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On the distribution of *Sympetrum croceolum* in the Russian part of its range (Odonata: Libellulidae)

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Abstract. We used literature data, museum collections, and fieldwork to compile a list of records and produce a distribution map of *Sympetrum croceolum* in the Russian part of its range from where the species was little known to odonatologists outside of Russia for a long time. A detailed description of the fourth record of the species in Western Siberia (Chernyy Mys village, Kolyvanskiy District, Novosibirsk Province), which is globally the northernmost record of the species, is given. We suppose that the West Siberian *S. croceolum* populations originate from westward migrations from the eastern core part of the species' range. Morphometric analysis of specimens from different populations showed that variation of the hind wing size is within the individual variability of *S. croceolum*. By breeding *S. croceolum* in an aquarium from an egg clutch, information on the period of embryonic development and morphometric characteristics of eggs and larvae of younger instars was obtained. The subspecies *Sympetrum croceolum fuscoatrum* Belyshev, 1964, is synonymised with the nominotypical subspecies.

Further key words. Dragonfly, Anisoptera, biology, ecology, Western Siberia.

Introduction

The palaearctic *Sympetrum croceolum* (Selys, 1883) (Fig. 1) was described from Japan based on a male specimen collected in Yokohama (Selys 1883, sub *Diplax croceola*). Selys received the holotype specimen from the Museo di Storia naturale Giacomo Doria in Genoa, Italy (Selys 1883: 18). Later, the holotype was deposited in the Institut royal des Sciences naturelles de Belgique (IRSNB) in Brussels, Belgium (Fig. 2).

For more than 100 years, the species' distribution was considered restricted to Southeast Asia. It was known from Japanese islands (Yakobson & Bianki 1905; Bartenev 1915; Asahina 1938, 1959, 1961; Tsuda 2000; Inoue

& Tani 2001), Northeast China (Needham 1930; Sui & Sun 1984; Tsuda 2000), the Korean Peninsula (*e.g.*, Asahina 1990; Lee 2001; Seehausen & Fiebig 2016), and the South of the Russian Far East (Belyshev 1964; Belyshev & Stepanchyuk 1965; Malikova 1995; Haritonov & Malikova 1998; Malikova & Ivanov 2001; Ivanov 2002; Malikova et al. 2007), in particular, Amur Province (Malikova 1997).

Then, in the 1980s, isolated populations of *S. croceolum* were detected in the South of Western Siberia, several thousand kilometres west of the core range of the species. These were recorded in the Northeast Altai (Kosterin 1987a, b), in the South of the Novosibirsk Province on the border to the Altai Republic (Haritonov 2000; Popova & Haritonov 2008), and in the city of Novosibirsk (Kosterin et al. 2001). Finally, *S. croceolum* was found by us in the North of Novosibirsk Province in Kolyvanskiy District in early autumn 2009 and 2010 (this article).

In this article, the distribution of *S. croceolum* in the Russian part of its range is described, and a description of the species' habitat in the North of Novosibirsk Province in Western Siberia is given. Information on the ecology and taxonomy of the species is provided, the development of the species in an aquarium is documented, and the migratory potential of *S. croceolum* is discussed.

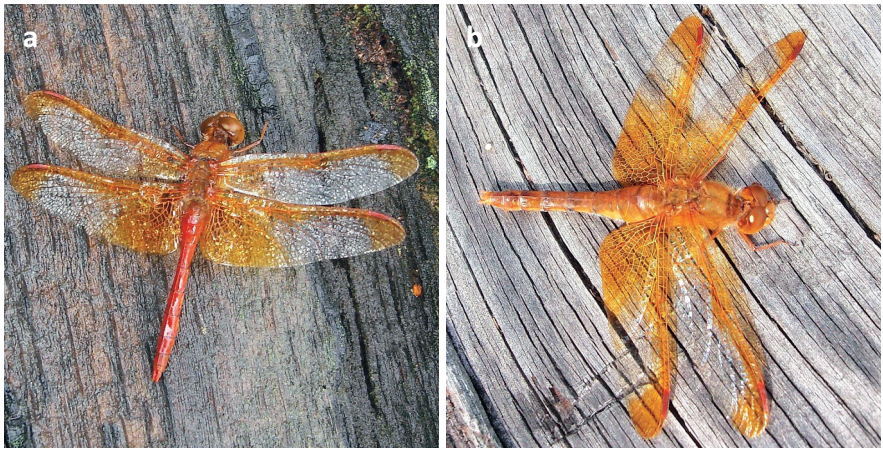

Figure 1. *Sympetrum croceolum* in life. a – Male; b – female. Town of Amursk, Khabarovskiy Kray, Far East, Russia (15-ix-2013). Photos: V. Bobov, Insecta.pro

Material and methods

Study region

The focus of the study was the distribution of *Sympetrum croceolum* in the Russian part of the species range, which includes southern West Siberia, the Amur region, and Primorje.

Data compilation

Four photographs of the holotype in coll. IRSNB (Fig. 2) were kindly provided by Malte Seehausen.

The majority of data concerning the distribution of *S. croceolum* was compiled from the literature. In total, 50 dry specimens from the collection of the Siberian Zoological Museum, Novosibirsk (SZMN), of the Institute of Systematics and Ecology of Animals of the Siberian Branch of the Russian

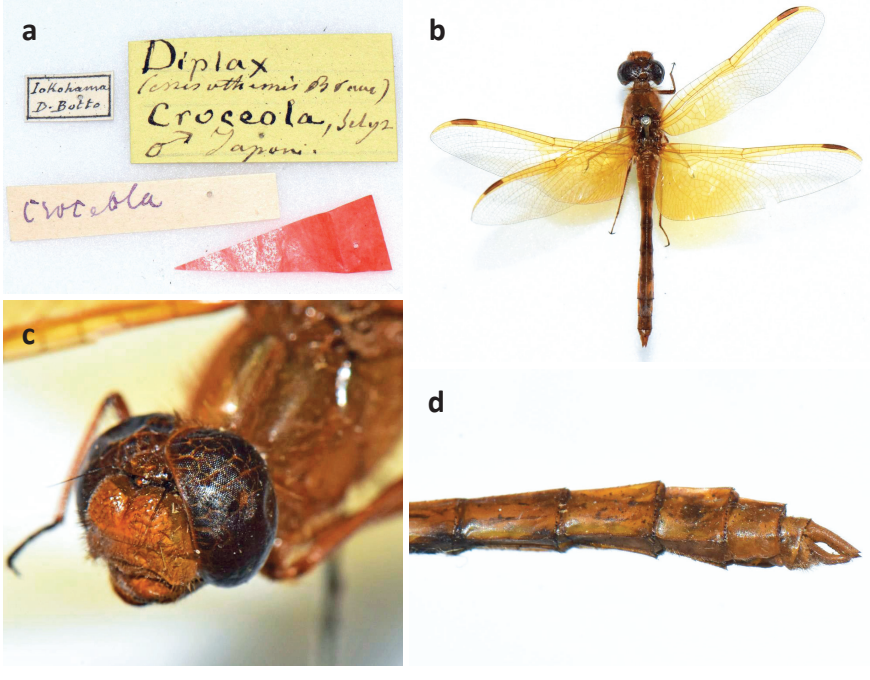

Figure 2. Holotype of *Sympetrum croceolum* (Selys, 1883) in the IRSNB, Brussels, Belgium. a – Labels; b – habitus in dorsal view; c – head in dorso-lateral view; d – end of abdomen and appendages in lateral view. Photos by courtesy of M. Seehausen

Academy of Sciences, Novosibirsk (ISEA) (cf. Fig. 3), were used for systematic analysis.

A distribution map of the species was kindly provided by Jean-Pierre Boudot using software Carto Fauna-Flora (http://zoologie.umons.ac.be/cff/). Geographical coordinates, if they were not available in the cited publication, were retrieved from a satellite image (Google Earth™, https://www.google.ru/maps).

Results

Fifty-five individuals of *Sympetrum croceolum* (29♂ 26♀) were recorded in 18 localities cited for the territory of Russia. Records of *S. croceolum* are available from five administrative units of the Russian Federation, viz. Novosibirsk Province, Altai Republic, Amur Province, Khabarovskiy Kray, and Primorskiy Kray.

Annotated list of localities with records of *S. croceolum* in the Russian part of its range

Locality numbering corresponds to that on the species distribution map (Fig. 4).

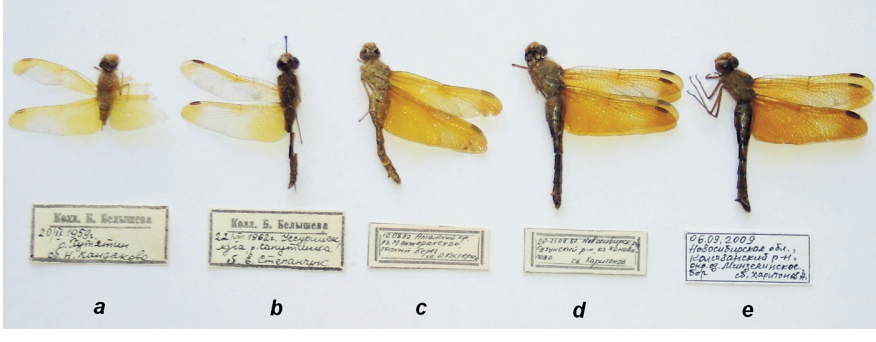

Figure 3. Specimens of *Sympetrum croceolum* from five Russian localities in the collection of SZMN. a – Teneral female from Putyatin Island, Primorskiy Kray; b – mature male from Komarovka River, Primorskiy Kray; c – teneral female from Lake Manzherok, Altai; d – mature female from Lake Konovalovo, Novosibirsk Province; e – mature female from a pine forest in the vicinity of Chernyy Mys village, Novosibirsk Province.

Novosibirsk Province (Siberian Federal Region)

Loc. 1. (this paper): Kolyvanskiy District, 9,5 km NE of Chernyy Mys village, left bank of the Ob' River, 5 km SE of Lake Minzelinskoye, a clearing in pine forest (Fig. 5), 55°33'N, 83°24'E, 158 m a.s.l., 06-ix-2009, 14 h NOVT (UTC +7): 12 individuals observed, 3♀ collected; obs. & leg. ONP & AYuH; same site, 07-ix-2010, 11 h: 3 individuals, obs. ONP & AYuH.

Loc. 2. (Kosterin et al. 2001): Novosibirsk City, Leninskiy District, bus stop and Kommunal'nyy bridge close to Gorskaya, left bank of the Ob' River, oxbow, 54°59'N, 82°55'E, 139 m a.s.l., 25-viii-2000: 1♀, 4 individuals observed in total, obs. & leg. E. Shtrecker.

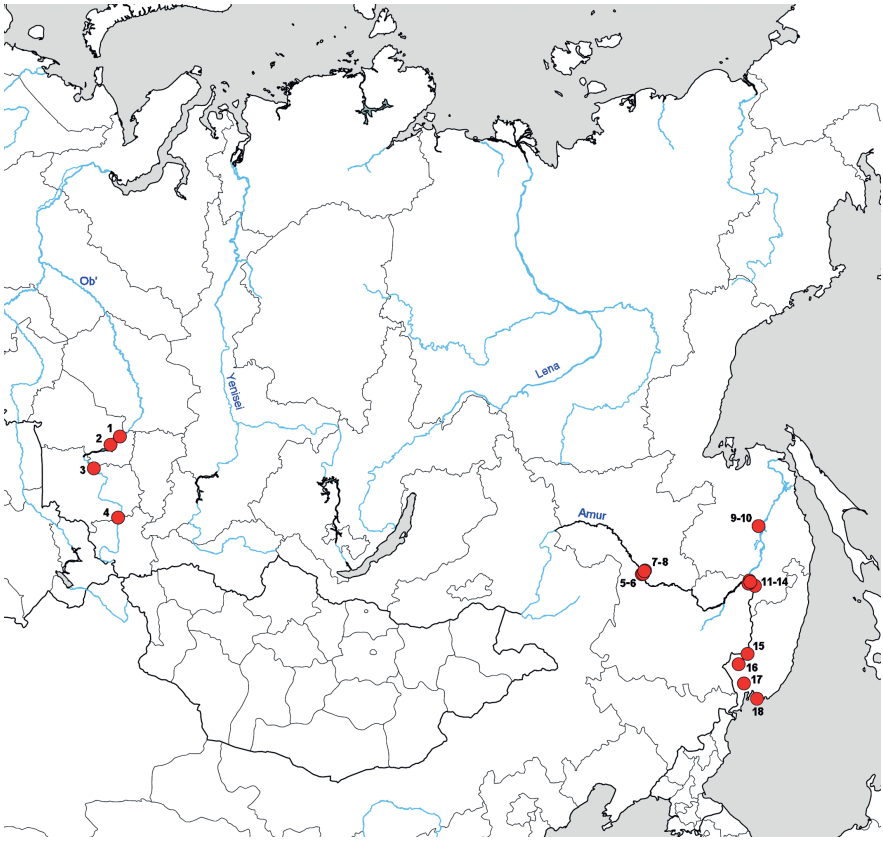

Figure 4. Distribution map of *Sympetrum croceolum* in the Russian part of its range. Locality numbering as given in the list of localities in the text. Map prepared on Lambert conformal conic projection by courtesy of Jean-Pierre Boudot.

Remarks. Later, this water body was repeatedly inspected in late summer and early autumn of 2002–2007. Not a single imago was seen, nor was a single larva of this species detected during collection of hydrobionts (Popova & Haritonov 2008). Therefore, it is unclear whether *S. croceolum* actually inhabits this oxbow in the city.

Loc. 3. (Haritonov 2000): Suzunskiy District, Meret' village, right bank of the Ob' River, Lake Konovalovo (Fig. 6), 53°34'N, 82°24'E, 120 m a.s.l., 20–21-viii-1987: 3♂ 4♀ (1 teneral, 6 adults) (Fig. 3d); 25-viii-2000: 2♂ 1♀ adult, leg. AYuH (this paper); same site, 04-ix-2002: 1♂ 2♀ adult, leg. ONP & AYuH.

Remarks. Lake Konovalovo is located in the Priobskaya forest steppe on a gently rolling and ridged plain with absolute elevations of up to 200 m bordering the Suzunskiy pine forest (Rikhter 1963). During our visits, the small, shallow lake was heavily overgrown with aquatic and semi-aquatic

Figure 5. Clearing in a pine forest – one of the sites where *Sympetrum croceolum* was found in Western Siberia. Novosibirsk Province, Kolyvanskiy District, near Chernyy Mys village (13-ix-2009). Photo: A.Yu. Haritonov

vegetation and had swampy shore areas. We estimated the size of the Suzun population of *S. croceolum* at its first discovery in 1987 at about 500 individuals. According to counts of imagines conducted in late August and early September 2000, 2002, and 2004–2007, there was a decrease in the population size to 100 individuals or less (Popova & Haritonov 2008).

Altai Republic (Siberian Federal Region)

Loc. 4. (Kosterin 1987a): Mayminskiy District, Lake Manzherok (Fig. 7), E and SE banks, 51°49'N, 85°49'E, 376 m a.s.l., 05-viii-1982: 1♂; 08-viii-1982: 1♀, 09--viii-1982: 1♀; 10-viii-1982: 2♂ 3♀ (Fig. 3c); 13-viii-1982: 1♀, leg. Kolosov & O.E. Kosterin (Kosterin 2007b); the same place, 20-viii-1994: moderately abundant; 06-ix-2001: many dozens of individuals estimated on a rather rainy day (Kosterin 2017); the same place, 16-ix-2016: 2♂, leg. O.E. Kosterin.

Remarks. Lake Manzherok is located in the mountain valley in the transition lane between the Priobskoye Plateau and the first mountains of northwestern Altai; it is at least 15–20 thousand years old (Rusanov 2015). The length is about 1 km, the maximum width is 0.4 km, the average depth is

Figure 6. Lake Konovalovo at Meret' village, Novosibirsk Province, Russia (15-vii--2010). Habitat of a *Sympetrum croceolum* population. Photo: A.Yu. Haritonov

1 m, and the maximum depth is 3 m. It is a eutrophic lake with a bottom composed of an up to 5 m thick layer of sapropel sediment (gyttja). All banks, except the north-western, were covered by swampy birch and pine forest, followed by quaking bogs that were up to 45 m wide. With up to 25 species, the lake was rich in aquatic vegetation (cf. Rikhter 1963). The water surface was marginally covered by a 5–60 m wide band of water-lily, *Nymphaea candida*, followed by a broad zone covered by rosettes of water caltrop, *Trapa* sp. In Altai, only the Manzherok population of *S. croceolum* is known so far, which has been monitored since 1982. The population size was moderately high with many dozens of individuals in 1982, 1994 and 2001, and with a declining population observed in 2016 (Kosterin 2017). Kosterin (1987a: 60) found *S. croceolum* only on the swampy shore areas in the East and the Southeast. There is no doubt that the species is able to breed in Lake Manzherok as an emergence was recorded in August 1982, while the species was not detected in nearby water bodies including Lake Aya (Kosterin 1987a).

Figure 7. Lake Manzherok, Altai Republic, Russia (16-ix-2016). Habitat of a *Sympetrum croceolum* population. Photo: O.E. Kosterin

Amur Province (Far-East Federal Region)

Loc. 5–8. (Malikova 1993): Middle Amur River basin, Blagoveshchenskiy District, from early August to mid September, 1988–1992: 5♂ 2♀, 5 exuviae, leg. E.I. Malikova.

Loc. 5. Verkhne-Blagoveshchensk village, the floodplain of the Amur River, a sometimes dried-up pond, 50°17'N, 127°23'E, 134 m a.s.l.

Loc. 6. Blagoveshchensk City, Astashinskiye Lakes and adjacent wetland, 50°17'N, 127°30'E, 134 m a.s.l.

Loc. 7. Snezhinka Recreation center, forest, 50°23'N, 127°38'E, 208 m a.s.l.

Loc. 8. Peschanoye Lake, the floodplain of the Zeya River, 50°25'N, 127°42'E, 134 m a.s.l.

Remarks. The southern part of Blagoveshchenskiy District, where *S. croceolum* was found, is located in the swampy, gently hilly Amur-Zeya Plain, which predominantly exhibits a forest steppe landscape. The bottoms of various river valleys abound with circular mossy swamps with depths of 0.9–1.5 m. Water caltrop and duckweed are found in the lakes (Vorobyov & Derevyanko 1989). Between 1988 and 1992, several isolated findings of *S. croceolum* were made in Blagoveshchenskiy District in diverse habitats: in the forest, in the city, in permanent and in temporary ponds.

Khabarovskii Krai (Far-East Federal Region)

Loc. 9–10. (Yakubovich & Kapkaev 2009): Komsomol'sk-na-Amure City, 50°33'N, 137°01'E, 36 m a.s.l.

Loc. 9. Silin Forest Park, 19-viii-2005: 2♂, leg. A.Yu. Kapkaev.

Loc. 10. Lake Balyay, 14-viii-2005: 4♂, leg. A.Yu. Kapkaev.

Loc. 11–13. Khabarovskiy Distrikt, Bol'shekhekhtsirskii State Natural Reservation.

Loc. 11. (Kosterin & Dubatolov 2005): near Bychikha village, 48°18'N, 134°50'E, 87 m a.s.l., 18-ix-2004: 1♀, leg. V.V. Dubatolov; (Malikova et al. 2007): 05-x-2006: 1♂, leg. V.V. Dubatolov.

Loc. 12. (Malikova et al. 2007): the mouth of the Chirki River, Chirki post of the Reservation, 48°12'N, 134°41'E, 35 m a.s.l., 20-vii-2007: 1♂, leg. V.V. Dubatolov.

Loc. 13. (Malikova et al. 2007): the Khekhtsirskiy Range forest (spruce, fir, and Daurian birch) with glades, *ca* 48°13'N, 134°51'E, 650 m a.s.l., 26-vii-2007: 1♀, leg. A.M. Dolgikh.

Loc. 14. (Yakubovich 2014): Lazo District, the lower course of the Ussuri River near Pereyaslavka village, 47°58'N, 135°03'E, 98 m a.s.l., 14-ix-2006: 4♂ 5♀, leg. V.S. Yakubovich.

Primorskiy Kray (Far-East Federal Region)

Loc. 15. (Ivanov 2002): east coast of Lake Khanka, Pospelovy Lakes, at the Vostochnyi post, 45°02'N, 132°51'E, 69 m a.s.l., 14-x-2000: 1♂, leg. Nikulina.

Loc. 16. (Ivanov 2002): south-western coast of Lake Khanka between the villages of Kamen'-Rybolov and Astrakhanka, 44°43'N, 132°03'E, 67 m a.s.l., 25-vii-1997: 1♂, leg. P.Yu. Ivanov.

Remarks. Lake Khanka lies on the Khankayskaya Plain in a savannah-like landscape with forests and grassland surrounded by mountains at the border between Russia and China and belongs to the Amur River basin. It is the largest lake in Primorskiy Kray (length 95 km, width 40–85 km, maximum depth 6.5 m, average depth 4 m), and 16 rivers run into the lake. The shore areas are partly swampy. The aquatic vegetation is well developed in shallow water. Meadow prevails on coasts, and pine forest reaches the lake at some places (Ivanov 2002).

Loc. 17. (Belyshev & Stepanchyuk 1965): near Ussurijsk City, the lower course of the Saputina River (presently Komarovka River), flood meadow, 43°46'N, 131°57'E, 18 m a.s.l., 22-viii-1962: 1♂ adult (Fig. 3b), leg. E.S. Stepanchyuk.

Remarks. The river is called Saputina in Belyshev & Stepanchyuk (1965) and Saputinka on the label of the voucher specimen (see Fig. 3b). This refers to the Chinese name Suputinka River, which was renamed Komarovka River in 1972. Ussurijsk City lies on the Komarovka and Rakovka Rivers in a depression between the hills in the Khanka Lowland. The Komarovka River runs down through wide valleys with tall-herbage meadows; the sides of the valley are covered with broad-leafed forest at the site where *S. croceolum* was found (Gerasimov 1969).

Loc. 18. (Belyshev 1964): Japan Sea, Putyatin Island, 35 km W of Nakhodka City, 42°52'N, 132°25'E, 0 m a.s.l., 01-ix-1959: 1♂ adul; 20-ix-1959: 1♀ (teneral) (Fig. 3a), leg. N.N. Kondakov.

Details of *S. croceolum* records in Kolyvanskiy District, Novosibirsk Province

The discovery of *S. croceolum* in Kolyvanskiy District succeeded in the pine forest in the surroundings of the village of Chernyy Mys, 5 km south-east of Lake Minzelinskoye (loc. 1). Chernyy Mys is located at the border be-

tween the forest and the north-eastern tip of the Barabinskaya forest steppe. Dragonfly monitoring has been conducted by us at this site since 1980, and *S. croceolum* was recorded there only in 2009 (12 individuals) and 2010 (3 individuals).

The first finding of *S. croceolum* took place on 06-ix-2009, around 14:00 h NOVT (UTC +7) on a clear day with a temperature of 18°C. At midday, we detected 12 individuals of *S. croceolum* in the pine forest in a sunlit, cluttered, wide clearing (Fig. 5). The dragonflies flew actively at 1.5–2.0 m above the ground, landing from time to time on prominent dry branches of brush or rough tree trunks, where they were perfectly camouflaged on the red-brown tree bark, making them almost invisible. Although the imagines of *S. croceolum* were very agile and quickly escaped when we approached them, we managed to catch three adult females with a butterfly net.

In further search of *S. croceolum*, we carefully inspected a clearing, a dirt track including adjacent forest, and the south-eastern bank of Lake Minzelinskoye during the rest of the same and the next day, however without success. A week later, on 13-ix-2009, we inspected this site again from 15:30–16:30 h NOVT but we did not see a single *Sympetrum*. The weather was clear, windless, with an air temperature of 14°C.

The second finding of *S. croceolum* took place exactly one year later on 07-ix-2010, 10:30–11:30 h NOVT, in exactly the same place. In the clearing of the pine forest, we saw three individuals of *S. croceolum* but failed to catch them. The weather conditions were clear and quiet, air temperature was 18°C.

Lake Minzelinskoye

At a distance of *ca* 5 km, the nearest water body to the site of the *S. croceolum* records is Lake Minzelinskoye (Fig. 8), which is likely to be the origin of a small population of this species. Therefore, a brief description is given. In addition, Lake Minzelinskoye resembles in its main features Lake Manzherok (Fig. 7), which is inhabited by a stable *S. croceolum* population but is ten times larger.

The length of the lake is about 12 km, the largest width 2.2 km, the depth ranges from 1 to 3.5 m. The lake has no tributary and is discharged by the Krutishka River, which enters the Ob' River. The lake is fed by spring floods,

precipitation, and ground water. It contains freshwater (salinity below 1 g/l) (Mal'tsev et al. 2014). The largely swampy lake is located in a forest (Siberian Spruce, Siberian Stone Pine, Common Pine, birch). Quaking bogs intersperse with extensive growth of macrophytes, dominated by *Myriophyllum sibiricum*, *Stratiotes aloides*, *Hydrilla verticillata*, and *Hydrocharis morsus-ranae*. *Phragmites australis*, *Typha latifolia*, and *Carex* spp. dominate in the coastal zone (Zarubina 2013). The lake has a thick layer of up to 10 m of sapropel sediment (gyttja).

Breeding of *S. croceolum* in an aquarium

We managed to obtain a clutch of 150 eggs from one of the *S. croceolum* females caught on 06-ix-2009. Freshly laid *S. croceolum* eggs were yellowish, and by the end of the first day in water they had become brown. The size of the ovate eggs was slightly larger than that of other species of the genus – the length was 0.60–0.63 mm, the maximum width (diameter) was 0.45 mm. The aquarium with the eggs was placed in a well-ventilated room with an

Figure 8. Lake Minzelinskoye, Kolyvanskiy District, Novosibirsk Province, Russia (15-viii-2006). Photo: A.Yu. Haritonov

air temperature of about 22–23°C and a water temperature of about 22.5–23.0°C throughout the entire breeding time. Thirty eggs blackened and died during the first two weeks. The first larvae hatched on 04-xii-2009 and hatching continued until 28-xii-2009. Thus, the period of embryonic development lasted from 89 to 113 days (3–3.5 months). Larvae hatched at different rates, with a decreasing trend throughout the hatching period (25 days): one a day at the beginning of the hatching period, one every 4–5 days during the middle, and one every 7 days at the end. Only 28 of 150 eggs (18.5 %) developed successfully to larvae. Small larvae were fed with brine shrimp, *Artemia salina*, bred in saturated saline solution, and were moved successively from one container with fresh water to another in order to remove the salt. The dragonfly larvae foraged actively and moved all over the aquarium. We were able to rear the larvae only up to the 3rd instar before they died. The duration of the first larval instar was 1–2 days and that of the second instar 10–11 days. According to our experience, the larvae of younger instars of *S. croceolum* differed significantly from those of other *Sympetrum* spp.: they were larger and the whole body had a pronounced pattern characterised by a combination of dark and light bands. The pattern changed from instar to instar. Head coloration and morphology in the dorsal view are described as follows: 1st instar – slight shading without a pattern; 2nd instar – medium part of the head darkish and proximal and distal parts pale; 3rd instar – upper part of the head completely light, with "horns" (rod-shaped outgrowths) between the eyes. The colour of the abdomen in the dorsal view was: 1st and 2nd instar – a pale middle part and dark proximal and distal parts; 3rd instar – a completely pale abdomen.

Systematic remarks

The strong variability of *S. croceolum* has attracted much attention. The body size varies greatly, in particular the length of the hind wing, to which Belyshev (1964) attributed taxonomic significance. Specimens (1♂ 1♀) from Putyatin Island were described as a distinct geographical subspecies, *S. croceolum fuscoatrum* (Belyshev 1964: 55), to which Belyshev then also attributed continental specimens from the surroundings of the city of Ussuriysk (Belyshev 1968: 432) (Figs 3a, b). Subsequently, all records of *S. croceolum* from the Russian Far East were listed under the subspecies *S. c. fuscoatrum*

(Belyshev 1973; Davies & Tobin 1985; Tsuda 2000). Belyshev (1964: 55) wrote that specimens of this subspecies »differ from the type entirely in black tarsus in male and black distal end of the tarsus in female«. However, this statement is not in accordance with the tarsus coloration (Figs 2b, c) of the holotype specimen from Japan with entirely black front tarsi and middle and hind tarsi that are black at the distal end.

Between the 1960s and 1980s, the amount of material from the Far East of Russia did not increase, but local populations of *S. croceolum* were found in the south of Western Siberia, in Novosibirsk Province, and the Altai Republic. Analysis of morphological features, usually mentioned in the literature (*e.g.*, Bartenev 1915; Belyshev 1973; Kosterin 1987a), of Far Eastern and Siberian specimens gave the following general picture. All teneral specimens have wings with exclusively tan, but not black veins; all adults have tan veins in the coloured part of the wing and black veins in the transparent part. The distribution of the dark colour on the tarsi can vary even in individuals from the same site; for example, in the *Suzun* population (Lake Konovalovo, Suzunskiy District, Novosibirsk Province), it ranges from the complete absence of dark colour via a dark proximal part of the tarsi to completely dark tarsi. The saturation of the dark colour of the tarsi depends on the age of the individual – the older it is, the more intense the colour. The inferior appendages of males from the Komarovka River as well as of the holotype specimen (Fig. 2d) reach the lower corner of the superior appendages, while inferior appendages of males from Lake Manzherok and Lake Konovalovo can either reach or slightly extend beyond the lower corner of the superior appendages. Some authors tried to find differences in the shape of the row of black teeth on the superior appendages – either straight (Bartenev 1915: 350) or curved (Kosterin 1987a: 57). In our opinion, this is quite a subjective feature as the view angle is important: in profile, the row is straight, while in dorso-lateral view it is curved. Thus, all characters of Far Eastern and Siberian specimens mentioned in literature more or less overlap.

The specimens available to B.F. Belyshev for the description of the new subspecies, *S. c. fuscoatrum*, had a hind wing length of 25–27 mm, whereas according to Bartenev (1915), the length of the hind wing of Japanese and

Chinese specimens is 29–31 mm, and according to Asahina (1961) 28–32 mm. The hind wing length of specimens of the *Suzun* population was 24.5–33.0 mm (mean 28.2 ± 0.8 mm), a span outperforming all the values given above, thus demonstrating the great variability of hind wing length within *S. croceolum*.

Therefore, the previously recognised Far Eastern subspecies, *S. c. fuscoatrum* Belyshev, 1964, is here designated a junior synonym of the nominotypical subspecies *S. croceolum* (Selys, 1883). All individuals of this species inhabiting the south of the Russian Far East, the Korean Peninsula, and the Japanese islands should be classified as *S. c. croceolum*. Hence:

Sympetrum croceolum croceolum (Selys, 1883) = *Sympetrum croceolum fuscoatrum* Belyshev, 1964, syn. nov.

Discussion

The analysis of available data on the flight period of *Sympetrum croceolum* indicates a tendency for an increasing time span on the wing from the western to the eastern parts of its range: in Novosibirsk Province and in Altai Republic it was recorded from August to September, in the southern Far East of Russia from July to October, in Korea from June to October (Lee 2001), and in Japan from June to December, with some individuals living until spring (Inoue & Tani 2001). This indicates the flexibility of the species' life cycle.

Sympetrum croceolum occurs on the continent at lower elevations. In the Russian part of its area, the absolute elevations usually range from 18 (near Ussurijsk) to 158 m a.s.l. (near Chernyy Mys, Novosibirsk Province) with the maximum at 650 m a.s.l. (Khekhtsirskiy Range forest, Khabarovskiy District). Seehausen & Fiebig (2016) reported *S. croceolum* from North Korea at 757 m a.s.l. (Hamgyong-pukto, Mayang Reservoir north of Chongjin, 42.0705°N, 129.5096°E). This site is only about 270 km away from the Ussurijsk records (loc. 17), and therefore, it is likely that *S. croceolum* can be found in Russia at elevations higher than 650 m a.s.l.

On the Japanese islands, *S. croceolum* is reported from high elevations only (Matsumura 1898; Asahina 1938, 1961; Inoue & Tani 2001). Unfortunately, there is no information on where exactly the species was found

on Putyatin Island (Belyshev 1964). The mountainous parts of the island are covered by forest and shrubbery, and the lower parts consist of wetlands with elements of relic flora (Gerasimov 1969). During a monitoring survey of Lake Koreyskoye (eastern coast) and Lake Gusinoye (western coast) of Putyatin Island in July 1999, *S. croceolum* was not found (Zorina et al. 2000).

The northernmost record of *S. croceolum* in Western Siberia is in Kolyvanskiy District in Novosibirsk Province (55°33'N, 83°24'E). The forested swampy massifs of the Vasyugan plain – a subzone of the southern taiga – are located further to the North. In 2006 and 2012, during two odonatological expeditions to the eastern part of Vasyugan, 43 dragonfly species were recorded but not *S. croceolum* (Bernard & Kosterin 2010; Popova & Haritonov 2013), although a presence of the species in the region could be possible. Probably, the expeditions (07–23-vii) were undertaken too early for *S. croceolum* to be on the wing.

In the Far East, *S. croceolum* has not yet been found north of Lake Peschanoye in Amur Province (50°25'N, 127°42'E) (Malikova 1993, 1995) and Komsomol'sk-on-Amur (50°33'N, 137°01'E) (Yakubovich & Kapkaev 2009).

Within its entire range, *S. croceolum* seems to have a patchy distribution. Lee (2001: 166) writes: »This species is locally distributed over the Korean Peninsula and Is. Jeju-do. It seems not common species«. It was listed in only 12 of 80 odonatological publications we were able to analyse concerning the South of the Russian Far East. Based on the reviewed literature (Needham 1930; Asahina 1961, 1990; Haritonov & Malikova 1998; Inoue & Tani 2001; Lee 2001; Malikova & Ivanov 2001; Wilson 2005) and our data, it can be concluded that abundant populations of *S. croceolum* are much less common than small populations. There are more or less stable and large populations of the species only in two of 18 Russian locations – on Lakes Konovalovo and Manzherok in Western Siberia. The remaining records concern single or few individuals only. However, different estimations of population sizes exist for the south of Khabarovskiy Kray – from rare (Malikova et al. 2007) to fairly abundant (Yakubovich & Kapkaev 2009; Yakubovich 2014).

For 100 years, *S. croceolum* was considered to have a Japanese-Manchurian range. Not until 1982 were new populations detected in Western Siberia, in Novosibirsk Province, and Altai, 4 500 km west of the core area.

The isolation of the *S. croceolum* recording sites in the South of Western Siberia – on Lake Manzherok and in the Suzun pine forest – prompted Kosterin (1987a, 2005, 2017) to regard them as relics of a once vast continuous range. There are speculations in the scientific literature that the pine forests at the foothills of the Altai are remnants of continuous pine forest once covering the entire south of Western Siberia in the Neogene, which ended about 2.6 million years ago, and that still contain faunal and floral relic elements (Martynov 1929; Krylov 1957; Belyshev 1962; Belyshev & Haritonov 1981). Kosterin (2005) introduced an alternative hypothesis for the East Asian dragonfly species in Western Siberia, including *S. croceolum*; they could have colonised Siberia during the climatic optimum of the Holocene, only 5 000 years ago, when a broad-leafed woodland belt existed in Siberia. After the end of the optimum, due to the stenotopic nature of the species, the range of *S. croceolum* could have receded back to the Altai refugium (Kosterin 2005).

The last hypothesis seems logical, especially since the moderate age of most water bodies where this dragonfly is found is almost consistent with it. In addition, the species appears not to be stenotopic, but it is able to inhabit various landscapes and types of water bodies. The absence of records of *S. croceolum* on a significant stretch along the south of Siberia – from Krasnoyarskiy Kray to Chita Province inclusively – can probably be explained as follows: inadequate research within this large territory; locality of distribution inherent for the species in general; and a temporary character of the populations in this area.

Apparently, *S. croceolum* has a considerable migration potential, which is inherent to the Libellulidae (*e.g.*, Dumont & Hinnekint 1973; Borisov 2011; Buczyński et al. 2014; Popova & Haritonov 2014; Popova & Eremina 2016). Therefore, Western Siberian populations of *S. croceolum* probably originate from migration of some individuals of the eastern population to the west during the last decades or centuries (see, *e.g.*, Kosterin 2005).

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References

Anderson R.C. 2009. Do dragonflies migrate across the western Indian Ocean? *Journal of tropical Ecology* 25: 347-358

Asahina S. 1938. Odonata of Hokkaido. *Tenthredo: Acta entomologica* 2 (2): 149-172

Asahina S. 1961. Odonata: Libellulidae. Insecta Japonica (I) 1: 1-90. Hokuryukan, Tokyo

Asahina S. 1990. The Odonata of Korean peninsula, a summarized review. Part 5. Libellulidae 2. *Gekkan-Mushi* 231: 15-19

Bartenev A.N. 1915. Insectes Pseudoneuroptères (Insecta Pseudoneuroptera). Vol. I. Libellulidae. Livraison 1. In: Nasonov N.V. (Ed.), Faune de la Russie et des pays limitrophes: 1-352. Academie Impériale des Sciences de Petrograd [in Russian, French title]

Belyshev B.F. 1962. [About some elements of tertiary odonatological fauna in pine forest massifs of the southern part of the West Siberian plain]. *Izvestiya Sibir. otdelenie AN SSSR* [Seria biologo-meditsinskikh nauk], Novosibirsk, 4 (5): 115-120 [in Russian]

Belyshev B.F. 1964. [Contributions to the knowledge of the fauna of dragonflies (Odonata) of Siberia. I]. *Fragmenta faunistica*, Warszawa, 11: 53-74 [in Russian]

Belyshev B.F. 1968. [Contributions to the knowledge of the fauna of dragonflies (Odonata) of Siberia. IV]. *Fragmenta faunistica*, Warszawa, 14: 407-536 [in Russian]

Belyshev B.F. 1973. The dragonflies of Siberia (Odonata). Vol. 1, part 1. Nauka, Novosibirsk [in Russian, English title]

Belyshev B.F. & Haritonov A.Yu. 1981. Geografiya strekoz Boreal'nogo faunisticheskogo tsarstva. Nauka, Novosibirsk [in Russian]

Belyshev B.F. & Stepanchyuk E.S. 1965. Interesnye v zoogeographicheskom otnoshenii nakhodki strekoz (Odonata) v Yuzhnom Primor'e. *Izvestiya Vostochno-Sibirskogo otdela geograph. obshchestva SSSR* 64: 15-18 [in Russian]

Bernard R. & Kosterin O.E. 2010. Biogeographical and ecological description of Odonata of Eastern Vasyugan Plain, West Siberia, Russia. *Odonatologica* 39: 1-28

Borisov S.N. 2011. Migrant dragonflies in Middle Asia. 2. *Sympetrum fonscolombii* (Selys, 1840) (Odonata, Libellulidae). *Euroasian entomological Journal*. 10: 415-421 [in Russian, English title and abstract]

Buczyński P., Shapoval A.P. & Buczyńska E. 2014. *Pantala flavescens* at the coast of the Baltic Sea (Odonata: Libellulidae). *Odonatologica* 43: 3-11

Corbet P.S. 1999. Dragonflies: Behavior and ecology of Odonata. Harley Books, Colchester

Davies D.A.L. & Tobin P. 1985. The dragonflies of the world: A systematic list of the extant species of Odonata. Vol. 2. Anisoptera. *Societas internationalis odonatologica rapid Communnications* (Suppl.) 5: i-ix, 1-151. SIO, Utrecht

Dumont H.J. & Hinnekint B.O.N. 1973. Mass migration in dragonflies, especially in *Libellula quadrimaculata* L.: a review, a new ecological approach and a new hypothesis. *Odonatologica* 2: 1-20

Gerasimov I.P. (Ed.) 1969. Prirodnye uslovia i estestvennye resursy SSSR. Yuzhnaya chast' Dal'nego Vostoka. AN SSSR, Moskva [in Russian]

Haritonov A.Yu. 2000. [Dragonfly saffron *Sympetrum croceolum* Selys, 1883]. Krasnaya Kniga Novosibirskoi Oblasti. Zhivotnye: 224-225. Kontinent KMK, Novosibirsk [in Russian]

Haritonov A.Yu. & Malikova E.I. 1998. Odonata of the Russian Far East: a summary. *Odonatologica* 27: 375-381

Haritonov A.[Yu.] & Popova O. [N.] 2011. Spatial displacements of Odonata in southwest Siberia. *International Journal of Odonatology* 14: 1-10

Inoue K. & Tani K. 2001. All about dragonflies. Tombow Publishing, Osaka

Ivanov P.Yu. 2002. [Odonatofauna of the Khanka Lake basin]. *Zhivotnii mir Dal'nego Vostoka*, Blagoveshchensk, 4: 47-60 [in Russian]

Kosterin O.E. 1987a. [Discovery of east-asiatic dragonfly (Odonata, Libellulidae) at the Mangerock lake (Altay)]. In: Cherepanov A.I. (Ed.), Nasekomye, kleshchi i gel'minty 9: 57-63. Nauka, Novosibirsk [in Russian]

Kosterin O.E. 1987b. [Population of dragonflies of Lake Manzherok]. In: Problemy formirovaniya naseleniya nazemnyh i vodnyh biotsenozov: 76-92. OmGPI, Omsk [in Russian]

Kosterin O.E. 2005. Western range limits and isolates of eastern odonate species in Siberia and their putative origins. *Odonatologica* 34: 219-242

Kosterin O.E. 2007a. [Dragonflies (Insecta, Odonata) of Akademgorodok]. In: Zhimulyov I.F. (Ed.), Priroda Akademgorodka: 50 let spustya: 74-91. SO RAN, Novosibirsk [in Russian]

Kosterin O.E. 2007b. [Saffron dragonfly – *Sympetrum croceolum* Selys, 1883]. Krasnaya Kniga Rispubliki Altay (issue 2). Zhivotnye: 47-50. GAGU, Gorno-Altaysk [in Russian]

Kosterin O.E. 2017. [Saffron dragonfly – *Sympetrum croceolum* Selys, 1883]. Krasnaya Kniga Rispubliki Altay (issue 3). Zhivotnye: 33-35. GAGU, Gorno-Altaysk [in Russian]

Kosterin O.E. & Dubatolov V.V. 2005. A dragonfly (Odonata) collection from the Bolshekhekhtsirskii State Nature Reserve (Khabarovskii Krai, Russia). In: Streltzov A.I. (Ed.), Zhivotnii mir Dal'nego Vostoka [Animal World of the Far East] 5: 9-14. BGPU, Blagoveshchensk [in Russian, English title and abstract]

Kosterin O.E., Haritonov A.Yu. & Inoue K. 2001. Dragonflies of the part of Novosibirsk Province east of the Ob' River, Russia. *Sympetrum*, Hyogo, l (7/8): 24-49

Kosterin O.E., Malikova E.I. & Haritonov A.Yu. 2004. Critical species of Odonata in the Asian part of the former USSR and the Republic of Mongolia. *International Journal of Odonatology* 7: 341-370

Krylov G.V. [The nature of the forests of Western Siberia and the direction of the use and improvement of forest resources]. *Trudy po lesnomu khozyaistvu* 3: 91-146. Zapadno-sibirskii filial AN SSSR, Novosibirsk [in Russian]

Lee S.-M. 2001. The dragonflies of Korean Peninsula (Odonata). Junghaeng-Sa, Seoul

Malikova E.I. 1993. [Dragonflies (Insecta, Odonata) of the surroundings of city of Blagoveshchensk]. *Problemy ekologii Verkhnego Priamur'ya*, Blagoveshchensk, 1: 91-101 [in Russian]

Malikova E.I. 1995. [Dragonflies (Odonata, Insecta) of the Russian Far East]. Dissertation, Novosibirsk [in Russian]

Malikova E.I. 1997. [Fauna of dragonflies (Insecta, Odonata) of Amur region]. *Problemy ekologii Verkhnego Priamur'ya*, Blagoveshchensk, 3: 109-116 [In Russian]

Malikova E.I. & Ivanov P.Y. 2001. [Fauna of odonates (Insecta, Odonata) of the Primorskii Krai]. *V.Y. Levanidov's biennial Memorial Meetings* 1: 131-143. Dal'nauka, Vladivostok [in Russian]

Malikova E.I., Kosterin O.E. & Dubatolov V.V. 2007. A dragonfly (Odonata) collection from the Bolshekhekhtsirskii State Nature reserve (Khabarovskii Krai, Russia). II. Seasons 2006 and 2007. In: Streltzov A.I. (Ed.), Zhivotnii mir Dal'nego Vostoka [Animal World of the Far East] 6: 5-9. BGPU, Blagoveshchensk [in Russian, English title and abstract]

Mal'tsev A.E., Lazareva E.V., Leonova G.A., Bobrov V.A. & Miroshnichenko L.V. 2014. Mineral composition and geochemistry of the holocene section sapropel in Minzelinskoye Lake (Novosibirsk region). *Geologiya i mineral'no-syr'evye resursy Sibiri*. 3c-2: 414-420 [in Russian, English title and abstract]

Martynov A.V. 1929. [Ecological preconditions for zoogeography of freshwater benthic animals]. *Russkii zoologicheskii Zhurnal* 12 (3): 3-34 [in Russian]

Matsumura S. 1898. Insects collected on Mount Fuji. *Annotationes zoologicae japonenses* 2: 113-124

Needham J.G. 1930. A manual of the dragonflies of China. A monographic study of the Chinese Odonata. *Zoologica sinica* (A, Invertebrates of China) 11 (1): 1-344, [index] 1-11. The Fan Memorial Institute of Biology, Peiping, China

Popova O.N. & Eremina E.E. 2016. *Sympetrum fonscolombii* (Selys, 1840) (Odonata, Libellulidae) in northernmost areal localities in Chelyabinskaya and Novosibirskaya Oblast's of Russia. *Euroasian entomological Journal* 15 (1): 45-59 [in Russian, English title and abstract]

Popova O.N. & Haritonov A.Yu. 1999. [Geographical distribution of dragonflies of the *Sympetrum* genus]. *Vestnik Chelyabinskogo gosudarstvennogo pedagogicheskogo Universiteta* (10) 1: 7-15 [in Russian]

Popova O.N. & Haritonov A.Yu. 2008. [Saffron dragonfly of *Sympetrum croceolum* Selys, 1883]. Krasnaya Kniga Novosibirskoi Oblasti. Zhivotnye, rasteniya, griby: 44-45. Arta, Novosibirsk [in Russian]

Popova O.N. & Haritonov A.Yu. 2013. Odonata of the East Vasyugan, West Siberia, Russia. *Euroasian entomological Journal* 12: 217-223 [in Russian, English title and abstract]

Popova O.N. & Haritonov A.Yu. 2014. Mass reproductive wanderings of dragonflies of the genus *Sympetrum* (Odonata, Libellulidae). *Entomological Review* 94 (1): 21-28

Rikhter G.D. (Ed.). 1963. Prirodnye uslovia i estestvennye resursy SSSR. Zapadnaya Sibir'. AN SSSR, Moskva [in Russian]

Selys-Longchamps de E. 1883. Les odonates du Japon. *Annales de la Société entomologique de Belgique* 27: 82-143

Rusanov G.G. 2015. About time appearance water nut in Manzherok and Kolyvan lakes of Altay. *Bulletin AB RGS* 3 (38): 30-34 [in Russian, English title and abstract]

Seehausen M. & Fiebig J. 2016. A collection of Odonata from North Korea, with first record of *Ischnura elegans* (Odonata: Coenagrionidae). *Notulae odonatologicae* 8 (7): 203-211

Sui J.-z. & Sun H.-g. 1984. Common species of dragonflies from China. Agriculture Publishing House, Beijing [in Chinese, English title]

Tsuda S. 2000. A distributional list of world Odonata. Privately published, Osaka

Wilson K.D.P. 2005. Odonata of Guangxi Zhuang Autonomous Region, China, part II: Anisoptera. *International Journal of Odonatology* 8: 107-168

Yakobson G.G. & Bianki V.P. 1905. [Orthoptera and Pseudoneuroptéres of Russian Empire and adjacent countries]. Saint-Petersburg [in Russian]

Yakubovich V.S. 2014. [To the fauna of odonates (Odonata) of the lower course of the Ussuri River, Khabarovskii Krai]. *A.I. Kurentsov's annual Memorial Meetings* 25: 41-48. Dal'nauka, Vladivostok [in Russian]

Yakubovich V.S. & Kapkaev A.Yu. 2009. [To the fauna of odonates (Odonata) of Komsomolsk-on-Amur and its vicinities]. *Shestye Grodekovskie chteniya*, Khabarovsk, 6: 88-90 [in Russian]

Zarubina E.Yu. 2013. Primary macrophyte production of three different-type sapropelic lakes in the south of West Siberia (within Novosibirsk Oblast') in 2012. *Mir nauki*, *kul'tury*, *obrazovaniya* 5 (42): 441-444 [in Russian, English title and abstract]

Zorina O.V., Ivanov P.Yu., Storozhenko S.Yu. & Kholin S.K. 2000. To the knowledge of insect fauna of Putyatin Island (South Primorye). *The North Pacific Islands biological Researches* 3: 1-12. Dal'nauka, Vladivostok [in Russian, English title and abstract]