

Review of the distribution of *Somatochlora sahlbergi* (Odonata: Corduliidae)

Asmus Schröter *

*Rasenweg 10, D-37130 Gleichen, Germany. E-mail: asmustim@gmx.de

"It's always nice to have at least one elusive species out there that will bring a big smile to your face when it's pulled out from the net."

John Hudson, by E-mail



Figure 1: Exuvia of *Somatochlora sahlbergi* in dorsal view (Norway)

Summary

Based on data collected from literature, museum collections, national databases and personal communications, an up-to-date map of the worldwide distribution of *Somatochlora sahlbergi* is presented. A new hypothesis is presented indicating that occurrences are at least regionally correlated with palsa mires. Two examples of larval habitats in Europe are illustrated and described, including the first observation of reproduction in Norway and the first record of co-occurrence with Zygoptera in Europe. The exuvia of *S. sahlbergi* is illustrated and distinguishing features briefly discussed.



Introduction

As the only dragonfly to have a primarily Beringian distribution (Cannings & Cannings 1985), *Somatochlora sahlbergi* Trybom 1889 occupies a unique position in the collective odonatological consciousness. The superlative “northernmost dragonfly” could be considered odonatological general knowledge and lead to a remarkable high level of awareness and recognition value of the name, even amongst odonatologists without any relations to northern latitudes. As hardly any other dragonfly species, *S. sahlbergi* widely represents a certain part of the world, evoking associations of the wild and vast Nordic landscape of its natural habitat. However, only a small minority of odonatologists has ever been lucky enough to find *S. sahlbergi* in the field. The difficulties to see this species, combined with its inhospitable and wild habitat, constitute an aura between mysteriousness and exclusivity.

The current known distribution of *Somatochlora sahlbergi* is restricted to the taiga biome. With the exception of possibly isolated populations in the mountains of Eastern and Southern Siberia (Belyshev & Ovodov 1961, Belyshev 1968, Kosterin 1992, 2004, Dumont et al. 2005, Haritonov & Malikova 1998, Kosterin & Lyubechanskii 2009, Kosterin & Zaika 2010), the circumboreal distribution of the species generally follows the latitudinal treeline across Canada, Alaska and Eurasia. Thus, the southern distributional limit of *S. sahlbergi* is situated further north than that of any other dragonfly (Corbet 1999: 179).

Despite the large size of its Holarctic distribution and recognition as a species for more than 120 years (Trybom 1889), little is known about the population dynamics and ecology *S. sahlbergi* (cf Wildermuth 2008: 432). The remoteness and inaccessibility of its habitat, and harsh weather conditions during the emergence period (cf Śniegula 2006, Wildermuth 2008, own obs.), are likely factors contributing to the lack of information about the species. Furthermore, despite increased interest in the species, very few records exist. Cannings & Cannings (1985) reported only 16 records worldwide and Kosterin (1992) reported 13 additional records, all located in Russia.

S. sahlbergi is the most rare dragonfly species in Europe. The first European record of *Somatochlora sahlbergi* was from Lake Imandra (Valle 1915, 1931). From the 1930s to the 1980s only a few additional records, consisting of single specimens from sites in Finland, were reported (Hämäläinen 1967, 1984, Sahlén 1987). However, since the 1990s, both the number of localities and the number of individuals collected at sites has increased, including the first adult records for Norway (Pedersen 1992) and Sweden (Sahlén 1994). Wildermuth (2008) provided a comprehensive summary of *S. sahlbergi* distribution in Europe.



Due to low abundances and general difficulties to detect adults of *S. sahlbergi*, comparatively many successful attempts have been made to collect larvae. However, the vegetation structure and composition of most of the known larval habitats in Europe (cf Valle 1931, Butler 1992) and elsewhere (Belyshev 1973, Cannings & Cannings 1985, 1997, Kosterin 1992, Dumont et al. 2005, McClory & Gotthardt 2006, Kosterin & Zaika 2010) are poorly described. Only 38 exuviae of *S. sahlbergi* have been collected worldwide, including only 16 exuviae from Fennoscandia (Table 1). As with the larval records, there is very little information on the habitat mainly bare figures are listed and virtually none of the bibliographical references include detailed information on circumstances under which exuviae have been found. The species's uniqueness is also impressively expressed by the fact that up to now only three photos showing naturally perching non-manipulated specimens have been published worldwide (Karjalainen 2010, Kosterin 2003).

Study Objectives

The primary objective of this study was to collect, evaluate, and map all existing distributional data for *S. sahlbergi*. Basic habitat and ecological information are also provided. The discussed distribution pattern and the presented correlation between the occurrence of *S. sahlbergi* and the climate conditions allowing the development of palsa mires in Europe, as well as its hypothesized generalisation on a worldwide scale, is based on description of climatic data of all 71 localities depicted on the map.

The second objective of this study was to summarize the available knowledge of the larval ecology of *S. sahlbergi*, supplying a small European piece of the mosaic to the still insufficient overall picture of the species we have. Essentially, due to the character of this review it implicitly refers to a meta-discussion on odonatological research, which might be considered the hidden third aim of this work.

Methods

S. sahlbergi records were obtained from publications, museum collections, national databases and personal communications. Additional records were obtained during two field trips in Fennoscandia by Jörg Arlt and the author in 2006 and 2010. Information on syntopic dragonfly species and vegetation in and around larval habitats were collected during these field trips. Climate data at the locations were taken from WorldClim (Hijmans et al. 2005) at a spatial resolution of 2.5 arcmin. Records were mapped using DIVA-GIS 5.4 (Hijmans et al. 2001).



Results - I *Somatochlora sahlbergi* worldwide

Distribution and abundance

The current global distribution of *S. sahlbergi* is represented by a total of 71 records from Russia, Norway, Finland, Sweden, Canada and the United States of America (Fig. 2-6).

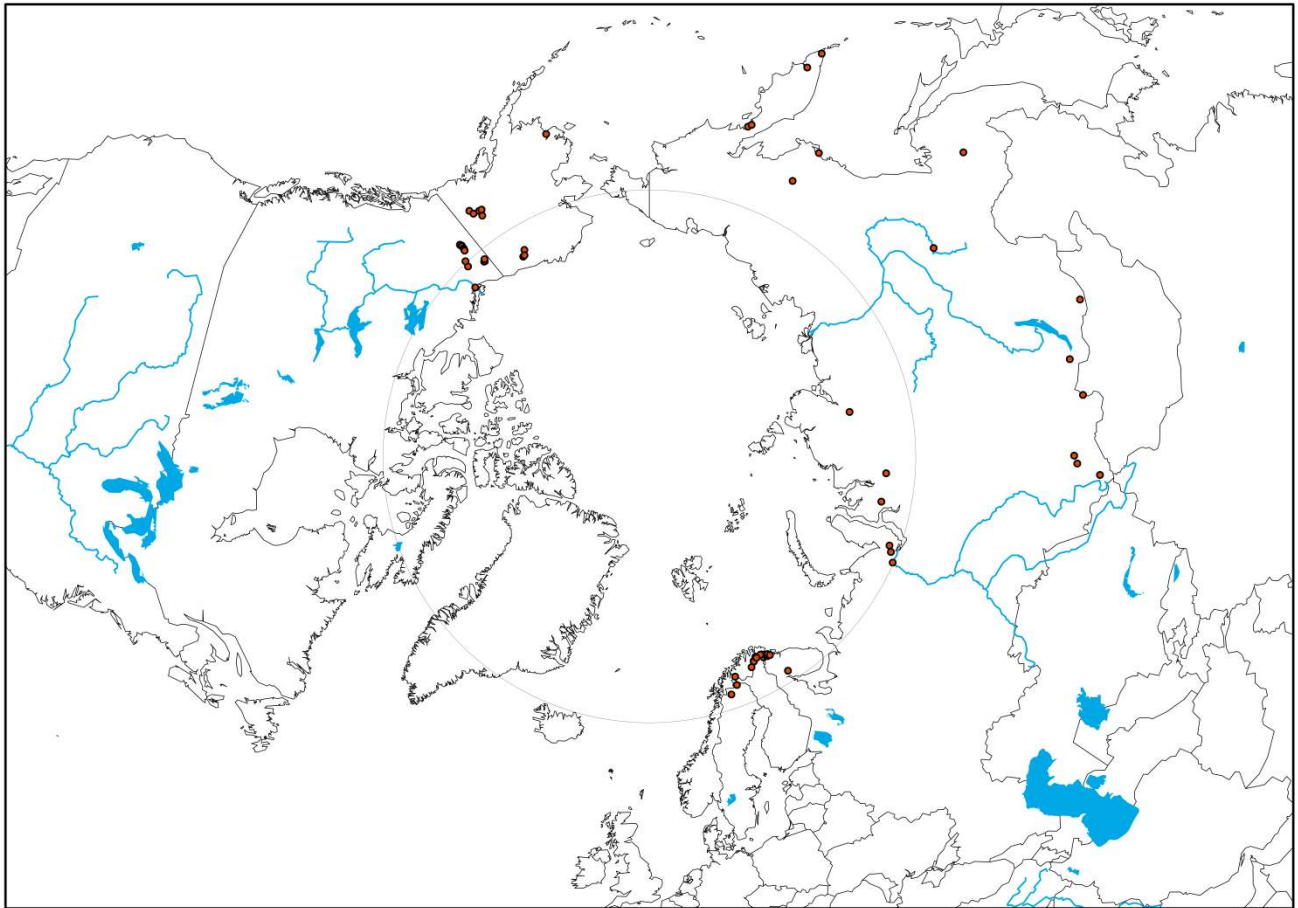


Figure 2: Global distribution of *Somatochlora sahlbergi*.



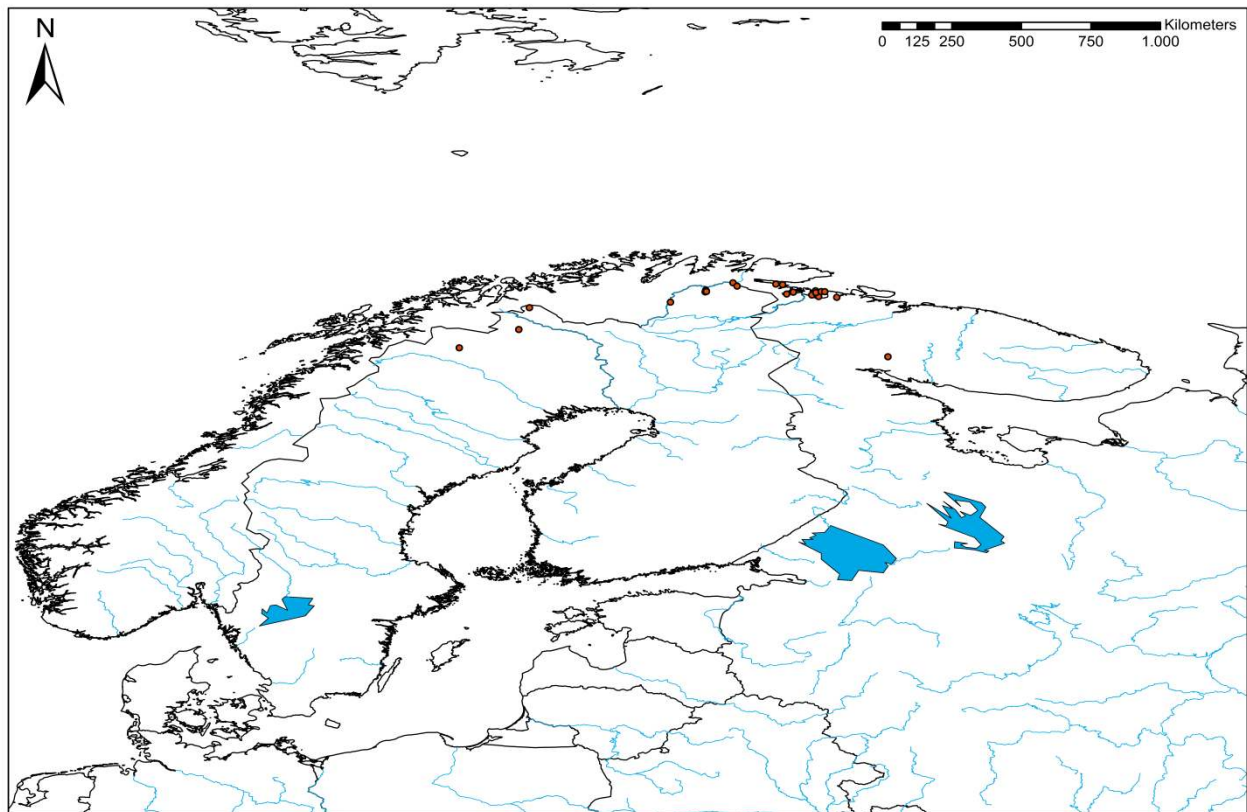


Figure 3: Detailed map of the distribution of *Somatochlora sahlbergi* in Europe.

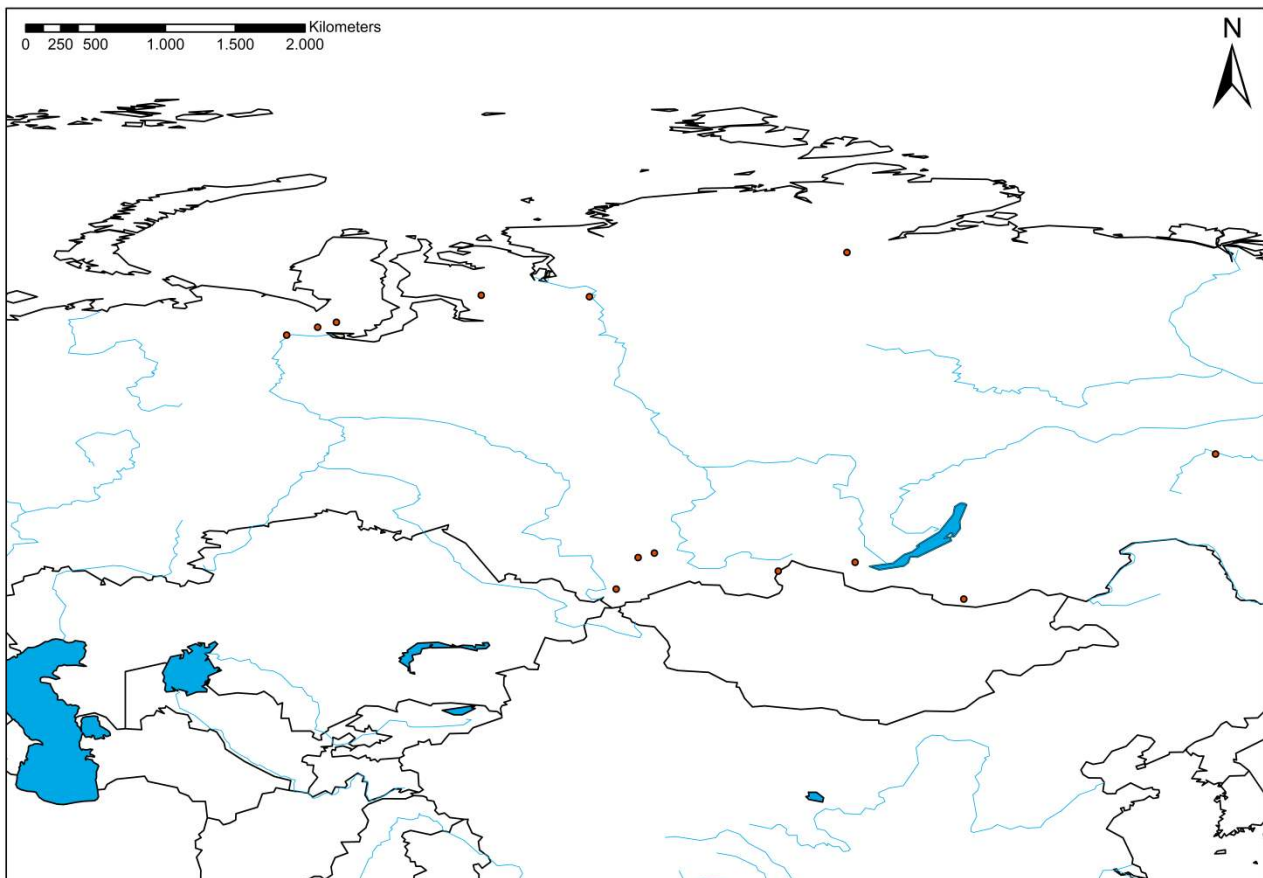


Figure 4: Detailed map of the distribution of *Somatochlora sahlbergi* in Western Siberia.



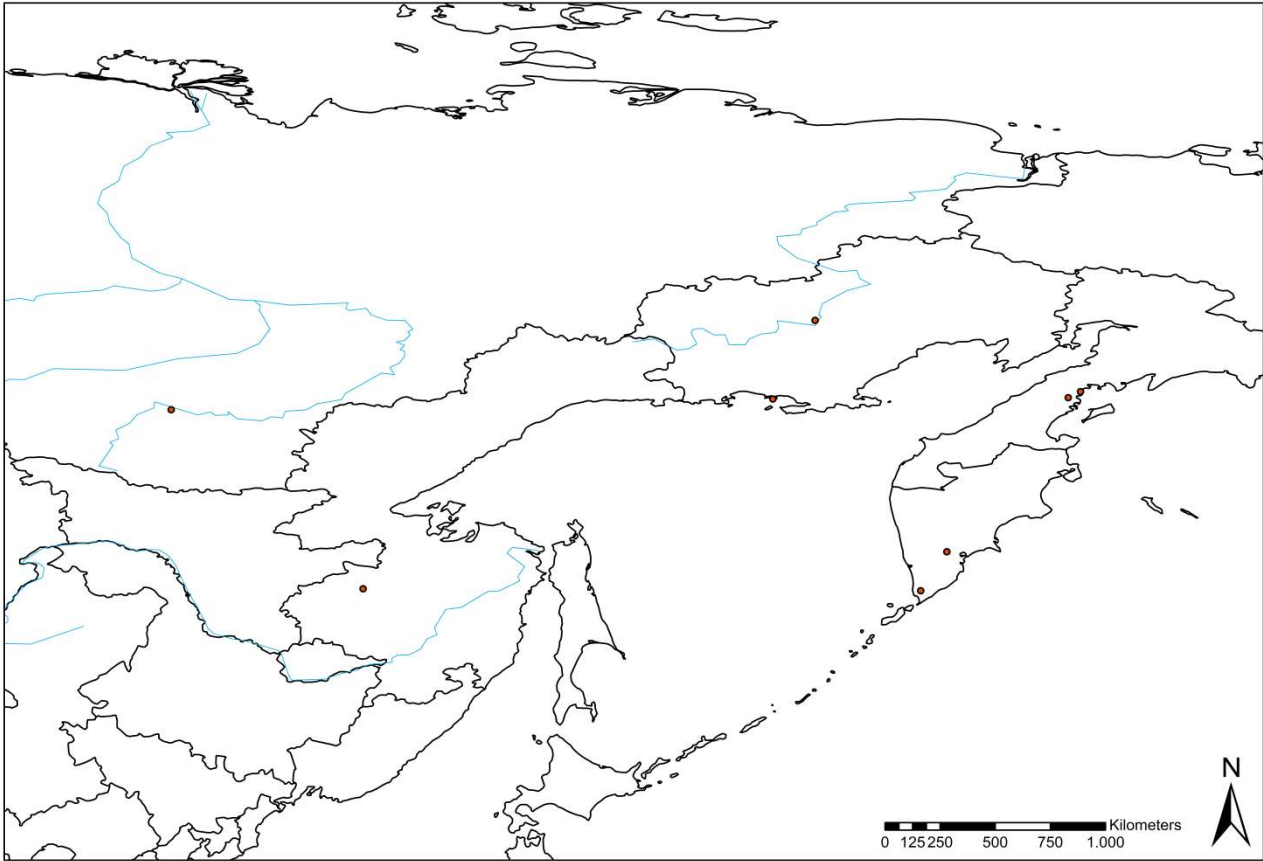


Figure 5: Detailed map of the distribution of *Somatochlora sahlbergi* in Eastern Siberia.

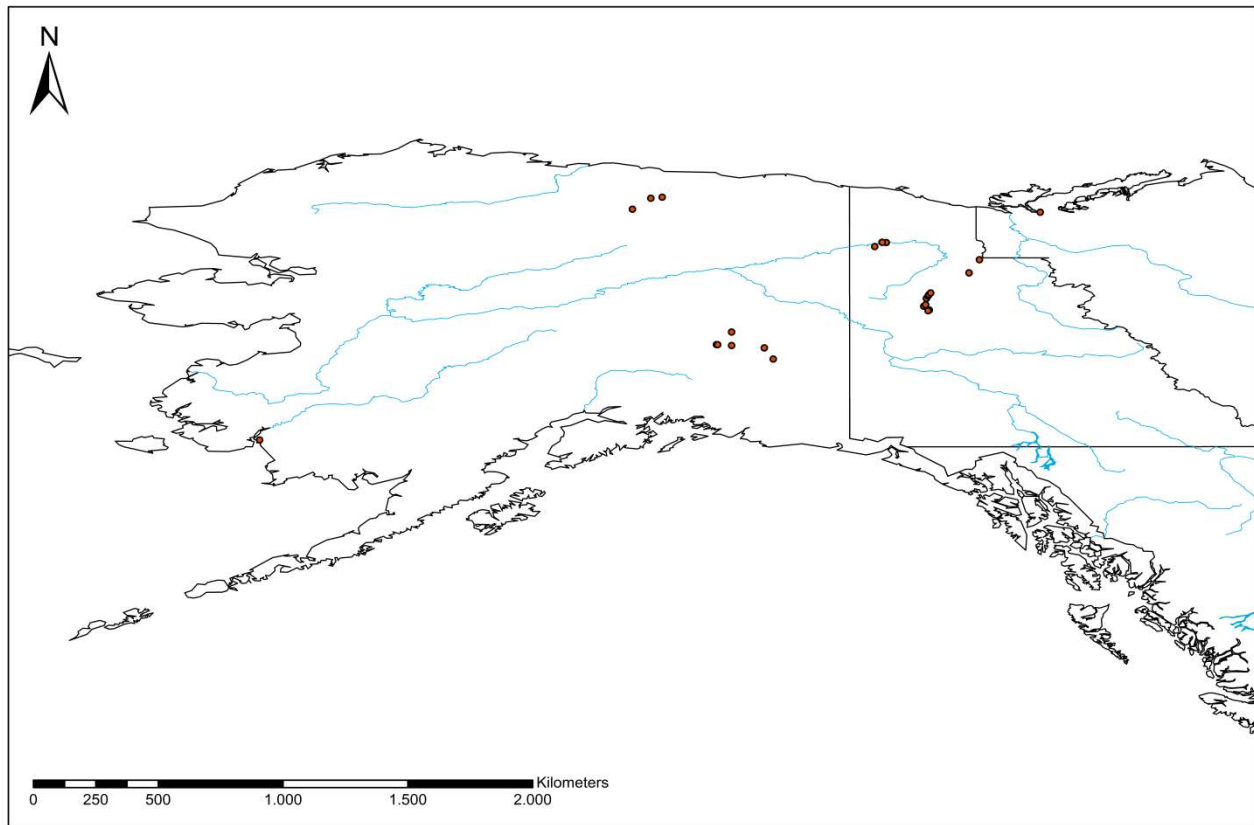


Figure 6: Detailed map of the distribution of *Somatochlora sahlbergi* in the United States and Canada.



Table 1: Distribution of records by country according to sex and kind of record (imagines, exuviae or larvae). *S. sahlbergi* has been recorded in all countries with national territories reaching the Arctic circle (66°34' N) except Danmark in Greenland. With the exception of Sweden, evidence of reproduction (the presence of exuviae or larvae), has been noted in all countries (for Norway this publication). X: Stated in literature, but no exact number given.

| country | male | female | exuvia | larva |
|----------|-----------|----------|--------|-------|
| USA | 13 | 1 | 0 | 22 |
| Canada | 76 | 6 | 19 | 4 |
| Russia | 106 | 20 | 3 | X |
| Finland | 25 | 12 | 7 | 13 |
| Norway | 3 | 1 | 9 | 0 |
| Sweden | 10 | 3 | X | 0 |
| Σ | 232 (84%) | 43 (16%) | 38 | 39 |

Most records of adults consist of observations of single or very few individuals while higher numbers of more than 10 individuals are exceptional (Fig. 7).

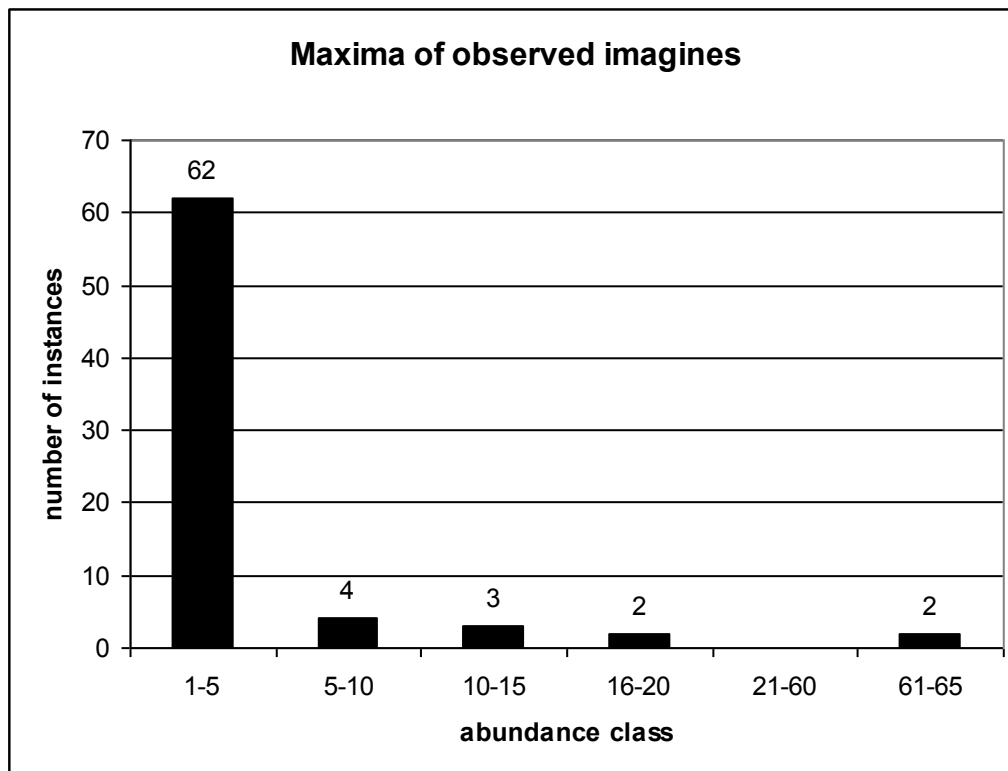


Figure 7: Maximal number of observed adults of *S. sahlbergi* of both sexes per day categorized into abundance classes. Note the gap in abundance classes. An exceptional high abundance reported by Dubatolov et al. (2004) with 15 individuals per 100 m shore line is considered here as equivalent with at least the magnitude 61-65 adults.



Precipitation and temperature

Annual precipitation at the 71 sites points to a rather dry climate, since most locations receive only 300-500 mm (Fig. 8). The wettest site where the annual precipitation reaches nearly 1000 mm is located on the Kamchatka peninsula (see outlier), while especially the area of the European populations of *S. sahlbergi* received less precipitation. European records were from palsa mires which typically develop under dry and cold conditions. The majority of *S. sahlbergi* records occurred at locations with annual mean temperatures below 0°C (Fig. 9).

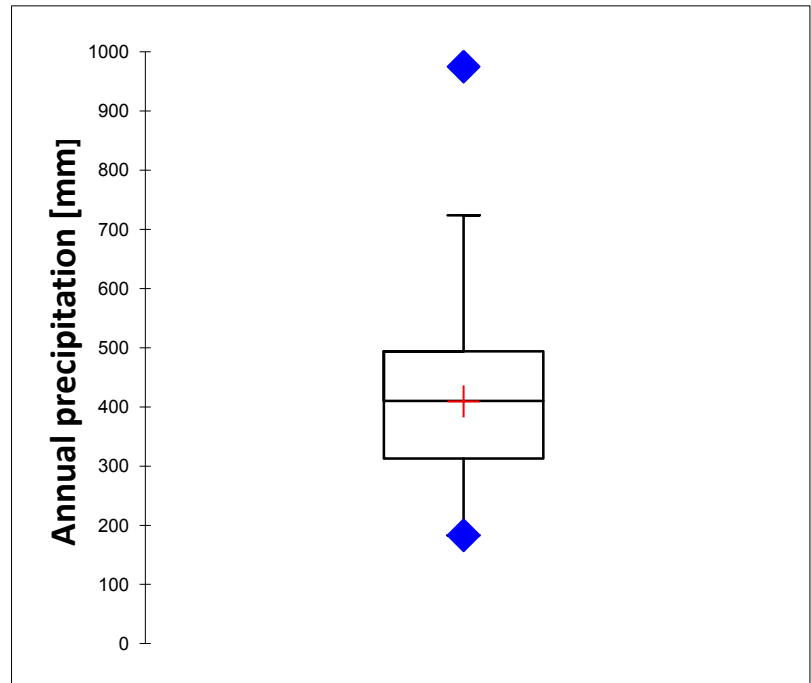


Figure 8: Annual precipitation at 71 worldwide localities of *S. sahlbergi*. The boxplot shows range, quartile and median, a cross indicates the mean. Blue dots represent outliers (see discussion).

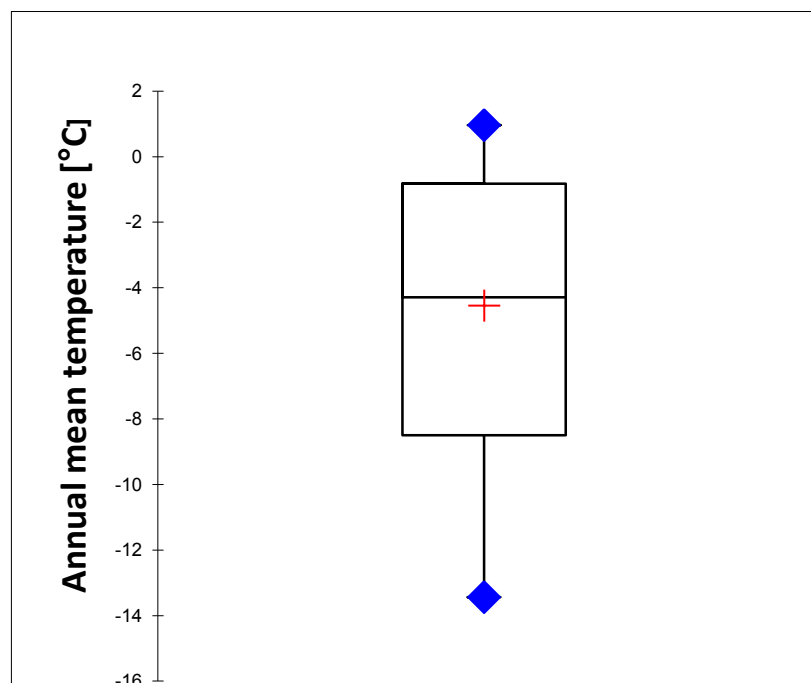


Figure 9: Boxplot of mean temperature at 71 worldwide localities of *S. sahlbergi*. The boxplot shows range, quartile and median, a cross indicates the mean.



Phenology

Data analysis of observed adults shows that flight season lasts from mid- June to mid-August with an exceptional observations made on 17th June in Alaska and on 3rd September in Russia (Fig. 10)

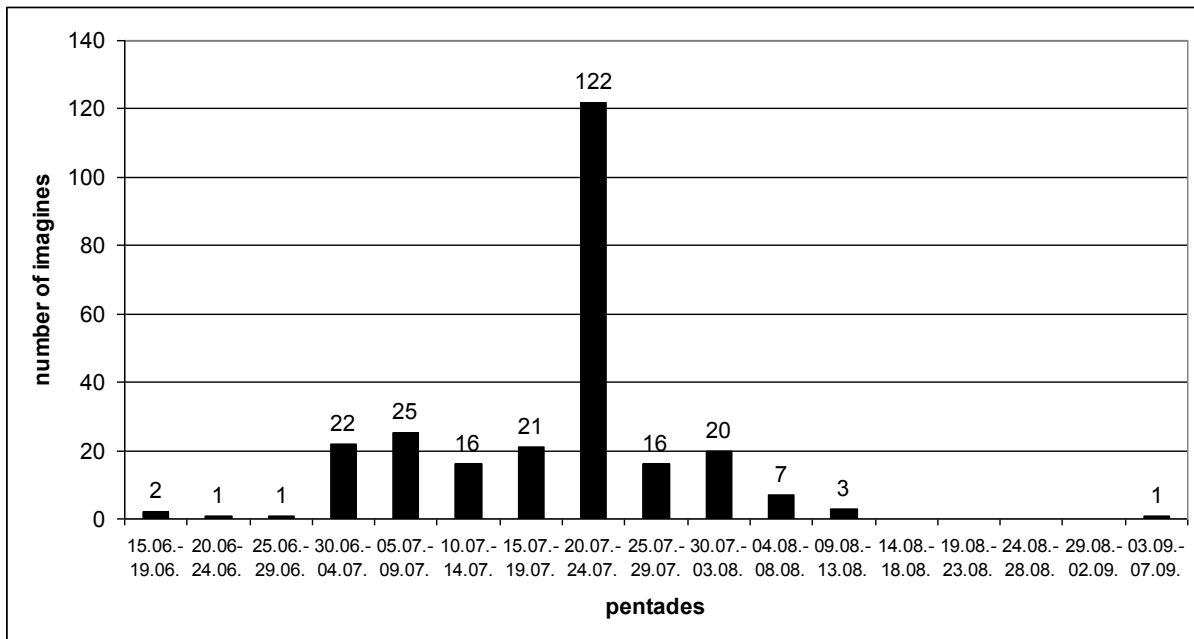


Figure 10: Number of recorded imagines of both sexes of *Somatochlora sahlbergi* worldwide per pentade from mid-June to beginning of September ($\Sigma_{\text{tot}} = 275$).

Results - II *Somatochlora sahlbergi* in Europe

Description of two European larval habitats

The following presentation of two European reproduction habitats consider the “how and where” at greater length, giving specific clues where to look for exuviae. The two given examples of habitats differ considerably as regards to latitude, macroclimate and vegetation composition and probably well illustrate and cover the variation range of habitat preference of *S. sahlbergi* in Fennoscandia, where the species has so far been found only beyond the polar circle and north of 67° N. Both habitats described below are classified as palsa mires being situated within the belt of discontinuous permafrost soil. Botanical nomenclature on species level corresponds to Hämet-Ahti et al. (1998), synsystematic classification of vegetation according to Dierssen (1996).



Habitat 1

Varanger Fjord, W Bugøynes/Norway 69° 59' 21.90"N 29° 29' 6.97"E



Figure 11: Habitat 1 (Norway) view from NW. The particular area where exuviae (n=9) could be collected is marked with a white ellipse. Notice the small overgrown peat hummocks at the water's edge in the background.

Morphology

Habitat 1 was a palsa mire lake with a diameter of approximately 50 m close to sea level at the lower part of a complex of mire lakes interconnected by streams. The mire lakes were arranged like terraces at the northern slope of the 200 m a. s. l. fjell at the southern sea shore of Varanger Fjord. The mire was situated in a small depression open to the sea to the north and thus was sheltered from prevailing western winds. The lake had a maximum depth of approximately 1 m and bottom sediments consisting of stones and boulders covered with a layer of decomposed organic matter. Due to the stream flowing through, pebbles and boulders at the central water current channel remained bare and beside this area the lake was almost completely overgrown with helophytes. The western, southern and eastern edges of the lake were surrounded by arctic *Salix* shrubs formation typical for the region, occurring in patches in sheltered parts of the tundra. The lake was fed by several springs and a



stream flowing in from the southern bank, where several degraded and vegetated palsas remained. The northern edge touched the embankment of a small coastal road under which the water of the outflow passed through towards the Arctic Sea.

Exuviae found

Nine exuviae were found on 7-vii-2006 floating on the water several meters away from the banks within a small defined area of approximately three times three meters in the broad *Eriophorum* lawn with a water depth of 50 cm (Fig. 11). Five exuviae are deposited in coll. J. Arlt/Delmenhorst, GER; one in coll. H. Wildermuth/Rüti, CH; one in coll. S. Karjalainen/Kirkkonummi, FIN; one in coll. F.-J. Schiel/Sasbach, GER; one in coll. author.

Habitat 2

Inari Lapland, S Utsjoki/Finland, 69°48'12.59"N 26°59'50.62"E

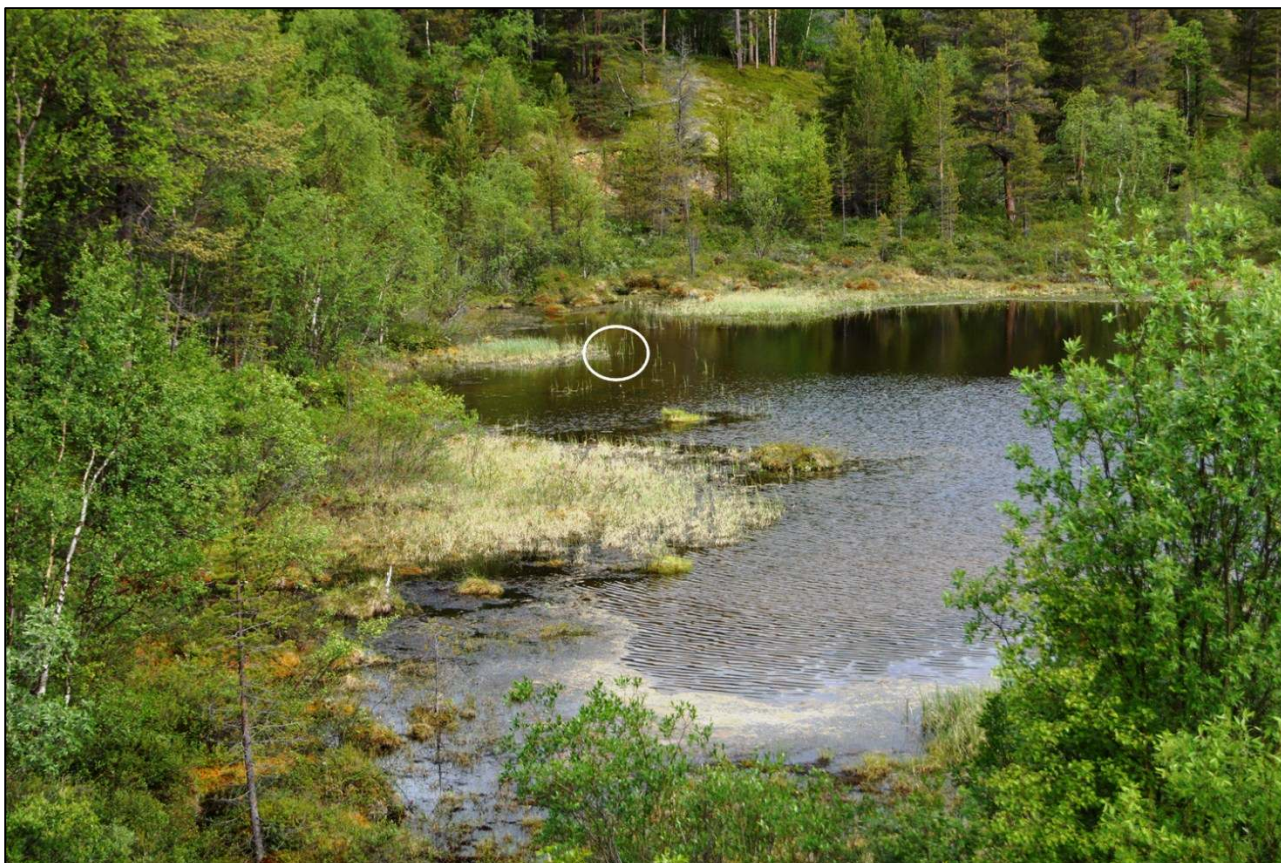


Figure 12: Habitat 2 (Finland) view from SE. The particular place where exuviae could be collected is marked with a white ellipsis. Notice also small overgrown peat hummocks at the shore in the background.



Morphology

This small palsa mire lake had a diameter of approximately 40 m and was surrounded by a closed canopy boreal *Pinus sylvestris* forest (Cladonio-Pinetum), situated in the sheltered valley of Utsjoki River. The lake was edged by helophytes, had a maximum depth of 1 m and was fed by several springs flowing in at the NW bank, where also a few small and partly degraded frozen peat hummocks (palsas) remained. Most of the lake bottom was covered with a layer of decomposing *Carex*-sludge. Pebbles and boulders in the centre of the lake were exposed due to a slow water current flowing through. Annotation: This locality belonged to a series of pools arranged like pearls on a chain along the Utsjoki River between Utsjoki town and Kevo Strict Nature Reserve. Localities stated in Butler (1992) were situated just a few kilometres away, indicating a continuous distribution of *S. sahlbergi* along this river section.

Exuviae found

On 13-vii-2010 two fresh exuviae were collected within a patch of *Carex rostrata* (fig. 12) Both exuviae were floating on knee-deep water with coarse *Carex* detritus. One exuvia is deposited in the collection of J. Arlt, Delmenhorst; GER, one in the collection of the author.

Syntopic occurrence with Zygoptera

On 12-vii-2010 a pair of *Coenagrion johanssoni* in tandem position (Fig. 13) encountered at habitat 2 indicated reproduction and represented the first record of syntopic occurrence of Zygoptera and *S. sahlbergi* for Europe.

Table 2: Syntopically reproducing dragonfly species in the two presented larval habitats of *Somatochlora sahlbergi*.

| Species | Habitat 1 | Habitat 2 |
|-------------------------------|-----------|-----------|
| <i>Coenagrion johanssoni</i> | | X |
| <i>Aeshna caerulea</i> | X | X |
| <i>Aeshna juncea</i> | X | X |
| <i>Somatochlora alpestris</i> | X | X |
| <i>Leucorrhinia rubicunda</i> | | X |
| <i>Leucorrhinia dubia</i> | | X |



Table 3: Vegetational characteristics of the two presented larval habitats of *Somatochlora sahlbergi*.

| | Habitat 1 | Habitat 2 |
|---------------------------------------|---|---|
| Plant communities | Scheuchzerio-Caricetea nigrae >Caricion lasiocarpae> indiff. type of <i>Eriophorum angustifolium</i> community | Scheuchzerio-Caricetea nigrae > Caricion lasiocarpae > Caricetum rostratae |
| Helophytes | <i>Eriophorum angustifolium</i> with nearly complete coverage, lesser <i>E. vaginatum</i> and very few stands of <i>Carex</i> spp. | <i>Carex rostrata</i> prevailing, less <i>Carex lasiocarpa</i> ; scattered low stands of <i>Carex limosa</i> did not exceed 1 m ² |
| Hydrophytes | Floating shoots of <i>Utricularia intermedia</i> within extensive <i>Eriophorum</i> lawn | Few shoots of <i>Utricularia intermedia</i> floating within patches of <i>Carex rostrata</i> |
| Characteristic plants of surroundings | <i>Salix lanata</i> , <i>S. glauca</i> , <i>S. lapponum</i> , <i>S. phylicifolia</i> , <i>Betula pubescens</i> ssp. <i>czerepanovii</i> , <i>Rubus chamaemorus</i> , <i>Pinguicula vulgaris</i> , <i>Empetrum hermaphroditum</i> , <i>Bartsia alpina</i> , <i>Geranium sylvaticum</i> , <i>Trollius europaeus</i> , <i>Pedicularis lapponica</i> , <i>Hippuris vulgatum</i> , <i>Antennaria dioeca</i> , <i>Salix herbacea</i> , <i>Carex magellanica</i> , <i>Carex nigra</i> ssp. <i>juncella</i> , <i>Carex vaginata</i> , <i>Carex bigelowii</i> , <i>Eriophorum scheuchzeri</i> , <i>Eriophorum russeolum</i> ssp. <i>russeolum</i> , <i>Polemonium acutiflorum</i> etc. | <i>Pinus sylvestris</i> , <i>Betula pubescens czerepanovii</i> , <i>Betula nana</i> , <i>Salix phylicifolia</i> , <i>S. hastata</i> , <i>S. myrsinites</i> , <i>Rhododendron tomentosum</i> , <i>Listera cordata</i> , <i>Drosera longifolia</i> , <i>Pinguicula vulgaris</i> , <i>Andromeda polifolia</i> , <i>Empetrum hermaphroditum</i> , <i>Vaccinium myrtillus</i> , <i>Vaccinium microcarpus</i> , <i>Vaccinium uliginosum</i> , <i>Pedicularis sceptrum-carolinum</i> , <i>Calamagrostis lapponica</i> , <i>Epilobium hornemannii</i> , <i>Carex rotundata</i> : Typical cryptogam communities at the inflow and lichens of northern <i>Pinus</i> -forests, like <i>Cladonia coccifera</i> and <i>Dicranum fuscescens</i> |





Figure 13: Mating pair in tandem linkage of *Coenagrion johanssoni* at habitat 2 (Finland).

Exuvia

Based on Valle`s description of the larva (1931) from the Kola peninsula Cannings & Cannings (1985) presented a comprehensive overview, including drawings and a key for the larvae of *S. sahlbergi* in comparison to *alpestris* and its closest Nearctic congeners (“*alpestris* group”). However, as photos of the exuvia of *S. sahlbergi* have never been published before, four photos of two different exuviae from two different European localities are presented here (Fig. 14, 15, 16 and 1).



Figure 14: Exuvia of *Somatochlora sahlbergi* in lateral view (Norway). Notice tufts of bristles, which might suggest dorsal spines or at least reinforce the impression of actual small rudimentary hooks as mentioned above.





Figure 15: Exuvia of *Somatochlora sahlbergi* in dorsal view (Norway). Notice the distinct lateral spines on segment 8 and 9, striped legs and the pale ground colour.

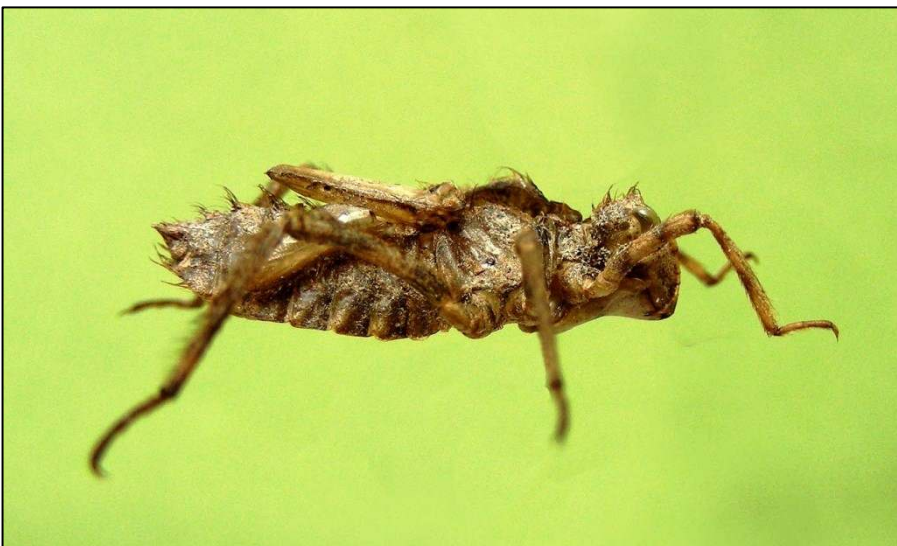


Figure 16: Exuvia of *Somatochlora sahlbergi* in lateral view (Norway), different individual than fig. 14.



Discussion

Abundance

The evaluation of data of *S. sahlbergi* in view of abundance impressively confirms the general scarceness and inobstrusiveness over its entire range of distribution, emphasized by the scarcity of records with more than five individuals. However, in a few cases *S. sahlbergi* has been encountered in surprisingly high abundances, for instance up to 60 males per day at one locality in Kamtchatka (Dumont et al. 2005) or 15 individuals per 100m shore line in the Sokhondo mountains of the southernmost population at all (Dubatolov et al. 2004: 85). Such exceptional high abundances appear like erratic blocks within the overall picture of the species we have, and are thus considerably hard to rate. In any case, these records once more put the finger on the weak spots of our yet only anecdotal and insufficient knowledge of autecology and population dynamics of the species. Interestingly, such outliers, which are challenging the overall picture of a rare and elusive species seems to be noticeably restricted to Siberia yet.

Syntopic occurrence with Zygoptera

In contrast to Siberia and the Nearctic region, where *S. sahlbergi* is known to co-occur frequently with regional damselfly species (cf Cannings & Cannings 1985, Dumont et al. 2005, Kosterin & Lyubechanskii 2009, Kosterin & Zaika 2010), in Europe no records on the co-occurrence of Zygoptera species and *S. sahlbergi* have been published so far and the absence of Zygoptera at sites of *S. sahlbergi* is stated repeatedly (e.g. Valle 1931, Butler 1992, Wildermuth 2008: 431). This seems even more surprising, as in view of latitude at least three damselfly species - *Coenagrion johanssoni*, *C. hastulatum* and *Enallagma cyathigerum* - widely overlap with *S. sahlbergi* in Northern Europe (Karjalainen 2010a, own obs.). Habitat preferences concerning microclimate and vegetation composition in Zygoptera and *S. sahlbergi*, however, seem to differ to some extent. As Zygoptera at these latitudes need at least a minimal offer of shielding tree growth, at habitats of *S. sahlbergi* in Europe and Western Siberia, under harshest climate conditions in treeless open tundra (like the above presented Norwegian habitat), Zygoptera are generally absent.

However, both the exact southern boundary line of the distribution of *S. sahlbergi* along the tundra-taiga ecotone and the extent of how far the species actually enters the northern zone of taiga are largely unknown. Therefore, it appears most likely that also in Europe targeted research at such habitats within the belt of the taiga-tundra transition zone would reveal more cases of syntopical occurrence of *S. sahlbergi* and regional Zygoptera species. Another observation (albeit not indicating reproduction) of a Zygoptera species at a reproduction habitat of *S. sahlbergi* referred to a single female of *Coenagrion lunulatum* on 23-vii-1998 (S. Karjalainen pers. comm.). This locality was situated only a few kilometres away from habitat 2.



First Norwegian record of reproduction

As the first records of *S. sahlbergi* in Norway referred to adults observed only with binoculars (Pedersen 1994), the collected exuviae presented above represent the first evidence of reproduction of *S. sahlbergi* in Norway.

Dorsal spines of exuvia

As far as proper identification of exuvia and confusion with related species is concerned, compared to the Nearctic region the situation in Eurasia appears to be rather comfortable. The exuvia of *S. sahlbergi* is easily recognized by the lateral spines on S8 and S9 and on the absence of dorsal spines, the latter trait distinguishing the “*alpestris* group” from the “*metallica* group”, whose members show prominent dorsal spines. The absence of dorsal spines in *S. sahlbergi* has been pointed out by Valle (1931), Haritonov (1975), Cannings & Cannings (1985), Norling & Sahlén (1997) and Wildermuth (2008). This trait, however, seems to vary to some extent and at least rudimentary, but clearly visible round dorsal hooks might appear more or less regularly, especially on the proximate segments. Three exuviae probably pertaining to *S. sahlbergi* reported from Kamtchatka (Dumont et al. 2005) even showed clear spines on S9 and further data and research is needed to shed light on the distribution and variation of this feature. In this regard it might be noteworthy however, that also in Europe depending on condition and age of the respective exuvia, tufts of bristles might suggest dorsal spines or at least reinforce the impression of actual small rudimentary hooks as mentioned above (Fig. 15 and 16).

Colour of exuvia

Compared to exuviae of *S. alpestris* in Europe, according to my current knowledge a clear tendency of a paler overall appearance could be stated which previously has not been established in literature. This difference in colour was distinctive even in the field when detecting exuviae of both *sahlbergi* and *alpestris* next to each other. With a bit of experience exuviae of *sahlbergi* are quite easily recognized with some certainty even from a distance by its distinctively light overall appearance alone. In this context it might be interesting that also Cannings & Cannings (1985) stated the distinctly lighter colour of pinned European larvae caught by Valle (Valle 1931) in comparison to material from the Nearctic region, whereas according to the authors this difference in colour was based on preservation methods. Even though Cannings & Cannings (1985) did not compare exuviae from Eurasia with Nearctic ones (but larvae), it appears likely, however, that the therein stated lighter colour of the European larvae was not based on a preservation artefact but rather corresponded to an actual tendency of European larvae to exhibit a lighter ground colour. Yet here, too, applies: only further research of more material from both parts of the world could confirm such tentative presumptions.



Preferred places of emergence

At both reproduction sites of *S. sahlbergi* described in this study exuviae of *S. alpestris* were more or less evenly distributed whenever suitable helophytes were available, including very shallow sections with water depth below 20 cm. Thus, no pattern of preferred emergence sites was recognizable. This was especially obvious at locality 2 (Norway). All eleven exuviae of *S. sahlbergi* from both habitats, however, were found exclusively within *Carex* and *Eriophorum* stands which grew in water depths of at least 40 cm. Although the number of exuviae was low ($n=11$), compared to *S. alpestris*, a tendency concerning the preferred emergence sites was looming and preliminary the conclusion might be drawn that *sahlbergi* larvae preferred deeper sections of the jointly inhabited waterbodies. Thus, the preferred places of emergence seemed to correspond widely with the preferred larval habitat (see following section).

Habitat preferences of the larvae and ecological differentiation

Both reproduction habitats described here were at least half a meter deep, supporting the findings of Butler (1992), who designated the minimum water depth of 50 cm “the only common denominator for *S. sahlbergi* sites”. According to my current knowledge, this applied for all European populations hitherto known. Also at the lower reaches of the Ob River in Siberia 50 cm seemed to be the critical depth for *S. sahlbergi* habitats (Kosterin 1992). In the Nearctic region *S. sahlbergi*'s obvious preference for rather deep water bodies seemed to indicate an ecological segregation to sympatric congeners (Cannings & Cannings 1985).

In Fennoscandia *S. alpestris* is distributed with blanket coverage over the region north of the polar circle (own obs.), clearly outnumbering its elusive congener at most places of syntopical occurrence. Whilst for the corresponding Central European species couple *S. alpestris* and *S. arctica* the gradual niche differentiation has been worked out in detail (Sternberg 1990, Wildermuth 1996, Wildermuth 2008), data with the complementary couple *sahlbergi/alpestris* of the North, is, as expected, extremely poor. Once more, we are far away from a data level of quantitative habitat parameters of *S. sahlbergi* allowing solid statistical analysis of its niche differentiation. Thus, relying on only anecdotal evidence in view of data, hardly more than preliminary conclusions could be drawn.

Collecting conditions

Due to often harsh weather conditions exuviae have been regularly found floating on the water (cf Butler 1992), which also goes for all eleven exuviae mentioned in this study. In all cases, however, exuviae were not floating freely, but being more or less fixed within dense *Carex* resp. *Eriophorum* stands and thus sufficiently sheltered from wind drift. Therefore, the finding place and the place of assumed emergence in my opinion might well be considered identical.



Distribution - palsa mire hypothesis

In view of the distribution of the species in large parts of Siberia, the extraordinary pattern of occurrence of *S. sahlbergi* in Fennoscandia and the Nearctic region remains puzzling. Subject to chronically insufficient data, the southern limit is particularly hard to understand. Whilst populations in mountains of southern and southeastern Siberia are reaching latitudes of the cities London and Berlin, in Fennoscandia, however, the species has been found only at the northernmost tip of the Scandinavian Mountains beyond the polar circle so far and thus north of 67° N (Wildermuth 2008, this study). This is astonishing, since the Scandinavian Mountain range extends without interruption 1700 km towards southwest, offering continuously permafrost habitats till at least 60° of latitude, superficially comparable to those actually inhabited in the north. However, even more surprising appears to be the situation in the Nearctic part of the species' distribution. Due to large-scale Atlantic circulation (Gulf Stream), Europe generally has a milder climate than parts of North America and Asia which are located at the same latitude. Therefore, the belt of boreal forest is shifted considerably northwards (roughly further north of 60° N), while the taiga biome in Northern America reaches southwards till about the 50° N. Curiously, records at 63° N from western Alaska represent the southernmost findings in Northern America at all (R. Cannings pers. comm.). The occurrence of *S. sahlbergi* is regularly connected with permafrost soil (Kosterin 1992, Sahlén 1994, Cannings & Cannings 1997). However, in vast parts of the world with permafrost soil, *S. sahlbergi* is notably absent. This applies not only for most of the high mountain areas like the Rocky Mountains, the entire Himalaya system, the Alps etc., but most surprisingly also for the entire central and eastern subarctic region of Northern America (Walker & Corbet 1975, Cannings 2006, Catling 2003; see Fig. 2 and 6). On a more localized scale, it is striking that in Fennoscandia *S. sahlbergi* notably seems to be confined to palsa mires. This type of mire is restricted to the most dry and cold regions, which are situated in the far north at the lee side of the Scandinavian Mountain ridge. Palsa mires are mire complexes of the subarctic and northern boreal regions characterized by elevated and permanently frozen peat hummocks (palsas), roughly 0.5 to 7 m high and up to 50 m in diameter, with interspersed wet hollows. The term palsa is a Finnish borrowing from Northern Sami language denoting a large peat hummock rising above the surface of a mire (Lundqvist 1969, Seppälä 1972, Nelson et al. 1992, Gurney 2001). In Eurasia palsa mires are distributed along a belt of discontinuous permafrost zone from Iceland across northern Fennoscandia and arctic Russia. The optimal environmental conditions for the formation of palsa mires are described as mean annual temperature between -3°C and -5°C, with a precipitation below 450 mm. Additionally, less than the half of this precipitation should be snow (Luoto et al. 2004, Seppälä 2006). Such areas correspond roughly with the northernmost tip of Finland, the adjacent western part of the Norwegian province Finnmark and a rather small area of the Swedish province Norrbotten at the border to Finland (cf Nordseth 1987). Thus, in Finland palsa mires are restricted to



regions north of 68° E 30' N latitude in the west and in eastern Lapland to the region north of Lake Inari, whereas the southern boundary of the palsa zone coincides with the -1°C mean annual air temperature isocline (Seppälä 1988, Ruuhijärvi & Hosiaisuus 1988, Laitinen et al. 2007, Seppälä 2006). Palsa mires in Sweden are typically found in regions with 200-210 days temperature below 0°C (Lundqvist 1962), while temperatures in Norwegian palsa mires are below -8°C for 120 days per annum (Åhman 1977). Minimum temperatures in palsa regions of northern Finland are often below -40°C, whilst the summer temperatures might reach +30°C (Seppälä 2006).

In Fennoscandia typically the strongest populations of *S. sahlbergi* were found in mires showing palsa formations in exemplary expression, like the mire area around Dávjavávrri, Torne Lapland, Sweden (own obs., see Sahlén 1994), lakes S Nuorgam in Inari Lapland (own obs.) for instance, the latter being home of the largest European population hitherto known (cf Karjalainen 2010b, Hämäläinen & Karjalainen 2010). Noteworthy, *S. sahlbergi* does obviously not enter the adjacent northern aapa mire zone (as defined in Laitinen et al. 2007). Thus, the pattern of palsa mires could possibly explain at least the distribution of *S. sahlbergi* in Europe. However, it can only be speculated if the presented climate correlations are in fact causal ultimate factors and if the correlation with palsa habitats could be predicted on a global scale. Hopefully, an intended study using ecological niche modelling methods will shed light on the global potential distribution and putative pleistocene refugia.

These results presented here allow to draw the preliminary conclusion, that in the context of strategic search for potential habitats of *S. sahlbergi*, palsa mires might function as a useful indicator and research might be most fruitful in dry and cold areas with climatic conditions under which palsa mires might develop. The results, however, might also cast fresh light on the still largely unknown nature of the notorious (probably) isolated populations of southern Siberia. After the first surprising records in the Tunkin Valley at 52° N close to the Mongolian border (Belyshev & Obodov 1961) these authors assumed that *S. sahlbergi* is distributed from the northern tundra throughout the entire taiga belt to the mountains of Southern Siberia. Subsequently this assumption was changed by Belyshev (1971), who considered his records from the southern Siberian mountains as glacial relicts and established even the new subspecies *relicta* Belyshev. However, later Belyshev himself never referred to this taxon in his further publications, such as the monograph on Siberian dragonflies (Belyshev 1973), and the former assumption of a broad Siberian distribution range of *S. sahlbergi* was again resumed (see Kosterin 1992: 23).

Thus, recent findings in the Siberian lowland, for instance in Sakha (Yakutia) in the valley of the major Aldan river at 59°0'0.41"N, 126°12'49.27"E at 280 m a.s.l. (Kosterin 2004), could be interpreted differently. On the one hand it might well support the



continuous distribution hypothesis. On the other hand, it is interesting to note, that of all things this particular location in Sakha (Yakutia) had an extreme continental climate with very little annual precipitation between 90-300 mm and a very short but comparatively hot summer (Kosterin 2004) and thus perfectly matched the proposed palsa mire hypothesis. Probably such dry climate conditions are confined to restricted areas and can hardly be generalized. On the contrary, rather than overall coverage of *S. sahlbergi* over the entire Siberian lowland, it is more likely, that this vast area is interspersed with climatic “islands” offering suitable mesoclimate dry enough for *S. sahlbergi*. Yet, here too, the inevitable *ceterum censeo* while dealing with *S. sahlbergi* applies: only further research and analysis of much more climate data could confirm such tentative presumptions. According to Oleg Kosterin (pers. comm.) however, probably the entire Sakha (Yakutia) has a similar climate and palsa mires are frequent within the larch taiga zone of Northeastern Asia. Thus, with the notable exception of Kamchatka, it may be assumed that the connection of *S. sahlbergi* with the palsa mire type of habitat applies for its entire distribution area on the Asian continent, stretching from Fennoscandia till Eastern Siberia.

The situation on Kamchatka, however, which is home to one of the strongest populations of *S. sahlbergi* hitherto known, on the Vachkazhets massif, seems to differ remarkably. This particular population received an annual precipitation of almost 1000 mm (see outlier dot Fig. 8), including huge amounts of snow. It is situated in the taiga but in the coastal zone of *Betula lanata* open stand with the specific Ochotian tall herbage (Oleg Kosterin pers. comm., Dumont et al. 2005). Thus, climatic and ecological conditions and habitat structure are not easily brought in accordance to assumed and evidenced habitat requirements of *S. sahlbergi* in the rest of the world. Yet, for a proper interpretation of the status and nature of this Kamchatkian population, further research and analysis of much more climatic and ecological data would be necessary and desirable. Thus, for the time being, I refrain from trying blend them in the ecological overall picture hypothesized in this paper.

Meta-discussion on research and future prospects

Due to its extraordinary distribution and elusiveness *S. sahlbergi* seems to be especially prone to fall through the cracks of scientific research and in many aspects this species could be considered a victim of inherent structures of the system of science. Compared to dozens of scientific research projects dealing with the ecology of several *Somatochlora* species, not a single university study has ever been worked out on *S. sahlbergi* and it is to be feared that it never will: the risk for any scholar, to be left empty-handed after returning from one or several exhausting field periods without finding even a trace of the study object is too high for both, the student and the university tutor. The result is scientific stagnancy. However, even though the state of



knowledge of all aspects of *S. sahlbergi* and the nature of the data set, which mainly consists of individual data obtained just by chance, could hardly substantiate any scientifically correct and justifiable hypothesis on its ecology and the whole issue remains on a speculative level - even a bad hypothesis has a higher heuristic value than no hypothesis! In the case of *S. sahlbergi*, however, after almost 120 years of near-stasis, familiar paths should be left and new ways should to be tried – or, to quote *Thomas Mann*: placet experiri! Thus, if this review would encourage to communicate and publish more courageously and freely also beyond the ossified structures of scientific correctness or boost every form of activities dealing with *S. sahlbergi*, the purpose of this work will be served.

Acknowledgement

This review could never have been realized without the support of many people. First and foremost I am grateful to Darius Stiels and Kathrin Schidelko (both ZFMK Bonn, Germany), who prepared the distribution maps, the visual silverware of the review and substantially influenced shape and content of the manuscript. Rob Cannings (Victoria, Canada) and John Hudson (Juneau, Alaska) spared no efforts to provide up-to-date data from the Nearctic region. This transatlantic cooperation was a most pleasant experience. Oleg Kosterin (Novosibirsk, Russia) gave valuable comments on the manuscript and kindly provided difficult to obtain literature. His fundamental publications on the Odonata of temperate Asia have been a major source of inspiration for my activities on *S. sahlbergi* throughout the years. Sami Karjalainen (Kirkkonummi, Finland) and Dietmar Ikemeyer (Zwillbrock, Germany) provided unpublished data on *S. sahlbergi*. Matti Hämäläinen (Helsinki, Finland), Hansruedi Wildermuth (Rüti, Switzerland), Arne Erpenbach and Anke Stein (both Göttingen, Germany) and Sami Karjalainen gave valuable comments on the manuscript. Jean-Pierre Boudot (Nancy, France) helped to complete my data base of European records. Steven Butler (All Stretton, United Kingdom) provided information on his pioneering work on *S. sahlbergi* in the late nineties. Hansruedi Wildermuth and Sami Karjalainen gave photo technical support (exuvia). John Hudson corrected the language and Martin Schorr provided literature. I am indebted to them all. Last but not least I thank Jörg Arlt (Delmenhorst, Germany) for being an invaluable travelling companion in the mosquito-infested northern wilderness and for making available his photos of our trips.



References

- Belyshev, B.F. & Ovodov, H. 1961. [Somatochlora sahlbergi Trybom (Odonata, Insecta) in South Siberia]. *Zoologicheskii Zhurnal* 12(40): 1892-1893.
- Belyshev, B.F. 1968. Contribution to the knowledge of the fauna of dragonflies (Odonata) of Siberia. IV: Geography of the dragonflies of Siberia. *Fragmenta Faunistica* 14(13): 407-536.
- Belyshev, B.F. 1971. [A new geographic form of the dragonfly *Somatochlora sahlbergi* (Odonata) from southern Siberia. New and little known species of the Siberian fauna 4: 5-6.
- Belyshev, B.F. 1973. The dragonflies of Siberia (Odonata) Vol. I. Part 2. Nauka, Novosibirsk.
- Belyshev, B.F., E.P. Bessolicyna, N.S Kostilia, P.E. Polyakova. 1978. [Additions to the odonate fauna (Insecta, Odonata) of northeastern Asia]. *Fauna Sibiri* 34: 39-46. [also cited as *Fauna Sibiri* Vol. 6]
- Butler, S.G. 1992. Notes on the collection and rearing out of the larva of *Somatochlora sahlbergi* Trybom from Finland (Odonata: Corduliidae). *Opuscula zoologica fluminensia* 84: 1-5.
- Cannings, S.G., R.A. Cannings. 1985. The larva of *Somatochlora sahlbergi* Trybom, with notes on the species in the Yukon territory, Canada (Anisoptera: Corduliidae). *Odonatologica* 14(4): 319-330.
- Cannings, S.G., R.A. Cannings, R.J. Cannings. 1991. The distribution of the dragonflies (Insecta: Odonata) of the Yukon Territory, Canada, with notes on ecology and behaviour. *Royal British Columbia Museum Contributions to Natural Science* 13: 1-26.
- Cannings, S.G. & Cannings, R.A. 1997. Dragonflies (Odonata) of the Yukon. In: Danks, H.V. & Downes, J.A. (Eds.): *Insects of the Yukon. Biological Survey of Canada Monographs* 2. 1034 pp: 169-200.
- Cannings, S. 2006. Checklist of the Odonata of the Yukon with conservation ranks and notes on distribution. In URL: http://www.royalbcmuseum.bc.ca/Natural_History/Insects-and-Relatives.aspx?id=2838 Last access 1.11.2010.
- Catling, P.M. 2003. Dragonflies (Odonata) of the Northwest Territories, Status ranking and preliminary atlas. University of Ottawa. 49 pp.
- Corbet, P.S. 1999. *Dragonflies: Behaviour and ecology of Odonata*. Harley Books, Colchester. 829 pp.



- Dubatolov, V.V., Kosterin O.E., Maksimenko, E. A 2004. Biodiversity of the Sokhondo nature Reserve. Odonata: 81-87 In: Biodiversity of the Sokhondo nature Reserve Novosibirsk-Chita, 2004, 416 pp.
- Dumont, H.J., Haritonov, A.Yu., Kosterin, O.E., Malikova, E.I., Popova, O. 2005. A review of the Odonata of Kamchatka Peninsula, Russia. *Odonatologica* 34(2): 131-153.
- Fronzek, S., M. Johansson, T.R. Christensen, T. R. Carter, T. Friberg & M. Luoto (eds.). 2009. Climate change impacts on sub-arctic palas mires and greenhouse gas feedbacks Proceedings of the PALSALARM symposium Abisko, Sweden 28–30 October 2008; 20 Reports of Finnish Environment Institute 3.
- Gurney, S.D. 2001. Aspects of the genesis, geomorphology and terminology of palas: perennial cryogenic mounds. – *Progress in Physical Geography* 25: 249-260.
- Haritonov, A.Yu. & E.I. Malikova 1998. Odonata of the Russian Far East: a summary. *Odonatologica* 27(3): 375-381.
- Haritonov, A.Yu. 1975. Ecological conditions of larval phases of dragonflies in the Arctic region. *Ekologiya* 6(3): 96-99.
- Hämet-Ahti, L., J. Suominen, T. Ulvinen & P. Uotila (eds.). 1998. *Retkeilykasvio (Field Flora of Finland)* Ed. 4. 656 pp. Finnish Museum of Natural History, Botanical Museum. Helsinki.
- Hämäläinen, M. 1967. *Somatochlora sahlbergi* Trybom (Odon., Corduliidae) Utsjoelta (InL). *Luonnon Tutkija* 71: 25.
- Hämäläinen, M. 1984. Odonata of Inari Lapland. *Kevo Notes* 7: 31-38
- Hämäläinen & Karjalainen. 2011. In: URL: <http://www.hatikka.fi>; Last access 1. 6.2011.
- Hijmans, R.J., J.M. Cruz, E. Rojas & L. Guarino. 2001. DIVA-GIS, version 1.4. A geographic information system for the management and analysis of genetic resources data. Manual. International Potato Center and International Plant Genetic Resources Institute, Lima, Peru.
- Hijmans R.J., S.E Cameron, J.L. Parra, P.G. Jones, A. Jarvis. 2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- Karjalainen, S. 2010a. Suomen sudenkorennot. Tammi, Helsinki. 239 pp.
- Karjalainen, S. 2010b. New records of *Somatochlora sahlbergi* from Finland. 1st European congress on Odonatology 2-5 July 2010 Portugal; program and abstracts.



- Kosterin, O. E. 1992. New distribution records of *Somatochlora sahlbergi* Trybom (Odonata, Corduliidae). *Acta hydroentomologica lativica* 2: 22-26.
- Kosterin, O.E & V.V. Zaika. 1995. [Materials on dragonflies (Odonata, Insecta) for the Red Book of the Altai Republic] Materialy po strekozam (Odonata, Insecta) k Krasnoy knige respubliki Altay. In: *Materialy k Krasnoy knige respubliki Altay (Zhivotnye)*. Gomo-Altaysk Gos. Univ., Gomo-Altaysk: 71-83.
- Kosterin, O.E. 2003. In: URL: <http://pisum.bionet.nsc.ru/kosterin/odonata/corduliidae/sahlbergi.htm>; Last access 1.11.2010.
- Kosterin, O.E. 2004. Some Odonata collected in Aldan Ulus of Sakha (Yakutia) Republic in late June 2002. *Notulae Odonatologicae* 6(3): 27-31.
- Kosterin, O.E. & I.I. Lyubechanskii. 2009. Odonata collection from the Bureinskii State Nature Reserve, Khabarovskii Krai, Russia. *Notulae odonatologicae* 7(3): 25-27.
- Kosterin, O.E & V.V. Zaika. 2010. Odonata of Tuva. *International Journal of Odonatology* 13(2): 277-328.
- Laitinen, J., S. Rehell, A. Huttunen, T. Tahvanainen, R. Heikkilä & T. Lindholm. 2007. Mire systems in Finland — special view to aapa mires and their water-flow pattern. *Suo* 58(1): 1–26.
- Luoto, M., Fronzek, S. & Zuidhoff, F. S. 2004. Spatial modelling of palsa mires in relation to climate in northern Europe. – *Earth Surface Processes and Landforms* 29: 1373-1387.
- Lundqvist, J. 1962. Patterned ground and related frost phenomena in Sweden. *Sveriges Geologiska Undersökning C* 583: 1-101.
- Lundqvist, J. 1969. Earth and ice mounds: a terminological discussion. – In Péwé, T.L. (ed.) *The Periglacial Environment. Past and Present*: 203-215. McGill-Queen's University Press, Montreal.
- Mann, T. 1924. *Der Zauberberg*. Fischer-Taschenbuch, Frankfurt 1991.
- McClory, J.G. & T.A. Gotthardt. 2006. Treeline Emerald. State Conservation Status, Element Ecology & Life History Edition. In: URL: <http://aknhp.uaa.alaska.edu>. Last access 1.11.2010.
- Nelson, F.E., K.M. Hinkel & S.I. Outcalt, 1992. Palsa-scale frost mounds. In: Dixon, J.C. and Abrahams, A.D. (eds.) *Periglacial geomorphology*: 305-325, John Wiley & Sons, Chichester.



- Norling, U & G. Sahlén. 1997. Odonata, Dragonflies. In: A. Nilsson (ed): The aquatic Insects of North Europe 2: 13-66. Apollo Books, Stenstrup.
- Pedersen, H. 1992. *Somatochlora sahlbergi* Trybom, 1899 (Odonata: Corduliidae) - a new species to Norway. *Fauna norvegica Ser. B* 39: 22.
- Ruuhijärvi, R. & V. Hosiaislouma. 1988. Mires 1: 1000000. In: Atlas of Finland. Folio 141–143. Map Appendix 2. National Board of Survey & Geographical Society of Finland, Helsinki.
- Sahlén, G. 1987. A new site for *Somatochlora sahlbergi* Trybom in Inari Lapland (Odonata, Corduliidae). *Notulae entomologicae* 67: 3-4.
- Sahlén, G. 1994. The dragonfly, *Somatochlora sahlbergi* Trybom, 1889, found in northern Sweden (Odonata, Corduliidae). *Entomologisk Tidskrift* 115(4): 137-142.
- Seppälä M. 1972. The term "palsa". – *Zeitschrift für Geomorphologie N.F.* 16: 463.
- Seppälä, M. 1988. Palsas and related forms. – In: Clark, M.J. (ed.): *Advances in periglacial geomorphology*: 247-278. John Wiley. Chichester.
- Seppälä, M. 2006. Palsa mires in Finland. *The Finnish environment* 23: 155-162.
- Śniegula, S. 2006. The adventure with *Somatochlora sahlbergi* Trybom, 1889. *Odonatrix* 2(2): 36-39.
- Sternberg, K. 1990. *Autökologie von sechs Libellenarten der Moore und Hochmoore des Schwarzwaldes und Ursachen ihrer Moorbindung*. – Dissertation. Universität Freiburg. 431 pp.
- Trybom, F. 1889. Trollsländor (Odonata), insamlade under Svenska expeditionen till Jenisei 1876. *Bihang till Kungliga Svenska vetenskapsakademiens handlingar* 15, IV, 4: 1-21.
- Valle, K.J. 1915. *Somatochlora Sahlbergi* Trybom. *Lapponia imandrensis*, Jokostrow, leg. R. Envald. Neu für Europa. *Meddelanden av Societas Pro Fauna et Flora Fennica* 1914-1915: 42.
- Valle, K.J. 1931. Materialien zur Odonatenfauna Finnlands. II. *Somatochlora sahlbergi* Trybom. *Notulae Entomologicae* 9: 41-51.
- Valle, K.J. 1938. Zur Ökologie der finnischen Odonaten. *Annales Universitatis Turkuensis A* 6(14): 1-76.
- Walker, E.M. & P.S. Corbet. 1975. *The Odonata of Canada and Alaska*, Vol. 3, University Toronto Press, Toronto.



Wildermuth, H. 1996. Niche overlap, niche segregation and habitat selection in *Somatochlora arctica* (Zett.) and *Somatochlora alpestris* (Sél.) in Switzerland (Anisoptera: Corduliidae). *Notulae odonatologicae* 4: 136.

Wildermuth, H. 2008. Die Falkenlibellen. Die Neue Brehm-Bücherei 653. 496 pp.

Åhman, R. 1977. Palsar i Nordnorge. – Meddelanden från Lunds Universitets Geografiska Institutionen, Avhandlingar 78: 1-165.

