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WESTERN RANGE LIMITS AND ISOLATES OF EASTERN ODONATE SPECIES IN SIBERIA AND THEIR PUTATIVE ORIGINS

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Macromia amphigena, Shaogomphus postocularis, and *Sympetrum croceolum*, ranging in NE China, Korea and Japan, have isolates at the NE margins of the Altai-Sayan mountain system: all 3 in SE West Siberia, *M. amphigena* and *S. postocularis* also in southern Central Siberia and *M. amphigena* in E Kazakhstan and W Mongolia. *Ophiogomphus obscurus, Nihonogomphus ruptus,* and *Calopteryx japonica* have continuous ranges protruding to the West from E. Asia to the Ob' River basin and to 60° N latitude. *Coenagrion ecornutum* has a similar range but extends N in Siberia to 65° N and has an isolate in the S Ural Mts. *C. lanceolatum, C. hylas* and *Somatochlora graeseri* reach 70° N and also extend westward to the Ob' River basin, but *C. hylas* has isolates in the Polar Urals and Bavaria, while *S. graeseri* is probably isolated in the Ural Mts. Of 4 other eastern spp. in Siberia, 2 reach 70° N, but *Somatochlora exuberata* extends westwards only to the sources of the Yenisey River and *Coenagrion glaciale* to Lake Baikal, while *Cercion v-nigrum* and *Anisogomphus maacki* just penetrate into SE Transbaikalia. Thus, 11 eastern odon. spp. have their western limits in Siberia (defined in a narrow sense, not including the Far East). In addition, 4 have more westerly isolates, 3 in the Urals and 1 in Bavaria. Siberia also includes the eastern limits of 21 western spp. 24 transpalaearctic spp. spread far to the N and 10 spp. occupy S Siberia only (or just occur locally), 2 Central Asian spp. barely penetrate into S. Siberia. *Aeshna viridis* is a doubtful amphipalaearctic species. Numerous palaeopalinological reconstructions suggest that during the Holocene climatic optimum, a continuous belt of broad-leaved forest was restored in Siberia, providing conditions for a recolonization of Siberia by Odon. Westward migrations of eastern spp. were favoured by the optimum occurring earlier in the east than in the west. Hence, many western spp. had no time to occupy all of Siberia and today the eastern limits of their ranges lie within the region. *M. amphigena, S. postocularis* and *S. croceolum* perhaps were the most stenotopic of those E. Asian spp. that colonized Siberia during the Holocene, and after the optimum, their ranges shrank to the peri-Altaian refugium. Their isolates there should be dated no earlier than 5-6 thousand yrs ago. *C. v-nigrum* and *A. maacki* are perhaps the least mobile of the eastern spp. in Siberia.

INTRODUCTION

Of all the types of ranges of plants and animals, disjunctive ones are the most intriguing; they often provide the clearest insights into the history of the biota. Dragonflies are powerful fliers and trophically unspecialized, allowing them to colonize a variety of suitable habitats far from their breeding places. For this reason, their ranges are often large and continuous, at least in the northern Holarctic. In Siberia, disjunctive ranges are scarce among Odonata. BELYSHEV (1973) and BELYSHEV & HARITONOV (1981) believed that populations of 13 species in the Upper Ob' River basin are isolated from their main ranges in Europe. They considered these populations to be pre-glacial (Tertiary!) relics preserved in a peri-Altaian refugium. They suggested that these were isolated from Europe first by the last climatic cooling and later by postglacial expansion over the West Siberian Lowland of vast freshwater lakes fed by melting glaciers in the North. However, more recent collections closed ten of these disjunctions (KOSTERIN, 1996a); all the relevant data are summarized in an unpublished thesis (SUKHACHEVA, 1989).

Most other range disjunctions in Siberia concern East Asian species. (New collections probably will eliminate some of these as well but, in general, Siberia is rather well studied odonatologically thanks to the efforts of B.F. Belyshev and his disciple A.Yu. Haritonov). These disjunctions motivated the present analysis of the longitudinal range limits of odonate species within Siberia, with special attention paid to eastern ones. Siberia is defined here in the present narrow sense, rather than in the broad sense of BELYSHEV (1973): it is bounded on the north by the Arctic Ocean; in the west by the Ural Mountains; on the south by the northern borders of Kazakhstan, Mongolia, and China; and in the east by the western borders of the Amur, Khabarovskiy Kray, and Magadan provinces of Russia.

In the boreal zone few species occur in eastern Eurasia only. However, in the more southerly Pacific part of the nemoral[1] broad-leaved and mixed forest zone (which is widely interrupted in the middle of Eurasia), many species form a characteristic East Asian fauna sometimes called Palaearchaearctic. In Russia, many of these occur in three provinces: Primorskiy Kray, Khabarovskiy Kray (in its southern part) and Amur province, which combined are now termed "the Russian Far East"and are not included in Siberia. Few of the East Asian odonate species penetrate into Siberia sensu stricto, and it is possible to consider all them here.

[1] The word 'nemoral' is used here as a term, opposed to 'boreal', for broad-leafed and (in the Far East) mixed forests occupying rather mild temperate regions in Europe and the Far East. In Russian this term sounds 'shirokolistvennyy' that means just 'broad-leafed'. However, one should note that in Siberia, widespread are birch and, to a less extent, aspen forests and groves which by many characteristics and genesis are boreal (not nemoral) in essence. In Russian they are termed 'melkolistvennyy' (small-leafed), that is not so correct since the asp have quite broad leaves.

DISTRIBUTION OF EASTERN ODONATE SPECIES IN SIBERIA

Three species of the East Asian Palaearctic fauna have intriguing isolates in southern West and/or Central Siberia, at the western extremes of the Altai-Sayan mountain system, but are absent from the rest of Siberia. They are *Macromia amphigena* Selys, 1871, *Shaogomphus postocularis* (Selys, 1869), and *Sympetrum croceolum* Selys, 1883.

The Siberian populations of *M. amphigena* were long known as *M. sibirica* Djakonov, 1926 (described from the Inya River at Novosibirsk). However, ASAHINA (1964), MALIKOVA (1995) and H. Dumont (pers. comm.) demonstrated that this is a synonym of the continental subspecies *M. amphigena fraenata* Martin, 1906, characterized by a smaller size and presence of a double yellow spot on the frons. Another synonym of this subspecies is *M. bartenevi* Belyshev, 1973, described from a teneral specimen preserved in the Siberian Zoological Museum at the Institute of Systematics and Ecology of Animals, the Siberian Division of the Russian Academy of Sciences (formerly 'Biological Institute') (MALIKOVA, 1995). Siberian records of the species are shown in Figures 1-2. It lives on rivers in Kemerovo province (Zolotoy Kitat, Inya, Mras-su, Kabyrza, Tamala, Kondoma), in eastern Novosibirsk province (Inya, Berd'), in eastern Altaiskiy Kray province (Nenya) and in northern Altai Republic (Lebed', Isha), that is, on rivers descending from the Kuznetskiy Alatau Mts, Gornaya Shoria Mts, Salairskiy Kryazh Range and the North Altai and belonging to the eastern catchment basin of the Upper Ob' River (BELYSHEV, 1973; DRONZIKOVA, 1998 and pers. comm.; KOSTERIN et al., 2001; S. Asyamova pers. comm.). It was recently recorded in the Kazakhstanian part of Altai[2]: in the westernmost Kalbinskiy Range of the West Altai in the valley of Sibinskie Lakes, 80 km S of Ust' Kamenogorsk (CHAPLINA, 2003) and at the Bukhtarminskoe Water Reserve (REINHARDT & SAMIETZ, 2003). Long ago DYAKONOV (1926), reported the species from the Krasnoyarsk area (Upper Yenisei basin); and it was unexpectedly collected in Mongolia on the Bulgan-Gol River, descending from the Mongolian Altai to Dzhungaria (PETERS, 1985). Beyond Siberia, this continental subspecies ranges in Amur province (MALIKOVA, 1993, 1995, 1997a), Primorye (BELYSHEV, 1973; MALIKOVA, 1995), in N and E China and Korea (ASAHINA, 1989b; TSUDA, 2000; LEE, 2001).

The gomphid species has exactly the same taxonomical history. Although *Gomphus epophthalmus* Selys, 1872 was described from "Irkutzk, par le Dr Maack" (SELYS LONGCHAMPS & McLACHLAN, 1872), this cannot be true, because it has never since been recorded in Irkutsk province. Irkutsk was probably men-

[2] In Russia, the names Ural and Altai (in singular) are applied both to the mountains and to the regions they reside in, in the case of Altai the region called so contains a lot of plains as well. Since the dragonflies considered inhabit foothills rather than the very mountains, here and on these names will be applied (in singular and without the article) to regions, following the Russian tradition.

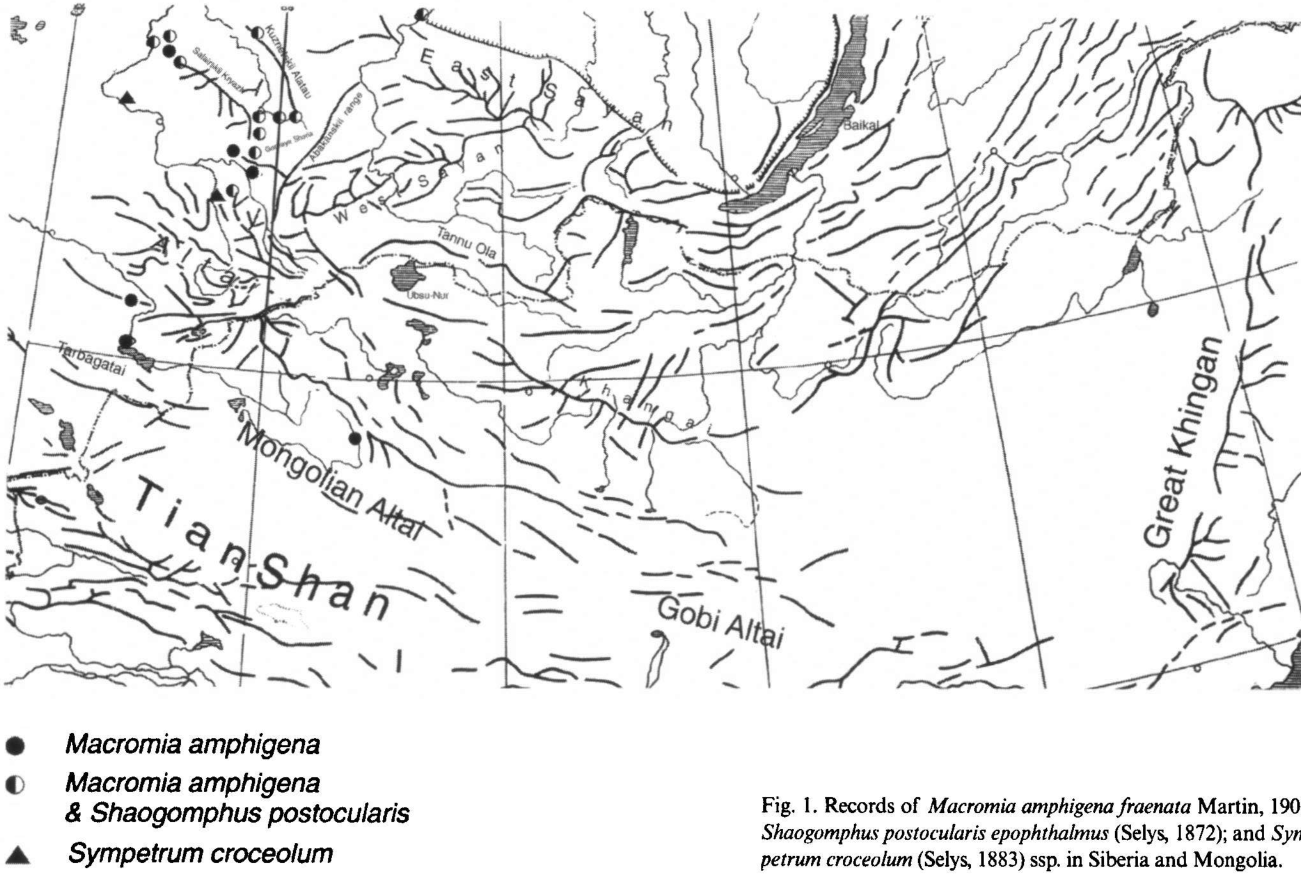

Fig. 1. Records of *Macromia amphigena fraenata* Martin, 1906; *Shaogomphus postocularis epophthalmus* (Selys, 1872); and *Sympetrum croceolum* (Selys, 1883) ssp. in Siberia and Mongolia.

tioned as simply the administrative centre of a vast territory. ASAHINA (1986) showed that this taxon is a continental subspecies of the Japanese *G. postocularis* Selys, 1869; later CHAO (1990) transferred it to *Shaogomphus* as a continental subspecies *S. postocularis epophthalmus* (Selys, 1872). However, the differences from the nominate form are minor, even on a subspecific level. In Siberia this species is almost invariably recorded at the same sites as *Macromia amphigena* (Zolotoy Kitat, Inya, Kos'ma, Berd', Kabyrza, Kondoma, Isha Rivers, at Krasnoyarsk) (Figs 1-2) (BELYSHEV, 1971, 1973, GAGINA, 1997; DRONZIKOVA, 1998 and pers. comm.; KOSTERIN et al., 2001). It is rarely absent from locations where *M. amphigena* occurs; it is perhaps less noticeable (and it was not found either in Kazakhstan or in Mongolia). Of the known localities it is apparently most abundant on the Inya River (where it has been monitored by A. Haritonov since 1979; see HARITONOV, 1981), which descends from the Kuznetskiy Alatau Mountains. to the west and joins the Ob' in Novosibirsk. Beyond Siberia, *Shaogomphus postocularis* is rare in Amur province (the Zeya River), Khabarovskiy Kray province (Sovetskaya Gavan'), and Primorye (Razdol'naya River) (MALIKOVA, 1997a and pers. comm.). Outside Russia, it lives in NE China, Korea and Japan (the nominate subspecies) (ASAHINA, 1989a; TSUDA, 2000; LEE, 2001)

The third and most surprising isolate is that of *Sympetrum croceolum* (Selys, 1883). I discovered this species in West Siberia at Lake Manzherok, N Altai, in 1982 and A. Haritonov at Meret' village, southern Novosibirsk province, in 1987 (KOSTERIN, 1987a, 1987b, 1996b; BELYSHEV et al., 1989; HARITONOV, 2000; KOSTERIN et al., 2001). In 2000, a single female was unexpectedly collected by A. Shtrekker (a student of A. Haritonov) in an Ob' floodplain oxbow in a Novosibirsk city park (KOSTERIN et al., 2001). In 2001 I examined this site thoroughly and failed to find the species, while on Lake Manzherok it flourished. BELYSHEV (1973) believed that in Russia this species was present only in Primorye, not north of Lake Khanka, but then MALIKOVA (1993, 1995, 1997a) found it common at Blagoveshchensk, Amur province. Its range extends to Japan, Korea, and NE China (NEEDHAM, 1930; ASAHINA, 1990; TSUDA, 2000; LEE, 2001). The West Siberian populations are remarkable for the extreme development of the orange colour on the wings; it occupies almost all the hind wing, leaving only a small window, and spreads widely from the fore wing apex. Moreover, the wing apices of mature individuals often show darker brown shading. In the Japanese nominotypical specimens, the orange coloration occupies only the basal wing parts and spreads to the apex along the costa, sometimes occupying the very wing tip as well. In Primorye and Amurland, the apical orange colouring is expanded, but not so remarkably as in West Siberia. BELYSHEV (1964) described the subspecies *S. croceolum fuscoatrum* Belyshev 1964 from Primorye (Putyatin Island is the type locality), and this name is suitable for the eastern continental populations of the species. I believe that the West Siberian ones also deserve subspecies status and shall publish the description elsewhere.

The three species considered above are represented by different subspecies in Japan and the continent. As Japan were last united by land with the continent during the last glaciation, the divergence of the subspecies occurred about 10-12 thousand years ago. This period is evidently sufficient for subspecies formation in Lepidopera (DUBATOLOV & KOSTERIN, 2000) but is thought to be insufficient for Odonata (LOHMANN, 1992). Anyway, the differences between these subspecies are not great.

The three mentioned species occur in Siberia only along the forested north-western margins of the Altai-Sayan mountain system and the adjacent lowlands at Novosibirsk (Figs 1-2). These mountain margins have well-developed forests of spruce, fir, and Siberian stone pine with a substantial component of birch and aspen, along with many woodland grass and herb species, that are usually associated with the European nemoral broad-leaved forests of oak, lime, elm, maple, and other trees that are absent or nearly absent from Siberia (see below). Especially rich are forests of Siberian fir associated with aspen and tall herbage; they are called 'chernevaya taiga' and are distributed along the western and northern Altai, the Kuznetsk Upland (including a low range of Salairskii Kryazh that protrudes into Novosibirsk province), and the northern slope of the Sayans (POLOZHII

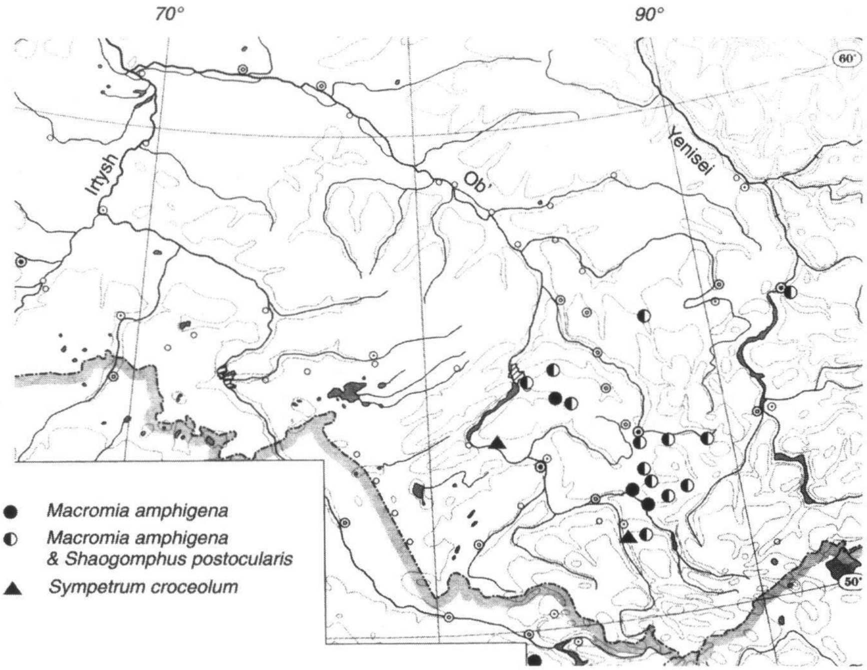

Fig. 2. Records of *Macromia amphigena fraenata* Martin, 1906; *Shaogomphus postocularis epophthalmus* (Selys, 1872); and *Sympetrum croceolum* (Selys, 1883) ssp. in West and Central Siberia.

& KRAPIVKINA, 1985; ERMAKOV, 1998). This plant community is termed subnemoral (ERMAKOV, 1998). Moreover, in the low mountains of Gornaya Shoria, there is a considerable area of natural lime forest (this lime tree species, *Tilia sibirica* Fischer, is considered distinct, although close to the European *T. cordata* L.) (KHLONOV, 1965; POLOZHII & KRAPIVKINA, 1985). In Lake Manzherok, where a population of *Sympetrum croceolum* lives, an endemic water chestnut *Trapa pectinata* V. Vassil. s. str. occurs. This plant is most closely related to *T. manshurica* Fler. s. str., which occurs in NE China, Japan and the Russian Far East (TSVELEV, 1995). Thus, the isolated population of an East Asian dragonfly has a parallel in the isolate of an East Asian plant.

The record of *Macromia amphigena* on a Mongolian river flowing through a desert is striking, but geographically the location belongs to Dzhungaria, not Mongolia, as it lies at the western foot of the Mongolian Altai. The main western slopes of this mountain chain receive much precipitation and support a luxuriant coniferous forest resembling those of the Central Altai (SAPOJNIKOF, 1911). Thus, the landscape upstream of the collecting site somewhat resembles that of the more northern spurs of the mountain system, and the dragonfly could descend along the Bulgan River to the low-lying desert landscapes. No doubt that when the climate was colder, it was Mongolian Altai, the southwestern main range of the Altai-Sayan mountain system, that supported refugia of subnemoral forest vegetation analogous to the forests present-day occupying the north-western spurs of the mountain system. The Irtysh River valley, as well as the so-called Dzhungarian Gates between the Saur and Dzhunragian Alatau mountains provided a gap in the latitudinal belt of Asian mountains through which thermophilic lowland species could retreat to the South and move North again during the various Pleistocene-Holocene climatic changes.

Three other eastern species range continuously westward in Siberia but the western limit of their distribution also lies at the NW margins of the Altai-Sayan mountain system. The western limit of *Ophiogomphus obscurus* Bartenev, 1909 is at Tomsk on the Ob' River (Fig. 3). This species inhabits forests, including Far Eastern mixed forests, but does not penetrate far to the north, hardly reaching 58°N in its western range (BELYSHEV, 1973; HARITONOV & BORISOV, 1990). *Nihonogomphus ruptus* (Selys, 1857) reaches the Ob' River at Novosibirsk, where it once was extremely rare (KOSTERIN et al., 2001); presently, it is becoming more and more common. In the Gornaya Shoria Mountains, also close to its western limit, it is abundant. To the North, it ranges to 60°N at the Podkamennaya Tunguska River (BELYSHEV, 1973) and to at least 58°N at the Aldan River, and therefore is the most northerly ranging gomphid in Siberia (Fig. 3). *Calopteryx japonica* Selys, 1869 ranges west to North Altai and the Gornaya Shoria Mountains. In the north, it reaches 60°N at the Podkamennaya Tunguska River (MALIKOVA, 1995) and 62°N at the Melyuk, Kil'lemtine, Vakunaika and Biryuk rivers in SW Yakutia (POPOVA et al., 2001; N.N. Vinokurov, pers.

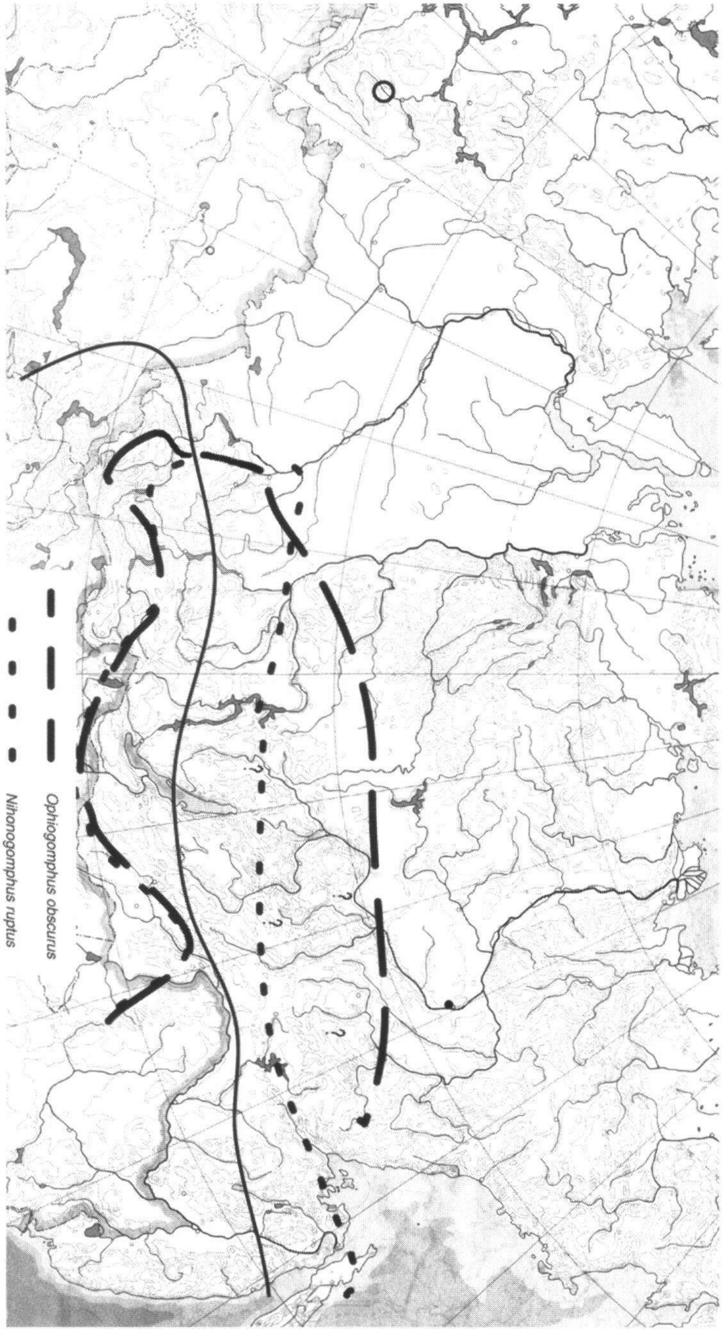

Fig. 3. Approximate range limits of *Ophiogomphus obscurus* Bartenef, 1909; *Nihonogomphus ruptus* (Selys, 1857); and *Coenagrion ecornutum* (Selys, 1872) in Ural and Siberia.

comm; KOSTERIN, 2004a) (Fig. 4). BARTENEV (1914), MIYAKAWA (1983, 1984) and MALIKOVA (1995) all showed its distinctness from *C. virgo* (Linnaeus, 1758), from which it differs in the wing shape, the nature of venation of the hind wing anal zone and, in males, the colour of the venter of the abdomen tip. In Altai and Central Siberia it is represented by the subspecies *C. japonica altaica* Belyshev, 1955, shown by MALIKOVA (1995) to belong to *C. japonica* but not to *C. virgo* (Linnaeus, 1758), within which it was originally described by Belyshev (1955). However, in the original description (BELYSHEV, 1955) it was compared with *C. v. virgo*, not *C. japonica*, and in fact its differences from *C. j. japonica* are weak – smaller body size, smaller false pterostigma in females and a highly variable labrum coloration (MALIKOVA, 1995). *C. japonica* has not been collected between Lake Baikal and Amurland, and perhaps there is a real gap in its distribution there. But since it penetrates so far to the North, it should find suitable habitats somewhere in this region as well.

Coenagrion ecornutum (Selys, 1872) was thought to have a similar range in the very South of Siberia from the upper Ob' River basin to Amurland. However, recently it was found as far North as 65°N at Yakutsk (FUKUI, 1992; KOSTERIN, 2004a), and an isolate was discovered by YANYBAEVA (1999) in the Bashkirskii Nature Reserve in SW Ural (Fig. 3). (The latter fact revives the old problem of its taxonomical relationship with a closely related, rare Euro-Caucasian species, *C. mercuriale* (Charpentier, 1940). A thorough comparative analysis of the Uralian specimens is necessary in this respect). In Siberia, *C. ecornutum* is obviously absent between Ural and Altaiskii Krai province, and it is unknown if the Yakutsk locality exists thanks to the unique conditions of the great Lena River valley isolated from the main range in southern Transbaikalia and Amur province (at least some more southern steppen species of plants and insects penetrate far North just along this valley), or it will be found in future somewhere in the Stanovoy Range or Aldan Upland.

Three eastern boreal species that thrive in the severe conditions of Central or East Siberia as far north as 70°N (BELYSHEV, 1973) also have the western limit of their ranges in Altai (Fig. 5). These are *Coenagrion lanceolatum* (Selys, 1872) (recently found by DRONZIKOVA (1998) in NE Altai); *C. hylas* (Trybom, 1879) and *Somatochlora graeseri* Selys, 1887. *C. hylas* has isolates on the Yamal Peninsula, in Polar Ural, and a notorious one in Bavaria (HARITONOV, 1974; BELYSHEV & HARITONOV 1980; 1981; LOHMANN, 1992); *S. graeseri* is isolated in Ural (Fig. 5) (BELYSHEV et al. 1989; YANYBAEVA, 1999).

Somatochlora exuberata Bartenev, 1910 ranges westward to the sources of the Yenisei River. Having observed it there (in the Todzha Hollow) sympatrically with *S. metallica* (Vander Linden, 1825) (KOSTERIN & ZAIKA, 2003), I am convinced that they are good species, differing somewhat ecologically. *Coenagrion glaciale* (Selys, 1872) reaches 70°N, but is not yet recorded west of the Baikal region, (BELYSHEV, 1973) (Fig. 5) although it probably occurs there.

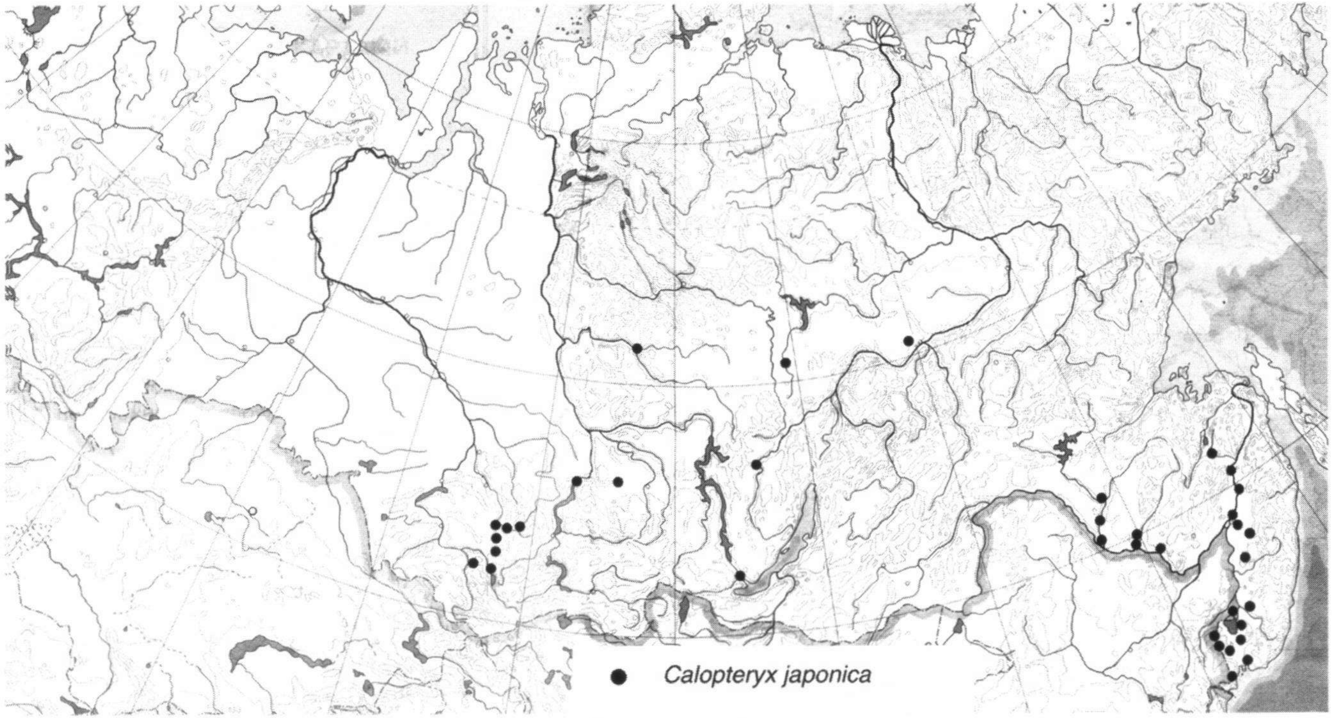

Fig. 4. Records of *Calopteryx japonica* Selys, 1869 in Siberia and the Russian Far East.

I recently found two more East Asian species, *Cercion v-nigrum* (Needham, 1930) and *Anisogomphus maacki* (Selys, 1872), in SE Transbaikalia in the Onon (both species) and Argun' (the latter species) river basins (KOSTERIN, 1999; 2004b).

Of all the western isolates of eastern species, the most striking is the report of *Sympetrum eroticum* Selys, 1863 in Lithuania by STANIONYTE (1989). It is a mysterious record, and an unintentional introduction cannot be excluded, so I omit it from the analysis.

LONGITUDINAL LIMITS OF OTHER ODONATE SPECIES WITHIN SIBERIA

As discussed, eleven East Asian odonate species have their western limits in Siberia and an additional three have even more westerly isolates in the Urals (*Coenagrion ecornutum, C. hylas, Somatochlora graeseri*) and in Bavaria (*C. hylas*). What do we find in the opposite direction – that is, how many western species have their eastern limits in Siberia? *Aeshna cyanea* (Müller, 1764) penetrates to Transuralia (V. Skvortsov, pers. comm.). Eight species reach the Upper Ob' River basin: *Lestes virens* Charpentier, 1825; *Coenagrion puella* (Linnaeus, 1758); *C. pulchellum* (van der Linden, 1825); *Gomphus vulgatissimus* (Linnaeus, 1758); *Somatochlora flavomaculata* (Vander Linden, 1825); *Sympetrum meridionale* (Selys, 1841); *Leucorrhinia pectoralis* Charpentier, 1825; and *L. albifrons* (Burmeister, 1839). Seven species reach the Yenisey River headwaters: *Lestes macrostigma* Eversmann, 1836; *Lestes barbarus* (Fabricius, 1798); *Platycnemis pennipes* (Pallas, 1771); *Aeshna affinis* Vander Linden, 1825; *Somatochlora metallica* (Vander Linden, 1825); *Orthetrum cancellatum* (Linnaeus, 1758); and *Sympetrum sanguineum* (Müller, 1764). Four species reach Baikal: *Calopteryx splendens* (Harris, 1782); *Ischnura pumilio* (Charpentier, 1825); *Aeshna grandis* (Linnaeus, 1758); and *Leucorrhinia caudalis* (Charpentier, 1840). *Ophiogomphus cecilia* (Fourcroy, 1758) reaches North Transbaikalia (KOSTERIN, 1999; 2004b) and *Calopteryx virgo* (Linnaeus, 1758) reaches Central Mongolia (MALIKOVA, 1997b). It is noteworthy that *Gomphus vulgatissimus* might have a disjunction between Europe and the Ob' basin, and *Leucorrhinia caudalis* between the Ob' and Baikal, but these gaps require proof. *I. pumilo* evidently has isolated populations in the N Altai and at Baikal (BELYSHEV, 1973). Hence, 21 western species have their eastern limits in Siberia compared to 11(+3) eastern ones. And only four of these western species – *C. splendens, C. virgo, S. metallica* and *A. grandis* – reach, or extend North of, 60°N latitude.

Siberian odonates ranging throughout Eurasia from Europe to the Pacific are mostly boreal species well adapted to the taiga zone. They may even penetrate into the forest-tundra zone; some of these also occur in North America. There are 24 of these northerly ranging trans-Siberian species: *Lestes dryas* Kirby, 1890; *L. sponsa* Hansemann, 1823; *Sympecma paedisca* (Brauer, 1877); *Coena-*

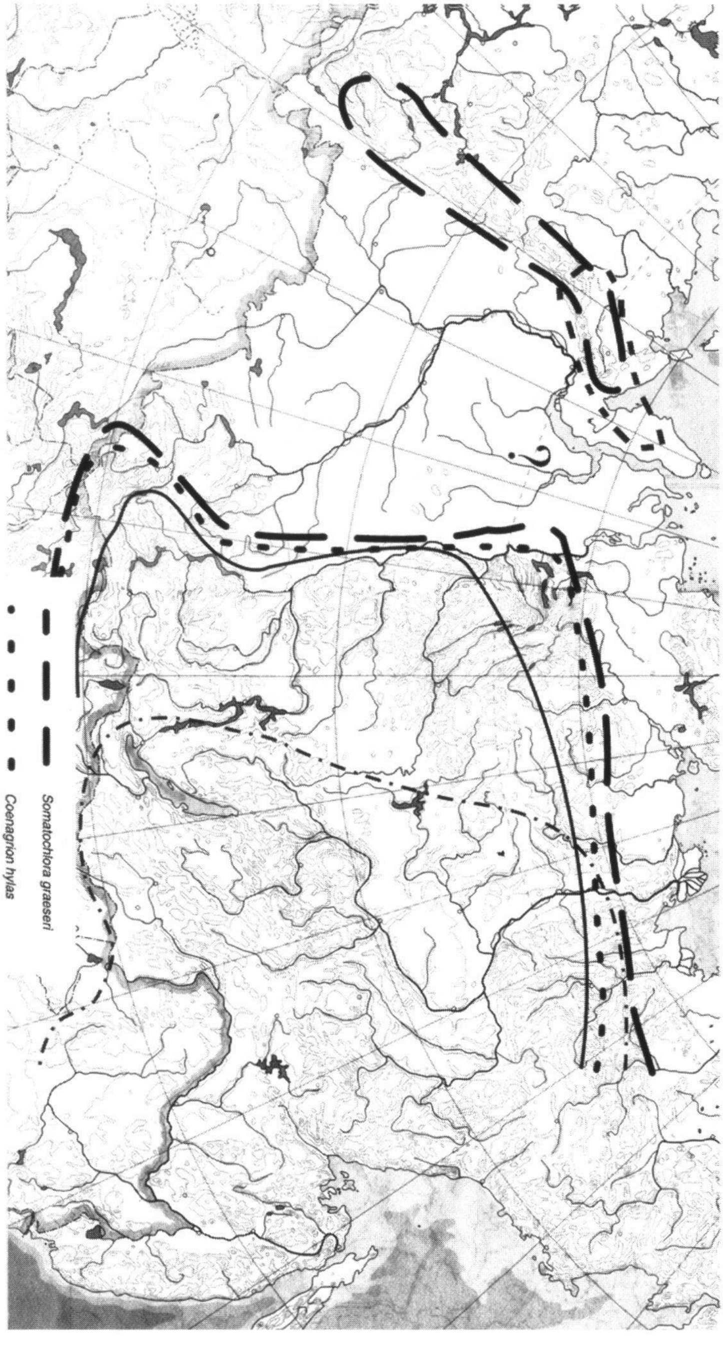

Fig. 5. Approximate range borders of *Somatochlora graeseri* Selys, 1887; *Coenagrion lanceolatum* (Selys, 1872); *C. hylas* (Trybom, 1879); and *C. glaciale* (Selys, 1872) in Ural and Siberia.

grion johanssoni (Wallengren, 1894); *C. armatum* (Charpentier, 1840); *C. hastulatum* (Charpentier, 1825); *C. lunulatum* (Charpentier, 1840); *Erythromma najas* (Hansemann, 1823) (including *E. humerale* Selys, 1887); *Enallagma cyathigerum* Charpentier, 1840 (including *E. risi* Schmidt, 1961 and *E. antiquum* (Bartenev, 1956) (= *E. continentale* Belyshev, 1956, = *E. nigrolineatum* Belyshev & Haritonov, 1975) see SAMRAOUI et al., 2002 and KOSTERIN, 2004b); *Aeshna caerulea* Ström, 1783; *A. crenata* Hagen, 1856; *A. serrata* Hagen, 1856, with an enigmatic range: it was thought to reach no farther than Transbaikalia (KOSTERIN, 1999, 2004b) and Central Yakutia (FUKUI, 1992; KOSTERIN, 2004a) in the East but was recently found in Kamchatka (DUMONT et al., 2005); *A. subarctica* Walker, 1908; *Epitheca bimaculata* (Charpentier, 1825); *Cordulia aenea* (Linnaeus, 1758); *Somatochlora arctica* (Zetterstedt, 1840); *S. sahlbergi* Tryböm, 1889; *S. alpestris* Selys, 1840; *Libellula quadrimaculata* (Linnaeus, 1758); *Leucorrhinia dubia* (Vander Linden, 1825) s. l. (including *L. orientalis* Selys, 1887); *L. rubicunda* (Linnaeus, 1758) s. l. (including *L. intermedia* Bartenev, 1910); *Sympetrum flaveolum* (Linnaeus, 1758); *S. danae* (Sulzer, 1776); and *S. vulgatum* (Linnaeus, 1758) (including *S. imitans* (Selys, 1886)).

Of those species distributed from Europe to East Asia, only ten inhabit the southernmost part of Siberia only or occur there locally: *Ischnura elegans* (Vander Linden, 1823); *Nehalennia speciosa* (Charpentier, 1840); *Aeshna mixta* Latreille, 1805; *Anax parthenope* Selys, 1839 s. l. (which penetrates into Siberia in North Altai (BELYSHEV & BELYSHEV, 1976), Kemerovo province (DRONZIKOVA, 1998 and pers. comm.), Tuva (KOSTERIN & ZAIKA, 2004, and unpubl.) and SE Transbaikalia (KOSTERIN, 1999)); *Stylurus flavipes* (Charpentier, 1825); *Pantala flavescens* (Fabricius, 1798) (penetrates into Transbaikalia (KOSTERIN, 1999; 2004b)); *Orthetrum albistylum* (Selys, 1842) (present in Siberia only in an isolated population at Lake Baikal associated with hot springs (BELYSHEV, 1973)); *Sympetrum depressiusculum* (Selys, 1841); and *S. pedemontanum* (Müller, 1766).

The range of *Nehalennia speciosa* (BELYSHEV & HARITONOV, 1981) is remarkable. The species is scattered in Europe to Ural; there are two reports from the West Siberian Lowland at Omsk (VALLE, 1832, although the location may be misleading) and in Khanty-Mansi Autonomous Region (KRASUTSKII & OLSHVANG, 2003), it occurs locally in the Upper Ob' River basin, including North Altai (BELYSHEV, 1973; KOSTERIN, 1987a; KOSTERIN et al. 2001); and, after a tremendous gap in Central and East Siberia, it reappears in Amurland (MALIKOVA, 1997a), China, Korea and Japan (BELYSHEV, 1973; BELYSHEV & HARITONOV, 1981; TSUDA, 2000).

The true range of *Aeshna viridis* Eversmann, 1836 is unclear. This western species inhabits West Siberia, where it is abundant; reaching the Altai and Kuznetskoe Alatau mountains in the east. There is, however, an old Bartenev's record at Ussuriisk in Primorye (cited by BELYSHEV, 1973; MALIKOVA, 1995). If *A. viridis* indeed occurs in the Far East, it would be the only true amphipalaearctic dragonfly species, present at the opposite ends of Eurasia but absent from the central parts of the continent. In the main part of its range this species is ecologically associated (but not so strictly as thought) with the water soldier (*S. aloides* L.) among the leaves of which its larvae dwell. *Stratiotes aloides* slightly extends farther East than the dragonfly, but only to the Yenisei River. This plant is absent in the East, but some other plant species might provide suitable larval habitat (e.g., *Ottelia alismoides* (L.) Pers).

Two species confined to Central Asia enter extreme southern Siberia – *Ophiogomphus spinicornis* Selys, 1878 occurs in S Tuva, S Baikal and Transbaikalia (KOSTERIN, 1999, 2004b) and *Sympetrum tibiale* (Ris, 1897) enters S Tuva (KOSTERIN & ZAIKA, 2004).

I have noted here all species (some accepted in the broad sense) present in Siberia (defined in the narrow sense). Other species that have been reported in the past are now considered synonyms of others; these synonymies are published or will be published elsewhere.

DISCUSSION

Thirty-four species do not range across all Siberia but do enter Siberia from the East or West. Twenty-five of these are rather southern species: they do not reach 60°N and prefer mostly the forest-steppe zone and/or the nemoral (broad-leaved) forest zone in either Europe or East Asia. The zone of nemoral broad-leaved forests is almost completely interrupted in Siberia and the diversity of deciduous tree

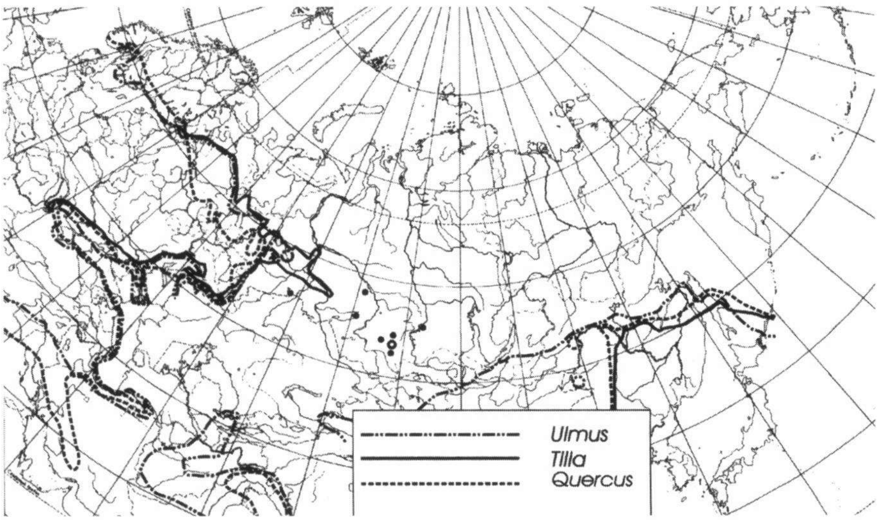

Fig. 6. Present ranges of three broad-leaved tree genera in Siberia (from DUBATOLOV & KOSTERIN, 2000).

species is strikingly poor, a fact that most inhabitants of North America, western Europe, and even European Russia, would find hard to imagine. The contemporary natural communities of Siberia lack such trees as maple, hornbeam, ash, beech, and are almost devoid of oak (only in easternmost Transbaikalia), lime (narrowly extending from the west to the Irtysh River; isolates in Altai, Kemerovo and Krasnoyarsk provinces), and elms (locally in the extreme West and East) (Fig. 6). In Siberia even the arboreal alder (*Alnus* s. str.) is rare – two species occur locally only in the very west and one species is widely distributed in East Siberia. Only deciduous birch forests (with aspen, willows, bird cherry and rowan tree) are extremely widespread in Siberia, either associated with boreal coniferous forests or alone forming groves in the forest-steppe zone. Traditionally in Russia, these forests are, for some reason, called "small-leaved" (although the aspen has rather large leaves), a term that corresponds to the North American "softwood". In NW Eurasia the abrupt limit of broad-leaved trees such as oak, maple and, to some extent, elm and linden coincides with the relatively low Ural Mountains (GORCHAKOVSKII, 1968). Insufficient humidity was once considered a key factor limiting the eastern spread of broad-leaved species (GORCHAKOVSKII, 1968). However, the low diversity of tree species in Siberia is probably due to past climatic conditions and biogeographical history rather than the result of contemporary climate because almost all these trees, if planted, grow well and propagate in South Siberia. The Siberian fauna in all major groups is impoverished compared to that of Europe and the Pacific regions. This depletion in bio-

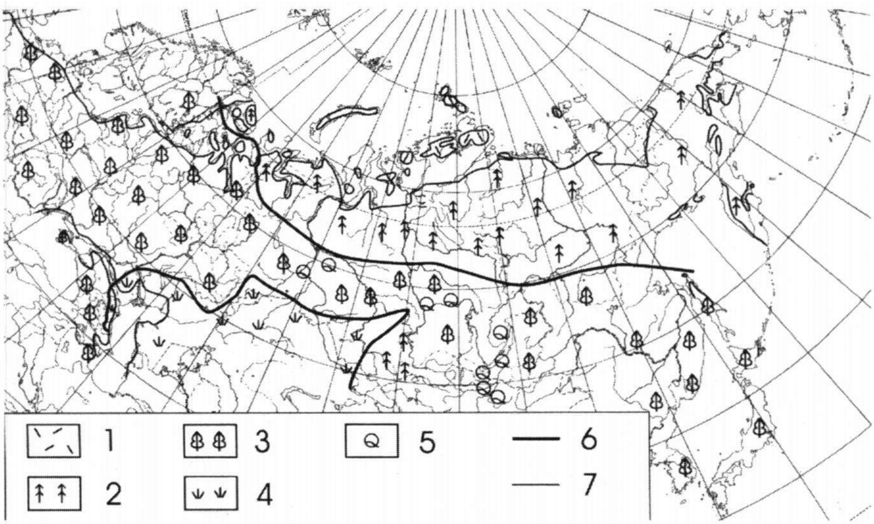

Fig. 7. Reconstruction of general zones during the Climatic Optimum of the Upper Pleistocene (the Kazantseva = Milulino = Riss-Würm Interglaciation). – 1: tundra; – 2: taiga; – 3: forests including broad-leaved trees; – 4: steppes; – 5: records of oak pollen; – 6: borders of the main vegetation types; – 7: coast line (from DUBATOLOV & KOSTERIN, 2000).

diversity is thought to result from the latitudinal orientation of major mountain chains that enclose Siberia to the South, a condition that prevented thermophylous biota from retreating to the South and subsequently moving North again during the oscillations of Pleistocene climate. The trapped biota was extirpated at the foot of the mountains. The relative aridity of the climate in the centre of the continent acted with the cooling temperatures to contribute to this empoverishment. Hence, during interglacial periods, including the Holocene, many components of rather thermophilous biotas had to recolonize Siberia from either the Far East or from Europe and, to some extent, from Turanian Central Asia, although the latter harboured mostly species of arid habitats.

I have been fortunate to work with Dr Vladimir Dubatolov, a productive lepidopterologist from Novosibirsk, on his thorough analysis of ranges of nemoral Lepidoptera species in Siberia (DUBATOLOV & KOSTERIN, 2000). Nemoral species are considered as those preferring or associated with broad-leaved forests. Most of the above considered odonate species that do not occupy all of Siberia from West to East roughly correspond to the nemoral complex by their environmental requirements as well as their distribution. Only few of such species reach 60-70°N and should be considered boreal, that is associated with the coniferous forest zone. However, odonates are less tied to ecological factors, much less precisely confined to vegetation types than are lepidopterans and thus can hardly be classified as "nemoral" or "boreal". DUBATOLOV & KOSTERIN (2000)

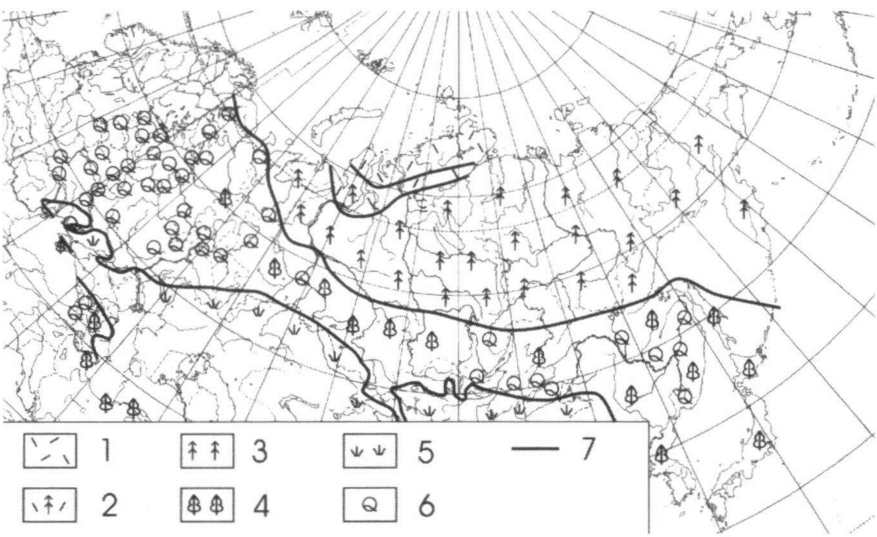

Fig. 8. Reconstruction of general zones during the Climatic Optimum of the Holocene (the Atlantic period). – 1: tundra; – 2: forest-tundra; – 3: taiga; – 4: forests including broad-leaved trees; – 5: steppes and deserts; – 6: records of oak pollen; – 7: borders of the main vegetation types (from DUBATOLOV & KOSTERIN, 2000).

calculated that 28 nemoral species of Lepidoptera demonstrate Amphipalaearctic ranges – those present in Europe, West to the Urals, and in the Far East but have a high range gap across Siberia. These species seem to have no counterparts among dragonflies, except for the problematic case of *Aeshna viridis*. Five lepidopteran species have disjunct ranges with parts in Europe, isolates in West Siberia (one species also has an isolate in Central Siberia), and the main range in East Asia (the Europe - West Siberia - Far East Disjunctive Ranges). Among odonates we find this range type in *Nehalennia speciosa*. Nine nemoral species of Lepidoptera are distributed in the Far East but have isolates in the extreme NW of the Altai-Sayan mountain system (the Altai-Far East Disjunctive Ranges), and hence are analogous in distribution to *Macromia amphigena, Shaogomphus postocularis* and *Sympetrum croceolum*. No nemoral Lepidoptera species demonstrate a range like that of *Coenagrion ecornutum*. Ten nemoral Lepidoptera species range continuously westward in South Siberia from East Asia to the Altai (the South Siberia - Far East ranges); *Calopteryx japonica, Nihonogomphus ruptus*, and *Ophiogomphus obscurus* are odonate examples. Thirty-eight (so many!) nemoral Lepidoptera penetrate from the Far East to Transbaikalia (the Transbaikalia - Far East ranges), but only two odonates, *Cercion v-nigrum* and *Anisogomphus maacki*, do. Seven nemoral lepidopterans are distributed from Europe to Transuralia (the Europe-Transuralia ranges), as does *Aeshna cyanea*. No nemoral Lepidoptera range from Europe to the Ob', Yenisei or Baikal basins, so 19 odonate species find no counterparts in this group, but there is a number of southern steppen and forest-steppen Lepidoptera species, not considered nemoral, which do share this range type.

Thus, many nemoral lepidopterans penetrate Siberia from the East, but hardly any do so from the West. In Odonata, the situation is almost the opposite. One of the reasons for this discrepancy is that the entities are not truly comparable. Odonata are not strongly associated with nemoral communities and thus the comparison should be made with all Lepidoptera, among which there are many meadow and steppe species penetrating from Europe to West or Central Siberia. Yet, as amphibiotic insects, odonates are associated with water and to some extent with forests and groves. One would expect them to have recolonized Siberia after the Pleistocene coolings from the east at least as easily as from the west. In Odonata, twice as many eastern range limits as western limits lie within Siberia. Depending on the speed of migration and the time allowed for these movements, this fact may be interpreted either as (1) a prevalence of migrating western species that managed to occupy Siberia to varying extents or (2) a prevalence migrating eastern species that occupied all of Siberia and became transpalaearctic while western species failed to reach the eastern border of Siberia in the time period allowed and thus have their present eastern limits within Siberia. BELYSHEV (1973) accepted the first interpretation. He believed that since Europe, with its ice-shield, suffered more from the Pleistocene cooling than had East Asia, the western species are, on average, more adapted to harsh climates, have acquired greater ecological plasticity and thus are more mobile. However, reconstructions of natural conditions in Siberia during the Holocene favour the second interpretation.

The disjunct distributions of southern species in various groups of temperate Eurasian animals are traditionally interpreted as remnants of pre-glacial continuous ranges. It is implied that some regions provided enough mild climate for these species to survive climate cooling and thus were refugia for them. Although it is known that former interglacial periods were warmer than the present one, for some reason most Russian scientists used to hypothesize that these refugia acted throughout the Pleistocene, while the continuous ranges existed only as long ago as the Tertiary. In view of the rich materials accumulated by Russian palaeoclimatologists and palaeobotanists (especially palinologists) in Siberia (ARKHOPOV & VOTAKH, 1973; VOLKOV et al., 1973; BELOVA, 1985; BAKHAREVA, 1985; VOLKOVA & BELOVA, 1980; ARKHIPOV & VOLKOVA, 1994; for a review see DUBATOLOV & KOSTERIN, 2000), this notion cannot be supported. Reconstructions show that the continuous trans-Eurasian belt of nemoral broad--leaved forests was restored during each interglacial period (BELOVA, 1985; BAKHAREVA, 1985; UKRAINTSEVA, 1988, 1996; ARKHOPOV & VOLKOVA, 1994), including the Holocene (KHOTINSKII, 1977; VOLKOVA & BELOVA, 1980; BELOVA, 1985; ARKHIPOV & VOLKOVA, 1994) (Figs 7-8). There is no doubt that the restoration of forest communities was accompanied by recolonization of these areas by a relevant, maybe somewhat impoverished, fauna, especially

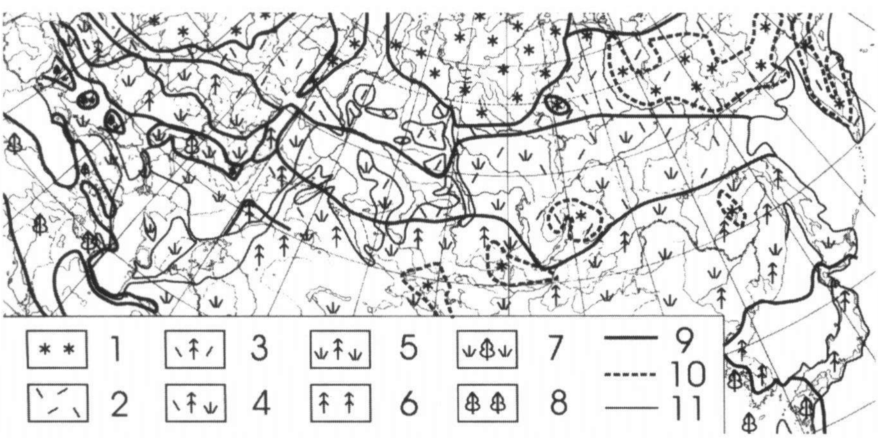

Fig. 9. Reconstruction of general zones during maximum glaciation of the Upper Pleistocene (the Sartan = Late Valdai = Late Zyryanka = Late Würm Glaciation). – 1: ice-sheets and mountain glaciers; – 2: arid tundra; – 3: cryophyte forest-tundra; – 5: forest-steppe without broad-leaved tree species; – 6: local coniferous forests; – 7: forest-steppe with some broad-leaved tree species; – 8: broad-leaved (nemoral) forests; – 9: borders of main vegetation types; – 10: borders of diffuse mountain glaciation in NE Asia; – 11: coast line (after DUBATOLOV & KOSTERIN, 2000).

of flying insects. On the other hand, during glaciations, conditions in the earlier supposed refugia were severe enough (although no ice-sheets developed) to prevent them acting as refugia (BELOVA, 1985; KOZHEVNIKOV & UKRAINTSEVA, 1992; ARKHIPOV & VOLKOVA, 1994) (Fig. 9). This allows dating of the disjunctions of the plant and animal species associated with nemoral forests to climate deterioration after the Holocene climatic optimum, not earlier than 5 to 6 thousand years ago. The western and northern piedmonts of the Altai, Kuznetskiy Alatau and Sayan Mts. indeed provided conditions mild enough for refugia for nemoral plants and insects, but these refugia acted not for 1.8 million years (as used to be supposed) but for only the 5 to 6 thousand years since the Holocene optimum. These regions became refugia through a combination of rather low latitude and the moderate elevations of the fronts of the South Siberian mountains, which capture a considerable amount of precipitation moving from the Atlantic. These conditions were sufficient for the development of chernevaya taiga, a close derivative of the extirpated nemoral forests (ERMAKOV, 1998).

Another very important fact revealed by the palaeobotanists is that the Holocene climatic optimum occurred earlier in the east and later in the west -- in the Atlantic period (about 8,000 YBP) in the Far East, in the Late Atlantic - Early Subboreal Period (about 6,000 YBP) at Lake Baikal and the Yenisey River, and in the Subboreal Period (about 5,000 YBP) in West Siberia (ARKHIPOV & VOLKOVA, 1994). This favoured westward migrations of eastern faunal elements. East Asian species had a better opportunity to occupy Siberia west to the Ob' River or to the Ural Mountains (and hence Europe) and become transpalaearctic (of course, some divided populations may have recolonized Siberia from both east and west). After further cooling, the distribution of those species more sensitive to climate change shrunk to various refugia, such as the peri-Altaian refugium. Thus the Holocene was a critical period in the formation of recent distributions of temperate zone species in Eurasia.

The Lepidoptera are almost as mobile as Odonata but, as a rule, they are strongly connected to their larval foodplants and therefore are less able to colonize new habitats. (However, the ranges of most of the above mentioned nemoral Lepidoptera species are smaller than those of their foodplants, and the insects could expand their ranges and still find the plants to feed on). The difference in the ratio of longitudinal range boundaries in Siberian Odonata and nemoral Lepidoptera result from (1) less strict climatic requirements in Odonata (so that the ranges of most species did not shrink or split after the Holocene climatic optimum) and (2) the greater speed of the spread of Odonata compared to Lepidoptera. These factors would allow many western odonate species (but only a few nemoral lepidopterans) to colonize western Siberia during the relatively short period after the late climatic optimum in the west. Those odonate species that earlier started colonizing from the east, moving west with the climatic optimum, and had enough time to get to Europe, today find suitable conditions throughout Eurasia and have continuous transpalaearctic ranges. Some of these species may have survived the last glaciation on both sides of Eurasia and restored a continuous range after the glaciation ended by occupying Siberia from both sides. However, some lepidopterans have not found suitable conditions in central Eurasia and so are still amphipalaearctic. Thus, the explanation proposed here is the reverse of Belyshev's; I suggest that it were eastern species, not the western ones, that managed to spread over greater distances during the Holocene.

The three species that today have isolates on the northwestern margin of the Altai-Sayan mountain system (*Shaogomphus postocularis*, *Macromia amphigena*, *Sympetrum croceolum*), are perhaps the most stenotopic of those East Asian species that penetrated into Siberia in the Holocene, while the two East Asian species that only reach Transbaikalia (*Cercion v-nigrum* and *Anisogomphus maacki*) maybe the least mobile. Therefore, the ranges of the latter two species resemble those of some eastern nemoral Lepidoptera. *Coenagrion ecornutum* and *Ophiogomphus obscurus* range more widely but yet did not occupy most of the West Siberian Lowland. Note that four of these seven species are rheophils. A western analog of such stenotopic species may be *Ischnura pumilio* (if its range is indeed so disjunct). *Nehalennia speciosa* is almost amphipalaearctic. It would not be surprising if *Aeshna viridis* proves to be the only true amphipalaearctic species, for it evidently is the most stenotopic of our dragonflies. Its aquatic 'hostplant(s)', and hence the dragonfly itself, could not expand fast enough in the Holocene for the eastern and western populations to meet.

A biogeographical explanation is needed for the few eastern boreal species that can live in Siberia's taiga zone at 70°N but that did not reach Europe. Figures 4-5 clearly show that their western limits coincide well with the mountainous or hilly relief: the Altai and Kuznetskiy Alatau Mts and the Yeniseiskiy Kryazh (the latter forms the western margin of the Central Siberian Plateau). These species avoid the West Siberian Lowland, especially its boggy northern half. This is especially understandable for the rheophils *Calopteryx japonica* and *Nihonogomphus ruptus*. *Somatochlora graeseri* and *Coenagrion hylas* managed to reach Ural, where they are probably isolated from their populations in Central Siberia. *C. hylas* reaches as far as Bavaria (note some boreal butterfly species, such as *Parnassius phoebus* (Fabricius, 1793), *Euphydryas intermedia* (Ménétriés, 1759), *Boloria napaea* (Hoffmansegg, 1804), *Erebia pandrose* (Borkhausen, 1788) also exhibit Alpine-Siberian disjunctions). These western isolates result from one of the last glaciations, most probably the ultimate one (LOHMANN, 1992).

Thus, the origin of Siberian species' disjunctions should be dated no earlier than a few thousand years ago. However, the repetitive nature of Pleistocene coolings, which alternated with interglacial periods, should have provided conditions for earlier disjunctions in species having continuous ranges in pre-glacial times or during earlier interglacial periods. The duration of glaciation(s) could be sufficient for speciation of isolated populations. Probably, such events produced pairs of species now living on the opposite sides of Eurasia. For example, the divergence of species pairs among nemoral Lepidoptera trophically associated with oaks is supposed to be associated with the last (Riss-Würm) interglacial period (DUBATOLOV & KOSTERIN, 2000). Among odonates, such species pairs include *Lestes virens* (Charpentier, 1825) and *L. japonicus* Selys, 1883; *L. barbarus* (Fabricius, 1798) and *L. temporalis* Selys, 1883; *Coenagrion mercuriale* (Charpentier, 1940) and *C. ecornutum* (Selys, 1872); *Pyrrhosoma nymphula* (Sulzer, 1776) and *P. tinctipennis* (McLachlan, 1894); these are reviewed in BELYSHEV & HARITONOV (1978, 1981). In these cases, disjunct amphipalaearctic ranges have been formed at the genus level.

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