominated by *Carex* spp. (*C. limosa*, *C. lasiocarpa*, *C. canescens*, *C. diandra*, *C. rostrata*) and locally by *Equisetum fluviatile*, *Menyanthes trifoliata*, *Potentilla palustris* or *Scirpus hudsonianus*, admixtures of *Drosera anglica*, *Eriophorum latifolium* and *Utricularia vulgaris*, and bushes of *Chamaedaphne calyculata*, *Betula nana* and *Salix lapponum* occurring locally; the locality was surrounded by pine and spruce forest (on karst). 5-7 July 2009.

Loc. 4: 7 km SE of the Krivye Ozera settlement (64°49'46"N, 43°19'06"E); chain of small, postglacial, non-acidic lakes fairly poor in nutrients and to some degree influenced by karst water; the lakes were surrounded by northern pine forest on poor soils; very clear water; emergent vegetation along the shores fairly sparse to fairly dense, consisting of low *Phragmites australis* and of *Carex rostrata*, *Carex acuta*, *Carex nigra*, *Eleocharis palustris* and very rare small *Hippuris vulgaris*; rare floating *Polygonum amphibium*; the whole bottom lined with mats of undetermined moss. 27 June 2009.

Loc. 5: Krivye Ozera, NE edge, 7.1 km SSE of the Krivye Ozera settlement (64°49'24"N, 43°17'27"E); large mesotrophic lake complex formed and fed by karst waters flowing from the more elevated parts of the karst plateau; clear water; dense *Carex acuta* and abundant *Phragmites australis* of medium height, with admixtures of large *Hippuris vulgaris* and *Utricularia minor*. 27 June 2009.

Figure 2: Site inhabited by *Coenagrion glaciale* and *C. hylas* — habitat mosaic near Khaimusovo (loc. 3), Arkhangelsk oblast, European Russia, 6 July 2009. Photo by BD.

Loc. 6: partly standing water bodies on the run of the Syrgovka stream, 3 km WNW of the northern end of Pinega village (64°43'17"N, 43°20'39"E); chain of small lakes fed by karst water, rather poor in nutrients, with clear water, sandy bottom, *Carex rostrata*, *Carex acuta* and Characeae. 30 June 2009.

Loc. 7: 1.2 km N of Okatovo, in the flood plain of the Pinega River (64°31'56"N, 43°16'50"E); a narrow (1 m wide), relatively deep, slow-flowing stream with sections along the shore that were overgrown with abundant *Equisetum fluviatile* and almost without a flow. 1 July 2009.

Methods

The study was carried out between 25 June and 7 July 2009 to find both spring and early summer odonate species after the late and cold spring of that year. Thirty-eight sites were visited in the environs of Pinega village and an additional two in the Arkhangelsk surroundings. The choice of sites was partly based on field accessibility and partly on habitat selection. We attempted to cover the whole spectrum of habitats, from various water bodies in flood plains through clear-water lakes influenced by karst waters up to diverse small lakes and pools situated in a mosaic karst and postglacial landscape and girdled by a vegetation dominated by *Sphagnum* and/or *Carex* species.

Due to frequent bad weather conditions, with low temperatures, dense cloud and long overcast periods, and showers, the studies focused on exuviae and teneral individuals, and to a lesser degree on mature imagines. So the data on imagines do not reflect the actual population numbers but only record rarely met individuals. Besides standard methods of observation and specimen collection, a search for inactive imagines was also undertaken among helophytes bounding the water table and among the herbaceous vegetation at the edge of surrounding forest and in nearby forest glade.

The collected material (imagines, exuviae, photographs) is in the authors' collections and in the Natural History Collections of the Adam Mickiewicz University in Poznań.

Results

In this paper, only the results for *Coenagrion glaciale*, *C. hylas* and *Aeshna serrata* are dealt with, although all species at localities 1-7 are listed in Table 1. Exhaustive faunistic data will be presented in a separate paper.

C. glaciale was recorded at three sites. At loc. 1: a few imagines, males and females, almost inactive in the transition mire vegetation; at loc. 2: a few imagines, males and one female; and at loc. 3: several imagines, males and females, the latter also observed at a small boggy glade 100-200 m from the complex. These localities

Table 1. Records of Odonata species at seven localities in the environs of Pinega village, Arkhangelsk oblast, Russia. Numbers of localities follow those given in the text. (*) foraging, probably allochthonous at the locality; (?) observed at the bog, originating from locality 2 or 1.

Species	Localities						
	1	2	3	4	5	6	7
Coenagrion armatum (Charpentier)	–	x	–	x	x	–	–
Coenagrion glaciale (Selys)	x	x	x	–	–	–	–
Coenagrion hastulatum (Charpentier)	x	–	x	x	–	x	–
Coenagrion hylas (Trybom)	–	–	x	–	–	–	–
Coenagrion johanssoni (Wallengren)	x	x	x	–	–	–	–
Coenagrion lunulatum (Charpentier)	–	–	–	x	–	–	–
Enallagma cyathigerum (Charpentier)	–	–	–	x	x	x	–
Aeshna caerulea (Ström)	–	–	x	–	–	–	–
Aeshna crenata Hagen	x	x	x	–	–	–	–
Aeshna grandis (Linnaeus)	–	–	x	–	–	–	–
Aeshna juncea (Linnaeus)	x	x	x	–	–	–	–
Aeshna serrata Hagen	–	x*	–	x	x	x	x
Aeshna subarctica Walker	–	x	x	–	–	–	–
Cordulia aenea (Linnaeus)	x	x	x	x	–	x	–
Somatochlora metallica (Vander Linden)	–	–	–	–	–	x	–
Leucorrhinia dubia (Vander Linden)	x	x	x	–	–	–	–
Leucorrhinia rubicunda (Linnaeus)	–	x?	x	x	–	–	–
Libellula quadrimaculata Linnaeus	x	x	x	x	x	x	–

were (1) situated in a mosaic of postglacial and karst lanscapes or a combination of them; (2) surrounded by at least partly spruce forest; (3) girdled by a transition mire zone (Fig. 1) or constituting a mosaic of open water and partly flooded bogs and fens (Fig. 2); and (4) characterized by the abundant presence of moderately dense (or mosaic: sparse to dense) low helophytes dominated by *Carex* species. The species was found neither in oxbows and other water bodies in the river valleys, nor in non-*Sphagnum* water bodies influenced by karst water. It was also absent from some small lakes and pools with *Sphagnum* and other moss species, especially those situated in pure pine forest and/or those poor in helophytes.

Individuals of *C. glaciale* were seen only within herbaceous vegetation and due to the bad weather no reproductive activity was observed. Inactive and slightly active females were found among sparse vegetation in sunny, warm and wind-sheltered places at the edges of glades and forests, mostly in a glade situated 100-200 m from the water body. Inactive males were seen perching vertically in fairly dense *Carex* vegetation in the transition mire zone above the water. In three cases it was observed that inactive individuals, when disturbed by the human observer, sidled round a stem to hide the body while still allowing unimpeded vision owing to the wide eye spacing. Active individuals, who had been caught by a dramatic weather change, were found perching in the upper parts of the *Carex* vegetation of the transition mire. In two cases, single individuals migrated between the forest edge and the denser *Carex* belt, always remaining very low above the moss and between the sparse and low vegetation.

Individuals of *C. glaciale* had the following distinguishing morphological features:

- The hind margin of the female pronotum showed in dorsal view a gentle, but distinct, median lobe (Fig. 3b), which in lateral view was even more prominent and slightly resembled a dog's head (Fig. 3a);
- The lower branches of the male cerci were variably, but mostly significantly, extending beyond the upper branches (Figs 3c, d);
- The male paraprocts were twice or almost twice as long as the cerci (Figs 3c, d);

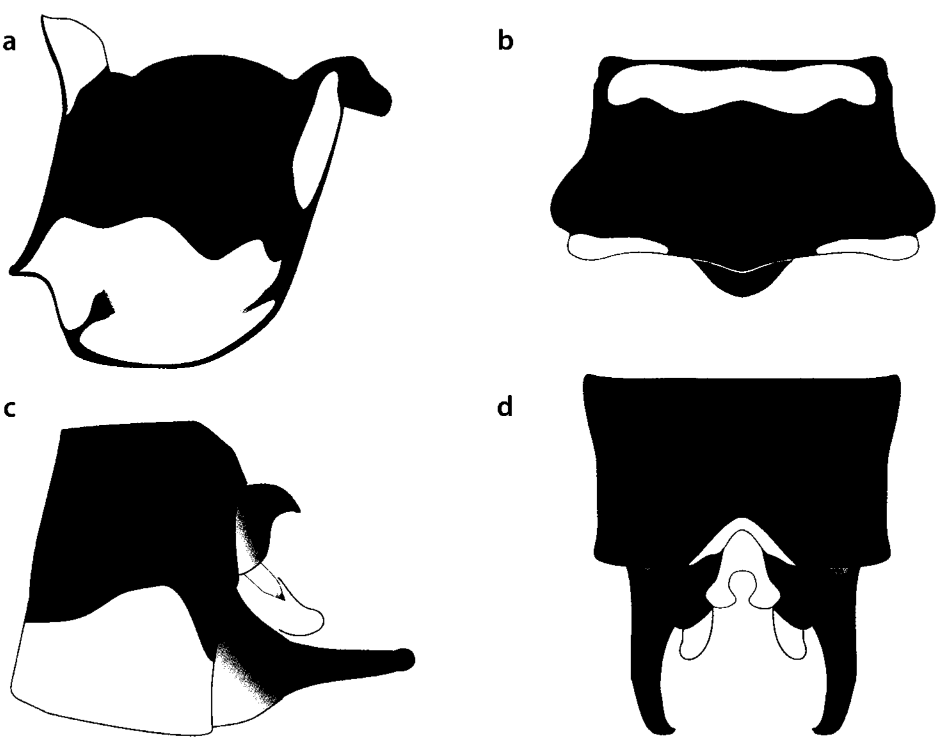

Figure 3: Morphological characters of *Coenagrion glaciale* — (a) female prothorax, lateral view; (b) female pronotum, dorsal view; (c) male cerci and paraprocts, lateral view; (d) same, dorsal view. Specimens collected from the environs of Pinega village, Arkhangelsk oblast, European Russia.

- The male abdominal pattern was predominantly black and included a distinctive large, black, U-shaped spot on the blue S2 (Fig. 4a, Plate Ia);
- Females combined an intensive deep blue background on the thorax, S1-2, S7-S9 and partly on S3 and S10, with the black abdominal pattern, especially characteristic on S8 where the proximal width of the black spot distinctively varied (Fig. 4b, Plate Ib);
- The occipital spots were horizontally elongate, with a slightly jagged hind margin (Figs 4a, b, Plate I);
- Small size: total length in five males 25.0 - 27.7 mm and in one female 29.0 mm.

C. hylas was found only at locality 3 where several individuals, mostly males, were recorded. This site was the only studied highly diverse locality that constituted a mosaic of water bodies and partly flooded *Sphagnum* bogs, transition mires and fens, with a clear but not predominating inflow of calcareous karst water and with manifold abundant and low vegetation reflecting interspersed oligo-/mesotrophic and acidic/slightly alkaline conditions. No clear association with

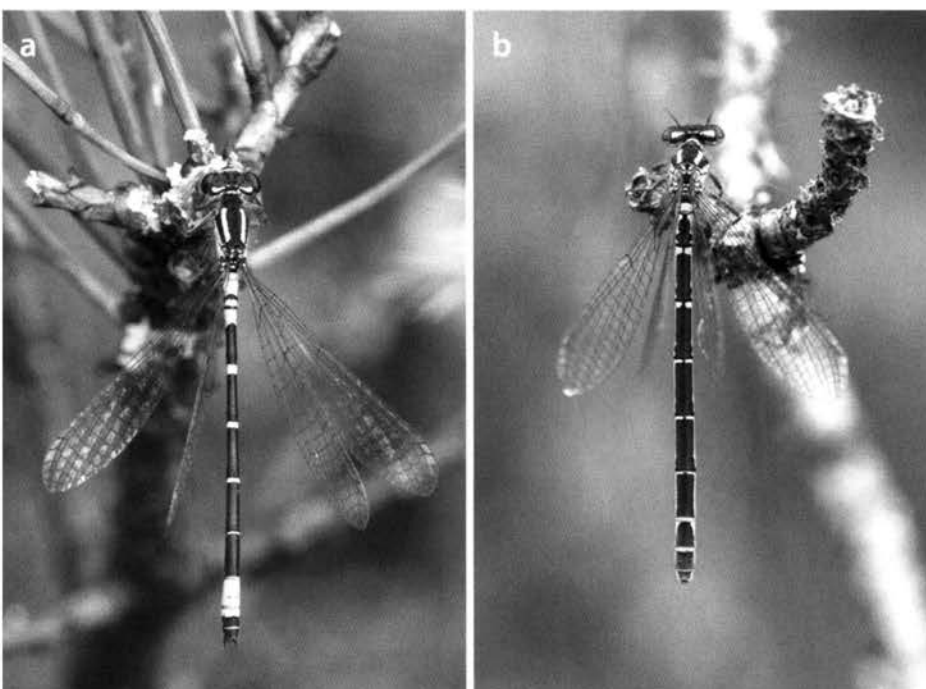

Figure 4: *Coenagrion glaciale* — (a) male, dorsal view, near Maletino (loc. 1); (b) female, near Maletino (loc. 2). Arkhangelsk oblast, European Russia, 7 July 2009. Photos by BD.

any vegetation type was recognized. Individuals were active only during a short episode of warmer and sunny weather in the late morning. However, even then the activity of the species was restricted to the warmest and totally wind-sheltered 'bay' of the complex of habitats. Individuals appeared to be quite 'lazy' and withdrew with the first clouds to shrubs and small trees at the forest edge.

In three of the four studied males of *C. hylas*, the median black spot on S2 was not connected with the lateral black stripes (Fig. 5) and in one male it was barely connected on one side. The lateral black stripes on S8 and S9 were well developed, broken in two males and unbroken in two other males. The ventral side of the thorax was black with bluish spots, which covered a slightly greater area than the black in at least one of the three males.

A. serrata was recorded at five sites. At loc. 2: one foraging female; loc. 4: numerous exuviae, some with teneral individuals; loc. 5: several exuviae, one with a teneral individual, and one probably immature imago; loc. 6: 1 exuvia; loc. 7: 1 exuvia. *A. serrata* was mostly recorded in clear-water, non-acidic lakes, at least partly influenced by karst water and with rather abundant fairly high vegetation predominated by *Phragmites australis* and completed by higher sedges. In a narrow stream and in a small lake situated in the course of a stream, the species presence was only marginal and restricted to lentic areas overgrown with high sedges or *Equisetum*.

Figure 5: *Coenagrion hylas* — male, lateral view, near Khaimusovo (loc. 3), Arkhangelsk oblast, European Russia, 7 July 2009. Photo by BD.

Discussion

Coenagrion glaciale in the Pinega region

C. glaciale seems not to be common in the study area, as it was recorded at only three localities, two of them being parts of the same complex of bogs and water bodies. However, this picture may change as a consequence of future studies when they are focused on habitats appropriate for the species. The observed low number of individuals certainly does not reflect the actual size of local populations. This was probably an effect of bad weather and being at the end of the flight period of this spring species. This was especially noticeable in the striking contrast between rare *C. glaciale* and numerous emerging and already abundant *C. johanssoni* during some warmer and sunnier moments at locality 3. Thus, a clear temporal segregation between these two species was observed. This segregation is possibly an effect of the rather similar body size of these *Coenagrion* species and their largely overlapping microhabitats or it may first of all reflect some differences in climatic and microclimatic requirements of these species.

The morphological features of *C. glaciale*, partly not presented or insufficiently emphasized in the original and subsequent descriptions by Selys (1872) and Belyshev (1973), are unmistakable in comparison with other coenagrionids. The hind margin of the female pronotum and the male cerci and paraprocts, which have only been rarely and rather sketchily illustrated in the literature so far (cf. Belyshev 1973), are highly diagnostic. The male abdominal pattern is also distinctive. Other features useful in the species determination are: (1) the intensive and ample blue on the female thorax and abdomen, combined with the black pattern on S8; (2) on average the occipital spots more elongate than those in congeneric species; and (3) the small size of the body, especially its length, on average even smaller than in *C. johanssoni*, making the species more similar to *Nehalennia speciosa* (Charpentier, 1840) than to other *Coenagrion* species. This effect is intensified by the behaviour of *C. glaciale*, being more associated with vegetation than related species. Concerning the variability of the black pattern, which in the past had been used to distinguish between two subspecies (Belyshev & Haritonov 1973) – later synonymized by Lohmann (1992) – the individuals from the studied populations represent the more black end of the species' clinal variation.

Coenagrion hylas in the Pinega region

It seems that in the study area *C. hylas* is rarer than *C. glaciale*, perhaps a consequence of its more specific habitat requirements, although the single population of *C. hylas* must have been fairly large as demonstrated during the only episode of sunny and warmer weather. The limited appearance in the breeding habitat at only the warmest sites and times was clearly recognizable and much more so than in co-occurring *Coenagrion* species, such as *C. glaciale*, *C. hastulatum* and *C. johanssoni*. This corresponds to the known rather weak activity of *C. hylas* which strongly prefers sunny weather and four hours around solar noon (Kiauta & Kiauta 1991; Müller 2001; Dijkstra & Lewington 2006). This preference also finds confirmation in the reaction of individuals to clouds passing overhead, i.e. in a rapid disappearance of all individuals from the waterside, which strictly resembles behaviour described by Kiauta & Kiauta (1991). This withdrawal of individuals from the breeding habitat to the edge of forest as well as the presence of one male in a small glade in the afternoon suggest that sparse forest and glades in forest are typical terrestrial habitats for the species.

The few individuals do not allow any generalisation, but the black pattern would suggest that North European *C. hylas* resemble Siberian rather than Central European individuals (cf. Belyshev & Haritonov 1974; Lohmann 1992).

Aeshna serrata in the Pinega region

The records of *A. serrata* at five sites in fairly distant areas and the frequency of exuviae at short sections of lake shores show the rather widespread and probably quite abundant presence of this species in the study area, although sightings of only single exuviae at localities 6 and 7 were probably an effect of female dispersal from more appropriate habitats in the surroundings. The female foraging at the peat bog (loc. 2) does not indicate that the adjacent small acidic lake was a breeding site as the species was absent from all other small acidic waters as well as from oxbows, karst forest pools and flooded fens, namely from all the kinds of water bodies generally overgrown with low vegetation.

The disjunct distributions of *C. glaciale* and *C. hylas*

The distribution of *C. glaciale* (Fig. 6) is largely restricted to Russia, where this East Palaearctic species occurs in eastern Siberia and in the Far East (Belyshev 1973). Apart from Russia it is only known from Manchuria in NE China (Bartenev 1914). However, the data concerning the species' distribution are generally poor and the run of its limits is mostly hypothetical. The known localities are mainly concentrated in a wide belt of southeastern Russia ranging from the Primorskii Krai and Khabarovskii Krai along the Amur River and a system of its western tributaries up to the region of Lake Baikal and the upper Angara River (Belyshev 1973; Malikova & Ivanov 2001; Kosterin 2004; Ketelaar et al. 2007; Malikova et al. 2007). The species is even common in Primorskii Krai, where it reaches the border of N. Korea (Belyshev 1966b; Malikova & Ivanov 2001; E. Malikova in litt.). Its occurrence in N. Korea is, therefore, very probable but not confirmed so far. For Manchuria, Bartenev (1914) mentions the species from the environs of Yimianpo (SE of Harbin), but the distribution in China is practically unknown. The

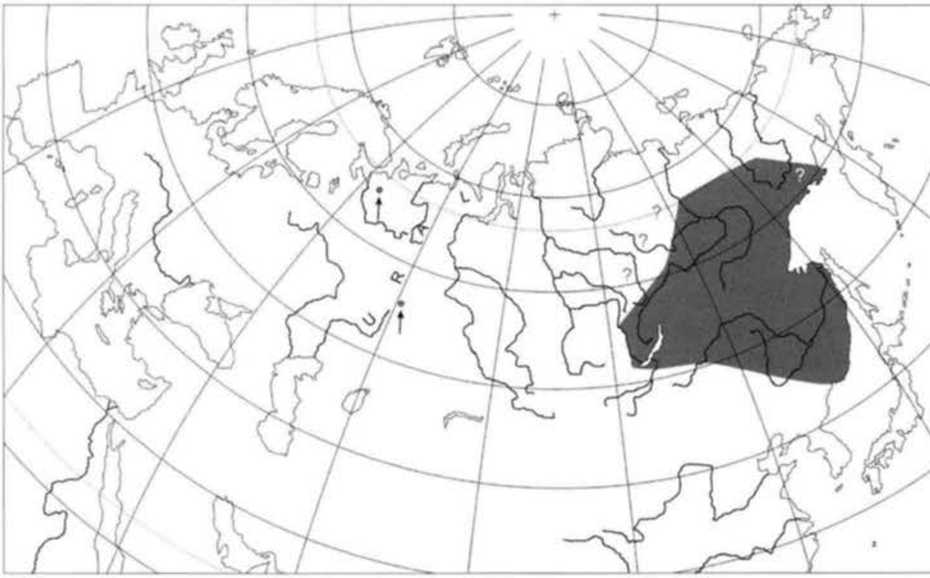

Figure 6: Disjunct range of distribution of *Coenagrion glaciale*. Relict postglacial isolates are indicated with arrows. The westernmost arrow shows the Pinega localities. White question mark indicates the theoretical range limit between the upper Moma River and the Okhotsk Sea. Dark question marks show an area where the species is unknown, but possibly occurs.

western range limit as given in Figure 6 connects several localities in its southern part, from the Tunka (= Tunkinskaya) Valley running northward along the upper Angara River up to the former Padun village (today a part of Bratsk) at 56°18'N and 101°48'E (Bartenev 1912a; Belyshev 1966a, 1973). However, north of this, the western limit is unknown. The next recorded localities are situated far to the north and east, i.e. in SW Yakutia, near the mouth of the Chayanda River into the Nyuya River, and in NW Yakutia, in the basin of the lower Lena River (Belyshev 1973; Kosterin & Sivtseva 2009). The given limit reaches its northernmost locality in the valley of the Nuorda (= Norda) River in Zhigansk and then runs south-eastward to the north of Okhotsk Sea, as only a small group of localities is known from this section, in the basins of the upper Indigirka and Moma Rivers (Kosterin & Sivtseva 2009). The distribution of *C. glaciale* is most probably larger than that drawn on the basis of collected data, especially in central Siberia and in the north.

Two probable isolates of *C. glaciale* were recently discovered far from the western limit of its hitherto known range (Fig. 6), the first in the Asian foothills of the South Ural Mountains in the Chelyabinsk oblast (Eremina 2009) and the second in the Pinega region in European Russia as described in this study. The northeastern European isolate is situated ca 3,200 km NW of the main known distribution range and ca 1,350 km NW of the south Ural isolate. The extent of occurrence of

C. glaciale, previously assumed to be compact and restricted to the East Palaearctic, has turned out to be much wider and disjunct, and is thus quite similar to that of *C. hylas*.

C. hylas is also an East Palaearctic species. The core of its range includes large areas of central and eastern Siberia, the Russian Far East, the southern half of the Kamchatka Peninsula, Sakhalin, eastern and northern Hokkaido, (partly?) North Korea – probably with an isolated locality far in South Korea –, northern Mongolia and northeasternmost Kazakhstan (Fig. 7) (Belyshev 1968, 1973; Lohmann 1992; Lee 2001; Dumont 2003; Kosterin and Zaika 2003; Kolesnikova 2004; Dumont et al. 2005; Kosterin 2005; Chaplina et al. 2007; Hirose et al. 2007; Kosterin & Sivtseva 2009). The species is also reported from northeastern China (Manchuria) by Zhu & Ou (2000), citing Asahina (1942). However, this reference is unsubstantiated, as Asahina's paper does not present original data and only refers to two papers ("Bartenev 1912, 1930") but provides no bibliographical data. Bartenev's papers published in 1912 or 1930 and including data from China or adjacent territories (Bartenev 1912a, 1912b, 1912c, 1930a, 1930b) only provide data on *C. hylas* from Russia or do not refer to this species at all. Additionally, the 'Manchurian' data mentioned by Belyshev (1968, 1973) refer to *Agrion convalescens* Bartenev, treated then by him as synonym of *C. hylas*, but actually pertain to *C. johanssoni*

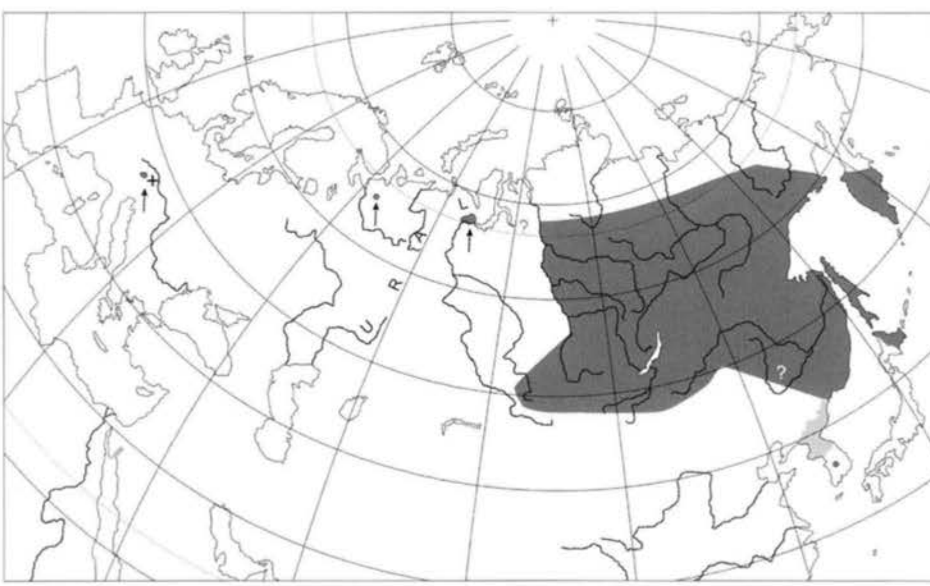

Figure 7: Disjunct range of *Coenagrion hylas*. Relict postglacial isolates are indicated with arrows. The middle arrow shows the Pinega locality. The white question mark refers to the hypothetical distribution in China. The light grey shade covering North Korea refers to an imprecisely reported occurrence. The dark question mark shows an area where the species is unknown, but possibly occurs.

(Belyshev & Haritonov 1974). *C. hylas* is also listed for northern China by Yang & Ou (1998), but the basis for this reference is unknown; possibly it is the same incorrectness as in the case of Zhu & Ou (2000). Despite all these shortcomings, *C. hylas* probably does occur in northeastern China given the species' status in the adjacent territories. Therefore, this area has been included in the species' range with a white question mark in Fig. 7.

So the range limits (Fig. 7) are still hypothetical, although in some sections they more or less mirror the actual state. The western limit of the main range probably runs along the Yenisei River, from the abandoned Plakhino settlement in the north (67°56'N) up to the river section situated to the south of Krasnoyarsk. Then it goes to the southeast through the upper Ob River basin and locally the Altai Mountains up to a single locality (49°N, 86°E) in their Kazakh ranges (Belyshev 1968, 1973; Chaplina et al. 2007). It seems that the species does not penetrate the plains of the West Siberian Lowland, being restricted to uplands and mountains. However, it has been suggested that the northernmost part of the species' distribution core may even reach as far as the Ural Mountains (Belyshev 1973).

Two isolates of *C. hylas* were previously known to the west of the main range (Fig. 7). The first isolate is situated in westernmost Asia, in the eastern foothills of the Polar Urals and their adjacent plains (Haritonov 1974, 1976; Belyshev & Korshunov 1976). Lohmann (1992) described it as a ca 12,000 km^2 large area situated in the forest-tundra zone at the base of the Yamal Peninsula, between the foothills of the Polar Urals and the Shchuchya and Ob Rivers; the lower Tanlovaya River, a tributary of the Shchuchya River should be added there (Belyshev & Korshunov 1976). Considering these data, the area of this isolate drawn by Kosterin (2005) is too large, although, in the light of new data not impossible. The second isolate is situated in central Europe at the northern edge and in the foothills of the central Alps (Bilek 1954; Heidemann 1974; Lohmann 1992). In fact, it consists of two parts – the German locality near Inzell, Bavaria, where the species is now extinct, and a group of a dozen or so localities situated 140-180 km WSW, in a small area of the Austrian Tyrol, in the valleys of the Lech and upper Inn Rivers, with the main concentration in the former (Müller 2001; Raab et al. 2007).

The newly described locality in northern European Russia, also probably representing only a part of an isolate, is situated ca 1,930 km W of the nearest known locality in the main range and between the two isolates described above – ca 1,070 km WSW of the Polar Ural isolate and ca 2,590-2,720 km NE of the nearest German and Austrian localities.

Palaeogeographical aspects

The present disjunct distribution of *C. glaciale* and *C. hylas* is believed to be a consequence of palaeoclimatic oscillations, i.e. both species had a much wider distribution in the past but retreated from the western part of their range, leaving just a few relict isolates. According to Lohmann (1992), *C. glaciale* and *C. hylas* are representatives of the Manchurian faunal element. They could have survived the glacial period in the Manchurian refugium, which became the origin of their postglacial expansion. Conversely, according to the interpretation by Brockhaus (2007), these species might have been members of the periglacial fauna which occurred in Europe during the whole Pleistocene series of glaciations with only a range shift to the north or to the south following successive climatic oscillations. Irrespective of the interpretation of the species distribution during glaciation, it seems that *C. glaciale* and *C. hylas*, as cold-stenothermal and taiga species, found the best conditions for expansion in the colder periods of a maximum birch and pine spread, i.e. near the end of the Pleistocene (in the Bølling-Allerød interstadial) and at the beginning of the Holocene, in the Preboreal and early Boreal (cf. de Lattin 1959; Lohmann 1992). This expansion might have had its first phase between 14,500 and 12,700 BP (all dates calibrated), and, after a phase of some regression in the Younger Dryas stadial, might have continued between 11,500 and 10,000 BP.

It is possible that this late glacial and postglacial expansion of eastern fauna led to different ranges in different species. The absence of some species from Europe west of the Urals (e.g. *C. glaciale*, *Coenagrion lanceolatum* (Selys), *Somatochlora graeseri* Selys) would suggest this interpretation. However, the discovery of the western isolate of *C. glaciale* in this study weighs rather more in favour of a common pattern of expansion reaching deep into Europe. This wave of eastern colonizers penetrating Europe most probably included, besides *C. glaciale* and *C. hylas*, such species as *C. johanssoni*, *Aeshna crenata*, *A. serrata*, *S. graeseri*, *S. sahlbergi* Trybom, and possibly also *A. caerulea* and *S. alpestris* (Selys).

According to Brockhaus' conception of periglacial fauna (2007), all these species might have continuously occurred there what is most likely for *A. caerulea* and *S. alpestris*. According to de Lattin's (1959) palaeogeographical conception, the regress of these species in Europe began between the Boreal and the beginning Atlantic, i.e. between 10,000 and 8,600-8,200 BP. As early as the late Boreal, pine, birch and hazel were reduced in favour of oak, elm, lime and alder, and the tendency for the spread of deciduous forest was deepened in the Holocene Climatic Optimum, i.e. in the Atlantic period, with the maximum reached in its late phase between 6,000 and 5,500 BP. Three main scenarios of odonate reaction can be recognized:

- The first, represented by Transpalaearctic eastern species with a large Siberian core of distribution, such as *A. crenata* and *C. johanssoni*, whose ranges shifted to the north – which was least affected by changes – but retained a relatively large area, compact structure and connection with the main Siberian range;
- The second, represented by Transpalaearctic northern and mountain, cold-stenothermal species which are associated with bogs, such as *A. caerulea*

and *S. alpestris*, whose distribution area shifted into two parts, boreo-arctic and mountain-alpine, the former quite compact or weakly fragmented and still more or less connected with the Siberian part of the range, and the latter disjunct and severely fragmented;

- And the third, represented by cold-stenothermal East Palaearctic species, such as *C. hylas* and *C. glaciale*, whose distribution areas shrank to the greatest degree when the species withdrew far to the east and survived only in rare isolates in Europe, probably mostly in the North and in the Urals and its foothills. These species are clearly postglacial relicts in Europe. *S. graeseri*, known so far up to the Yenisei and upper Ob Rivers and then in a large isolate in the Urals (Haritonov 1976; Yanybaeva et al. 2006), also may belong to European postglacial relicts and its discovery in northeastern Europe seems to be only a matter of time.

The question of the changes in the areas of distribution in later periods remains open. In shorter colder phases, e.g. in the beginning of the Subboreal, ranges of some species were most probably partly rebuilt, and in warmer periods, as in the Subatlantic, they probably shrank again. However, it seems that the course of changes and the extents of the species occurrence generally followed earlier patterns. In the species representing the third scenario, these changes, if they occurred at all, certainly were the smallest. Additionally, human impact might have also influenced the species area of occupancy in almost all these species, especially in central and western Europe.

The northeast of European Russia was touched by the Holocene climatic oscillations, and especially by its climatic optimum, to a lesser degree than Central Europe. In the Preboreal and partly in the Boreal, birch forest predominated. Spruce forest played a great role there beginning in the Boreal and especially in the Atlantic, at first in the form of the north and central taiga variants, and during the warmest peak in the south taiga variant together with mixed spruce-deciduous forest. In the Subboreal and Subatlantic, north spruce forest and pine-spruce and birch-spruce forests became leading forest types (Puchnina 2000). Therefore, cold-stenothermal and taiga species could always find appropriate conditions, at least here and there.

Aeshna serrata in Europe

A. serrata is a mainly northern and central Asian species, probably polyrefugial, but primarily is a representative of the Mongolian-Kazakh faunal element. Therefore, its quite extensive occurrence in the European north could be expected according to the first scenario. However, only a relatively small and isolated area inhabited by the species was previously known in Europe, comprising the coastal area of the Baltic Sea in Estonia, Finland and Sweden, and also reaching deeply inland in the last country (Dijkstra & Lewington 2006), and this view of 'isolate' seems to resemble the third scenario. The very rare and terse reports about the occurrence of *A. serrata* in other places in Eastern Europe, i.e. in the Komi Republic (Sedykh 1974) and in the Ukraine (Oliger 1980) were treated as doubtful or not confirmed (Peters 1997; Gorb et al. 2000). The new data from the Pinega karst area suggest an extensive occurrence of this rather Transpalaearctic than East Palaearctic species in the European northeast. The distribution area there may be fragmented, but possibly it is relatively continuous and connected first of all with the Siberian core of the range on the one side and even with the Baltic part of the range on the other side. In this light, the data from the Komi Republic have become more reliable and even the Ukrainian data could be treated more seriously, showing a possible southern belt of the distribution area going from the South Urals through the former steppe areas.

Ecological conclusions

It remains unknown whether *C. glaciale* and *C. hylas* in the European northeast occur only in the 'Pinega' isolate or in a fragmented belt extending through the major part of the far northeast. Therefore, it is impossible to define all the important conditions for the survival of these species there. However, it seems that besides continuous appropriately severe climatic conditions karst could also play an important role in this survival. The karst influence appears in: (1) a greater habitat diversity; in the study area the spectrum of waters is broad and not so dominated by boggy landscapes as in many other areas of the north (cf. Study Area and Methods), and such richness offers suitable conditions for species not restricted to boggy waters; (2) contrasting and locally more severe microclimatic conditions both on land and in water, recognizable e.g. in more persistent accumulations of cold air in land depressions and, what is especially important for cold-stenothermal dragonflies, in low water temperatures; (3) higher mineralization of some waters with their still fairly low or moderate trophic status.

C. hylas is a cold-stenothermal species and prefers cold and clear water rather poor in nutrients. Therefore, it frequently occurs in water bodies that are deeply frozen for a long time and/or fed by a cold inflow. These requirements are especially evident in the marginal zone of its distribution including the study area, where this species is highly stenotopic (cf. e.g. Belyshev 1966a; Belyshev 1973; Müller 2001). Karst conditions can be especially favourable for *C. hylas*, as it often inhabits seepage waters and shallow pools, not infrequently calcareous and situated in mountainous or hilly landscapes. The association with rich diversified relief is recognizable in the core of its distribution range, which does not penetrate the West Siberian Lowland, i.e. does not cross the Altai and Kuznetski Alatau Mountains and the Yeniseiskii Kryazh, the latter forming the western margin of the Central Siberian Plateau (Kosterin 2005). The rich relief and/or higher elevation are also crucial for the species occurrence at the southern limit of its extent, in Kazakhastan, the Tyva Republic and Mongolia (Dumont 2003; Kosterin & Zaika 2003; Chaplina et al. 2007). The Pinega environs are lowland (25-150 m a.s.l.) and the species locality is situated at an altitude of only 27 m. Karst landscapes serve here as an equivalent of rich relief providing appropriate microclimatic and physico-chemical conditions.

C. glaciale inhabits standing waters, but its habitat spectrum seems to be generally broader than that of *C. hylas* and also includes e.g. acidic waters (Belyshev 1973), which has been confirmed in the Pinega area. Three main habitat factors have been recognized so far (cf. Belyshev 1973; and the data from the Pinega area): (1) Forest or bushes bounding the locality/area of activity and providing the wind protection necessary for this small and delicate species; this is also important because of the spring flight period of the species when winds are generally more frequent and cooler; (2) The appropriate texture of vegetation providing enough space for imaginal activity and some wind-shield; the *Carex*-vegetation of diverse density and with admixtures of other plants is especially preferred by this species which is quite closely associated with vegetation; (3) Low temperatures of water, deeply frozen for a long time and/or fed by a cold inflow, the factor typical for cold-stenothermal species.

It should also be stressed that localities of both species in the Pinega environs are situated in at least partly spruce forest. This shaded and cool neighbourhood additionally influences the local microclimate making it more severe.

In the context of the habitat requirements described above, a specific combination of severe climate and habitat and microclimatic conditions largely influenced by karst is assumed to be crucial for the survival of *C. glaciale* and *C. hylas* in the study area from the Preboreal through the last 10,000 to 11,000 years. If the Pinega karst area is an isolate of these species, it may be 5,000-6,000 years old (an age of fragmentation); for the Central European isolate Lohmann (1992) suggested an age of 7,000-8,000 years.

Studies on diverse plant and animal groups in the Pinega State Nature Reserve (Pinezhskii Zapovednik), which borders our study area, have shown similar results to ours on *C. glaciale*, *C. hylas* and *A. serrata*. This reserve and generally the karst territories of the White Sea-Kuloi Plateau, are distinguished among other taiga areas at these latitudes by their unusually rich flora and fauna which also includes, besides taiga species, a much broader than expected representation of arctic, subarctic and arctic-alpine species (e.g. Puchnina 2000, 2008; Babenko 2008). Typically for the whole NE Europe, the percentage of Siberian species is larger than in other parts of the continent. However, even in this matter, the Pinega karst area seems to be distinctive. This is clearly recognizable in the relatively well-explored collembolans. East Palaearctic Collembola are represented there by 14 species whose distributions are largely concentrated in the boreal and arctic zones of Siberia. The nearest localities of several of these species are known far to the East, i.e. from the Yamal or Taimyr Peninsulas, and from the Yenisei basin or Putoran Plateau (Babenko 2008). The Pinega karst area constitutes the western range limit not only for these collembolans, but also for 14 plant species (Puchnina 2000) and the typically cold-stenothermal amphibian *Salamandrella keyserlingii* (Rykov 2008). All these authors stress that the richness and distinguishing features of the flora and fauna of the broad environs of Pinega village result from the karst influence followed by high habitat diversity and specific microclimate.

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