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Odonata of Tuva, Russia

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Abstract

The odonate fauna of Tuva in Siberia, Russia, is documented, based mainly on data from expeditions in 1990, 2000 and 2004, and examination of collections preserved in Novosibirsk. The checklist of Tuvinian Odonata presently includes 47 species. In the southern Ubsu-Nur depression 29 species were recorded (two just there); in the Central Tuvinian depression 34 species (six just there) and in the Todzha depression 32 species (nine just there). The fauna of the more humid taiga region of Todzha, separated from the arid remainder of Tuva by the Obruchev Mts, contained some forest species but lacked seven species found elsewhere in Tuva. In spite of Todzha's position in the north-east, its fauna showed a more western character and included a population of *Calopteryx splendens* with a high proportion of androchromic females and males with wings coloured to the tips. Todzha was also inhabited by *Enallagma c. cyathigerum* with a variably melanized abdomen, while in the Central Tuvinian and Ubsu-Nur depressions, *E. c. risi* occurred. In Turan and the Upper Kaa-Khem basin, intergradation between both taxa took place. In Todzha, *Somatochlora exuberata* and *S. metallica abocanica* were sympatric without intermediate forms and with habitat segregation, thus proving their status as separate species. Todzha was also inhabited by *Ophiogomphus obscurus* while the rest of Tuva harboured *O. spinicornis*.

Introduction

The Tyva Republic, Russian Federation, acquired its present name in 1993. In past centuries it was known as Uryankhaiskiy Kray or Soyotskiy Kray, and in the USSR as Tuvinskaya Avtonomnaya Sovetskaya Socialisticheskaya Respublika. In Russian, it is better known under the traditional name Tuva (rather than Tyva), used further in this text. Its capital Kyzyl is the geographical centre of Asia. This vast territory, embracing the headwaters of the Yenisey River, was hitherto unexplored for Odonata, although some Tuvinian specimens were mentioned by Valle (1942), who treated Tuva as part of Mongolia. Earlier we published our own preliminary faunal lists (Zaika & Kosterin 1992; Kosterin & Zaika 2001) and a travelougue (Kosterin & Zaika 2003). *Ophiogomphus spinicornis* was included into the Red Data Book of Tyva Republic (Kosterin 2002). Additionally, four abstracts mentioning some odonate species were published by Zaika (1996, 1999, 2003, 2005). Here, we summarize all knowledge on Tuvinian Odonata.

Material and methods

Geography of Tuva

Tuva is bordered to the north by the West Sayan Mts (altitude up to 2,858 m a.s.l.), to the north-east by the East Sayan Mts (up to 3,044 m), to the west by the Shapshal'skiy (up to 3,201 m) and Chikhacheva (up to 3,278 m) ranges of the Altai Mts. The territory of Tuva lies between 49°45' - 53°43'N and 88°48' - 99°15'E and embraces mountain chains dividing it into several huge intermontane depressions. In the NW, the volcanic Alash Plateau (up to 3,122 m) is adjacent to the West Sayan Range. The Kropotkin Range of East Sayan, eastern border of Tuva, includes two Quaternary extinct volcanoes, the Kropotkin and Peretolchin cones. In the south are the large Tannu-Ola Highlands. This is an east-west oriented mountain system with an almost uneroded and level upper surface of a peneplain type at altitudes of 2,000-2,500 m (up to 2,967 m), a structure explained by its relative geological youth; it restricted drainage from W Mongolia to the Yenisey in the Quaternary (Suslov 1954). In the south-west of Tuva, the Shapshal'skiy and West Tannu-Ola Ranges are connected with the short range of Tsagan-Shibetu (up to 3,577 m). Its highest massif, the Mongun-Taiga, is situated (up to 3,970 m) in the SW corner of the Republic. In the SE, the southern chain of uplands is extended with the Khorumnug-Taiga Range (up to 2,856 m) and the Sangilen (or Sengilen) Highlands (up to 3,276 m). This chain of mountains of South Tuva forms the northern border of the great Ubsu-Nur depression (with a minimum alt. of 750 m at Lake Ubsu-Nur) and is the watershed between the area of outflow to the Northern Ocean and the area of internal drainage. Most of the depression is in Mongolia; only its northern part is in Tuva. The depression is an area of rapid accumulation of fine tertiary and Quaternary sediments (Suslov 1954), thus Lake Ubsu-Nur and its tributary, the Tes Khem River, have no terraces, while small rivers descending from the mountains soon disappear, forming peculiar dry deltas, called 'sairs'. To the north of the Tannu-Ola are two large depressions: the Khemchik depression in the west, which is the Khemchik River catchment basin and descends to 650 m, and the Central Tuvinian depression in the east, which is the Ulug-Khem (Yenisey) River catchment and descends to 527 m a. s. l. These two depressions are divided by the low (up to 1,914 m) range of Adar-Dash. In the north, the small Uyukskiy Range (up to 2,492 m), a spur of the West Sayan, isolates the small Turan depression (descending to 660 m) from the Central Tuvinian depression. In the north, the Turan depression is closed by the Kurtushibinskiy Range, a spur of the West Sayan Range. The Taskyl Range (up to 2,615 m) and the Academician Obruchev Highlands (up to 2,895 m), together with the ranges of the West and East Sayans, embrace the extensive (ca 250 km longitudinally and 70-100 km latitudinally) and thinly populated Todzha depression (descending to 800 m) in the north-east of Tuva. Most of its territory is a hilly elevated plain with a relief of glacial origin, as ca 18,000 years ago it was occupied by a vast (30,000 km^2) glacier (Molokova & Kartashev 1999) and now encompasses numerous lakes. The mountains of eastern Tuva (the Obruchev Highlands, Khorumnug-Taiga Range and Sangilen Highlands), sometimes referred to as the East Tuvinian Highlands, are ancient, whereas the elevations of West Sayan and the Tannu-Ola Highlands are younger. Hence, the isolation of the Todzha depression is of great age (Suslov 1954), reflected in the history of its biota.

The main rivers of Tuva are Biy-Khem, or Bol'shoy [Greater] Yenisey, which has the Todza depression as its catchment basin, and the Kaa-Khem, or Malyy [Lesser] Yenisey, with its catchment basin bordered by the Academician Obruchev Highlands in the north and the Khorumnug-Taiga and Sangilen Mts in the south. These two rivers join at the city of Kyzyl to form the Ulug-Khem, or Yenisey, which flows west and then cuts through a narrow gorge, crossing West Sayan to the north, to leave Tuva. Just before the gorge through the West Sayan, the Ulug-Khem receives water from the Khemchik River flowing north-eastward from the Khemchik depression. The main river of the Ubsu-Nur depression is the Tes-Khem, descending from the western spurs of the Hangai Highlands. Numerous smaller rivers descend from the mountains of Tuva. The largest lakes of Tuva are: Ubsu-Nur (Mong. Uvs-Nor), with only a small NE section belonging to Tuva (and Russia); Tore-Khol' in the south-east, Tere-Khol' in the east; and numerous lakes, of glacial origin, of Todzha: Noyan-Khol', Many-Khol', Kadysh (with an area of ca 2,500 ha each) and Azas, or Todzha-Khol' (5,470 ha). In the Central Tuvinian depression occur the large mineralised lakes Cheder and Khadyn and the freshwater lake Chagytai.

Situated in the centre of Asia, Tuva has a continental climate characterised by a low mean annual temperature (-4°C) and wide daily and annual amplitudes (from +40°C in summer to -54°C in winter). Unless otherwise stated, the climatic data are cited according to Suslov (1954). The Central Tuvinian and, especially, Khemchik depressions reside in the rain shadow of the Altai and the West Sayan Mts, causing low annual precipitation (200-220 mm) (Shaktarzhik 1993). The driest and hottest desert climate, with an annual precipitation of 190 mm, is found in the Ubsu-Nur depression. The climate of the Todzha depression is moderately humid, with an annual precipitation of 343 mm, and an mean annual temperature of 5.5°C. The winter in Tuva lasts for 160-170 days, and is severe and dry. In the mountains, the climate is milder and snow deeper, in the north-eastern mountains the precipitation increases up to 600-800 mm. On the steppes, the spring starts in April and has an explosive character: the difference between mean temperatures of March and April can reach 22°C, with daily fluctuations of 15-20°C. Trees produce leaves mostly in late May. The summer is hot, although frosts may occur throughout. Maximum precipitation occurs in summer, mostly as showers. The autumn starts in late September, when the daily temperature fluctuation may reach 30°C, and mean temperature becomes negative after mid-October.

In Tuva, where Siberia borders on Inner Asia, forest and highland converge with dry steppe. The depressions of Ubsu-Nur and, partly, Central Tuva are occupied by dry steppes, ranging to semideserts and areas of almost unvegetated sand. In the mountains, altitudinal zonation is well marked. The forest belt occupies the greater area but in the south-western mountains it is missing so that the steppes merge directly into highland tundras. In the forest belt, *Larix sibirica* predominates; closer to the tree line, it is admixed with *Pinus sibirica*. The highlands are occupied with different types of mountain tundra and the so-called highland steppes, in the bottoms of cirques there are patches of alpine meadows. In Tuva, the so-called expositional forest-steppe is well represented, with northern slopes covered by forest and southern slopes by steppe. In floodplains of steppe rivers, there are strips of riparian forests dominated by *Populus laurifolia*, *Betula microphylla* and *Salix* spp., with some larch. In contrast to the rest of Tuva, the more humid Todzha depression is mostly occupied by taiga. There are fragmentary steppes and forest-steppes (at 850-900 m), a subtaiga belt of grassy mixed forests of *Betula pendula* and *Larix sibirica* (at 900-110 m), mountain larch taiga (at 100-1,300 m), forests of *Pinus sibirica* (at 1,200-1,700 m) and *Pinus silvestris* L. (at 1,000-1,700 m), and open woodland of *Pinus sibirica*, rarely *Larix sibirica* (at 1,700-1,900 m). Presently the predominating stands at low levels of Todzha are curiously composed of tall *Pinus silvestris* and to some extent *Larix sibirica*, while the dense understorey is provided by young *Pinus sibirica*. In river valleys patches of *Picea obovata* taiga are common. More details are provided by Maskaev et al. (1985).

Collections

This paper is based on adult specimens collected (1) on expeditions by OK in 1990, 2000 and 2004, and (2) by VZ during his hydrobiological exploration of Tuva for ca 20 years. We also examined all available odonate specimens from Tuva in the collection of the Siberian Zoological Museum at the Institute of Systematics and Ecology of Animals of the Siberian Division of the Russian Academy of Sciences in Novosibirsk (SZMN). Most of OK's specimens will be deposited with that institute, while VZ's specimens are kept at his laboratory.

Collecting sites

The collecting sites are denoted by numbers, referred to in the species list and the map (Fig. 1). Administrative designations of sites to "kozhuuns", a local term (of Mongolian origin) for districts, are given. Coordinates and elevations are interpolated from a 1:1,000,000 map or from GPS readings, and are given for the collecting sites rather than for entire lakes, terrains etc. Dates of collecting and collectors' names, if available, are provided.

Turan depression

1. Small lake with ca 50 m in diameter at Arzhaan village (52°03-05'N, 93°41'E, 850 m), Pii-Khem Kozhuun, 25 vii 2004 (A. Saaya).
2. Salt lake Ak-Khol' (52°04'N, 93°43-44'E, ca 800 m): 3.2 g/l of sulphates, 3.5 km^2, 1.5-2 m deep, surrounded with reeds, 6 km E of Arshaan village, Pii-Khem Kozhuun, 25 vi 2008 (VZ).
3. Kislye Lakes (52°01-03'N, 93°44-45'E, ca 850 m): numerous shallow freshwater and brackish lakes in a bogged and slightly saline valley with thickets of *Achnatherum splendens*, Pii-Khem Kozhuun, 22-25 vii 2004 (A. Saaya); 25 vi 2005 (I.I. Lyubechanskii).
4. Turan village (52°08'N, 93°57'E, ca 1,000 m), Pii-Khem Kozhuun, 28 vii 1960 (Ovodov).
5. Uyuk River at Uyuk village (52°04-05'N, 94°01-02'E, ca 800 m) and its floodplain with tussocks and pools from 2-3 m in diameter, Pii-Khem Kozhuun, 04 viii 1949 (Perevozchikova leg., Cherepanov's expedition), 24 vi 2008, 16 vii 2009 (VZ)
6. Uyuk River at Sush village (52°04'N, 94°12-13'E, ca 800 m): 3-5 m wide, 0.5-1 m (to 2 m during floods) deep, silt over shingle, Pii-Khem Kozhuun, 24 vi 2008 (VZ).

Khemchik depression

7. Moraine pools (51°21'N, 89°27'E, ca 1,400 m) 1 km SW of south end of Lake Kara-Khol' or Bai-Taiga on the Alash Highlands, Bai-Taiga Kozhuun, 23 vi - 01 vii 2003 (N. Priidak).
8. Bogs and northern end of Lake Kara-Khol' or Bai-Taiga (51°27'N, 89°29'E, ca 1,400 m), 13 x 2 km, freshwater on the Alash Highlands, Bai-Taiga Kozhuun, 20 viii 2002 (VZ).
9. Monagy River 3-4 km upstream of its mouth to Lake Kara-Khol' (51°29'N, 89°30'E, ca 1,400 m), damp meadow on a slow river reach with beavers present, Bai-Taiga Kozhuun, 08/09 vi 2008 (I. Lyubechanskii, R. Dudko).

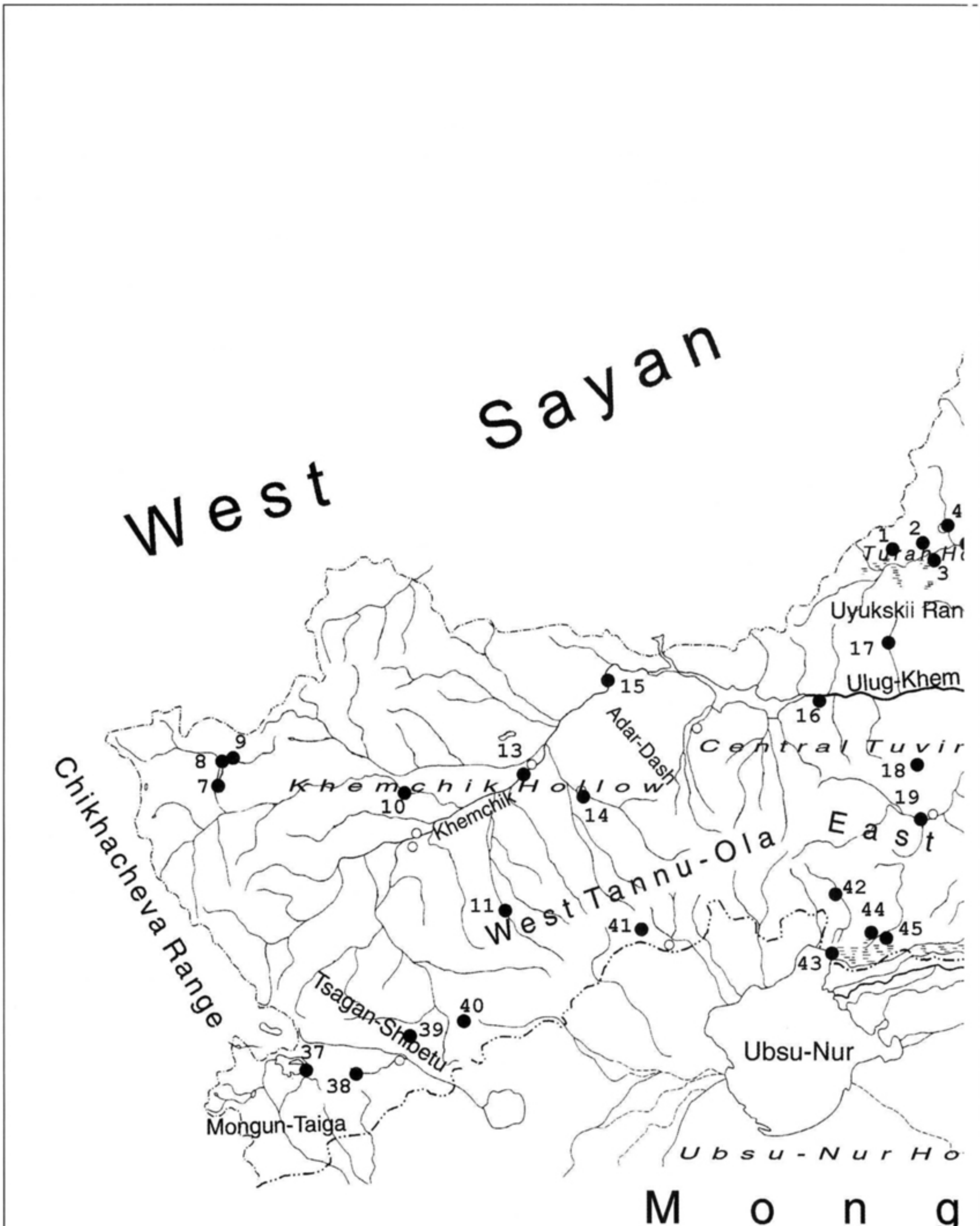
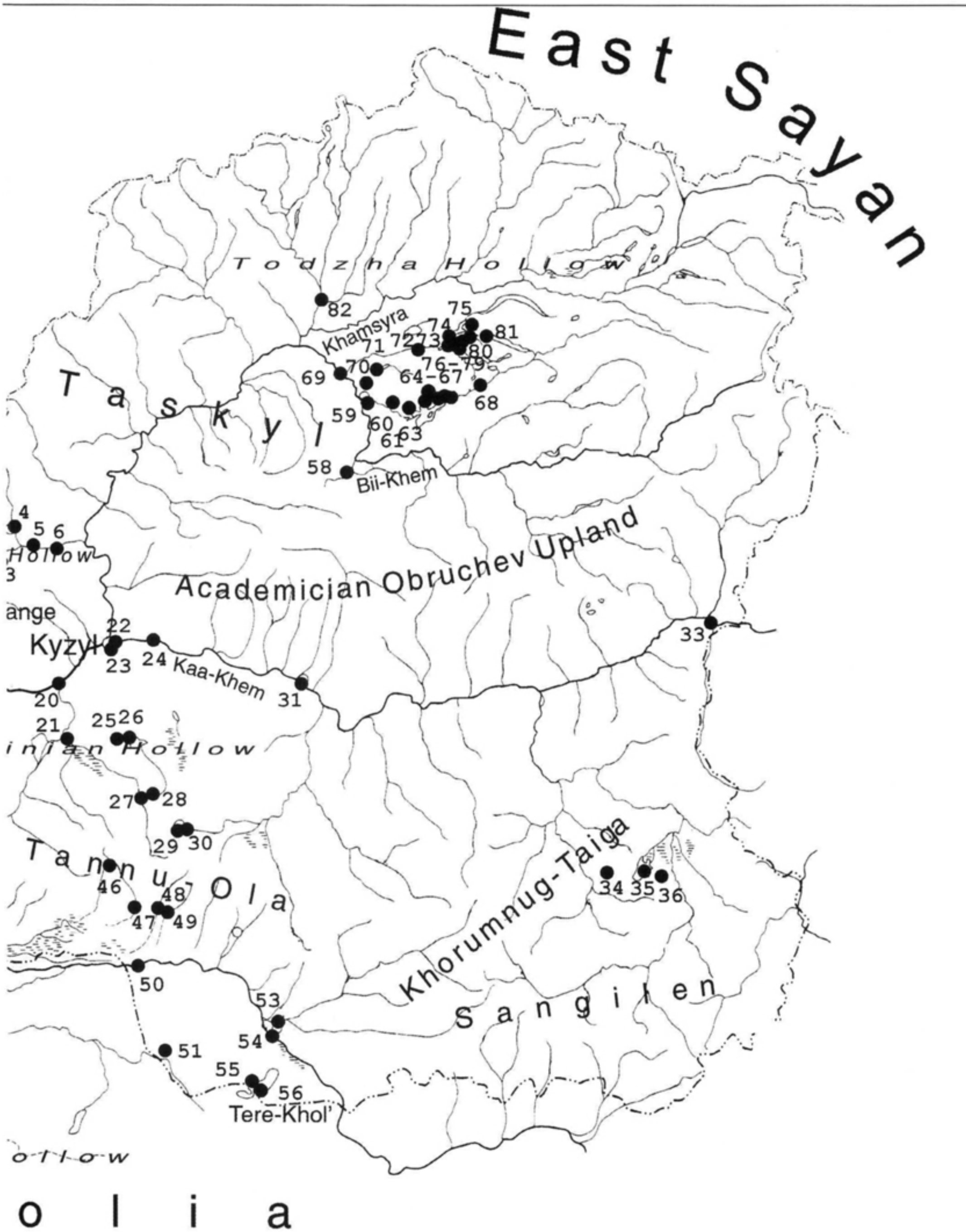


Figure 1: A schematic map of Tuva showing the collecting localities. Names of rivers and the city of Kyzyl are given in Roman script, mountain ranges and uplands with spaced Roman script, intermontane depressions by spaced Italics.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10. Alash River valley where crossed by road Abaza-Ak-Dovurak (51°23'N, 90°33'E, ca 950 m), Barun-Khemchik Kozhuun, 26 vi 2003 (I.I. Lyubechanskii).
11. Eldig-Khem village (50°52'N, 91°07'E, 1,400 m), Dzun-Khemchik Kozhuun, 09 viii 1999 (collector unknown).
12. Khemchik River valley, locality not specified, 25 vii 1963 (L.A. Violovich).
13. Khemchik River, here 50 m wide, at bridge on road to Sut-Khol' (51°22'N, 91°15'E, 723 m), Sut-Khol' Kozhuun, 01 viii 2000 (VZ).
14. Chadan River, right bank, site not specified, probably at Chadan village (ca 51°00'-51°30'N, 91°20'-92°00'E), Dzun-Khemchik Kozhuun, 04 vii 1974 (collector unknown).
15. Khemchik River in its lower reaches at Idig-Khonchu cordon (51°43'N, 91.55°E, 622 m): swiftly flowing in steep gorge between Khor-Taiga and Khemchik Ranges, Chaa-Khol' Kozhuun, 01-04 vii 2004 (OK).

Central Tuvinian depression

16. Small right oxbow of Ulug-Khem (Yenisey) River at the limestone Khayyrakaan Mt. (51°34'N, 93°03'E, 550 m), at the oxbow with *Potamogeton crispus, Sagittaria natans, Persicaria amphibia*, some reeds and abundant *Acorus calamus*, Ulug-Khem Kozhuun, 05 vii 2004 (OK).
17. Mountain slope in Khem-Bazhi valley (51°45'N, 93°30'E) in Bayan-Kol River basin: small mountain rivulet, ca 2 m wide, 0.5 m deep, with a boulder bottom, Kyzyl Kozhuun, 28 vii 1995 (VZ).
18. Brackish lake Kak-Khol' (51°20'N, 93°54'E, 1,100 m): surrounded with moist meadows, where dragonflies emerged, and ploughed fields in a depression within a coniferous forest, Tanda Kozhuun, 09 vii 1994 (VZ).
19. Ulug-Sailyg River headwaters near Khovu-Aksy village (51°06'N, 93°37'E, 1,000 m), the Elegest River basin, a mountain torrent with waterfalls in a taiga-clad gorge, Tanda Kozhuun, 07 viii 1993, 22 vii 1999 (VZ).
20. Ulug-Khem River bank at Ust'-Elegest village (51°33'N, 94°05'E, 600 m), Kyzyl Kozhuun, 02 vii 1965 (collector unknown).
21. Mezhegei River floodplain at Mogai mountain and at Kochetovo village (51°22'N, 94°05'E, 700 m), near its junction with Elegest River: an inundated, small tussock bog on a treeless floodplain, Tanda Kozhuun, 01 v 1995, 03 ix 2000 (VZ)
22. City park of Kyzyl (51°43'N, 94°27'E, 650 m): oxbows on Kaa-Khem River left bank floodplain covered with open riparian poplar forest, Kyzyl Kozhuun, 01 v 1988 (V.K. Zinchenko), 16 ix 1993, 22 viii 1997, 16 vi, 20/21 vii, 10/19 ix, 08 x 1998, 25 vi, 15/19/29 vii, 27 ix 1999, 08 v, 25 vi 2000 (VZ), 09/10 vii 2000 (OK), 19 vii 2000 (VZ), 26 vii 2000 (A. Bosenko), 28/29/31 vii 2000 (OK), 04/05/14 viii, 07 ix 2000, 23 iv, 09/19 v, 22 vi, 19 viii, 16 ix, 06 x 2001, 04 viii

2002, 30 v, 04 vi 2004 (VZ); 22 vi, 06/07 vii 2004 (OK); 16 v, 11/12/16/21 vi, 16/24/27 vii 2009 (VZ).

23. Rivulet Donmas-Sug (51°42'N, 94°27'E, 650 m) flowing within Kyzyl along an ancient bed of the Ulug-Khem under its upper terrace, 2-4 m wide, with a current up to 0.5 m/s, solid banks, grassy or with willow thickets, with some small bogs and open water with reeds on its floodplain springing from ground sources, hence unfrozen in winter, Kyzyl Kozhuun, 16/23 vi, 24/26 viii 1997 (VZ); 29 vi, 07 vii 2004 (OK).
24. Kaa-Khem River floodplain meadow 30 km upstream of Kyzyl (51°38'N, 94°50'E, 650 m), Kaa-Khem Kozhuun, 24 vii 1998 (VZ); 23 vi 2004 (OK).
25. Salt lake Dus-Khol' (51°22'N, 94°22'E, 750 m), Tanda Kozhuun, 21 vii 2000 (collector unknown).
26. Lake Khadyn (51°22'N, 94°27'E, 750 m): brackish, with small reed thickets (more developed at the Khadyn River mouth), Tanda Kozhuun, 20 viii 1968 (Grigoryev), 17 vi 1989, 02 x 1999 (VZ), 18 vi 2003 (A. Saaya), 25/26 vi 2004 (OK).
27. Durgen River floodplain downstream of Durgen village (51°12'N, 94°30'E, 900 m), with small pools, northern slope of the East Tannu-Ola Mts, Tanda Kozhuun, 01 vii 1992 (VZ).
28. Sosnovka village (51°10'N, 94°31'E, 950 m), Tanda Kozhuun, 05 vii 1949 (Cherepanov's expedition).
29. Lake Chagytai (49°58'-51°00'N, 94°41'-94°45'E, 1,004 m): large (6.2 x 6 km) and deep (10-15 m), freshwater, Tanda Kozhuun, 12 vii 1949 (Cherepanov's expedition), 25 vii 1963 (L.A. Violovich), 08 viii 1993, 17 vii 1995, 08 vii 1996, 11 vii 1997, 23 vi 1998,; 03, 22 vii 1999, 21-23/25/27/28 vi, 03 vii 2000, 25 vi 2001 (VZ).
30. Mazhalyg River outflows from Lake Chagytai (51°00'N, 94°45'E, 1,004 m): with sedge, reed and rush swamps, Tanda Kozhuun, 17/23 vi 2000, 17 vi 2004 (VZ).
31. Small rivulet flowing on the Kaa-Khem floodplain and falling into the latter at Saryg-Sep village (52°04'N, 95°33'E, 1,700 m), with grassy banks or with willow thickets, Kaa-Khem Kozhuun, 06 vii 1999 (VZ).
32. Znamenka village(52°04'N, 95°33'E), an old name for Saryg-Sep village Kaa-Khem Kozhuun, 22 viii 1948 (Cherepanov's expedition).

Upper Kaa-Khem River basin

33. Environs of Ush-Beldir village (51°28'N, 98°03'E, 1,200 m), where three rivers, Shishkhid-Gol, Bus and Bilin, join almost concurrently to form the Kaa-Khem River: numerous river arms, oxbows, pools and springs, overgrown with spruce taiga, Tere-Khol' Kozhuun, 13 vii 2008 (VZ).

34. Chergalandy terrain (50°38'N, 97°10'E, 1,400 m) 25 km WNW of Kungurtug village, a brook in a meadow, Tere-Khol' Kozhuun, 27/28 vii 2004. (I.I. Lyubechanskii.)
35. Small lakes along the Lake Tere-Khol' southern bank and Por Bazhin island (50°35-37'N, 97°20-28'E, 1,300 m), with famous Uigur fortress ruins, Tere-Khol' Kozhuun, 28/29 vi 2003 (A. Saaya), 30 vi 2003 (I.A. Artemov), 01/03 vii 2003 (A. Saaya), 29 vii 2008 (VZ).
36. Environs of Kungurtug village (50°36'N, 97°31'E, 1,300 m), steppe, forest edge and river bank, Tere-Khol' Kozhuun, 16 vi 2004. (I.I. Lyubechanskii).

Mongun-Taiga area

37. Eastern bank of the large Lake Khindiktikh Khol' (50°21'N, 89°56'E, 2,305 m), 9 x 15 km, Mongun-Taiga Kozhuun, 24 vii 2000 (VZ).
38. Mongun-Taiga Massif, 15 km SW of Mugur-Aksy village (50°32'N, 90°42'E, 2,500 m), a larch forest on northern slope, surrounded by 'tundrosteppe', Mongun-Taiga Kozhuun, 26 vi 2003 (V.V. Ivonin).
39. Tsagan-Shibetu Range, a road to Mugur-Aksy village (50°25'N, 90°30'E, 2,000 m). 27 vii 2000 (VZ).
40. Barlyk River valley at the Onaacha brook mouth (50°30'N, 90°44'E, 1,715 m), the Kargy River basin, at the border between Mongun-Taiga and Ovyur Kozhuuns, 03 viii 1998, 29 vii 2000 (VZ).

Ubsu-Nur depression

41. 14 km N of Khandagaity village (50°51'N, 92°05'E, ca 1,600 m), stones on mountain top, Ovyur Kozhuun, 25 vii (year and collector unknown).
42. Irbitei River (50°40'-60°00'N, 92°55'-93°10'E), Ovyur Kozhuun, 13 vi, 21 vii 1963 (L.A. Violovich).
43. The northern (Russian) bank of Lake Ubsu-Nur (Uvs-Nor) at the Khoolu River mouth (50°37'N, 93°02'E, 750 m): high reeds and freshwater shallows of otherwise brackish huge lake, Ovyur Kozhuun, 26 vii 1970 (I.B. Knor), 18 vii 1993 (A.V. Barkalov); 15 vi 1995, 20/21 vi 2003 (VZ).
44. Surroundings of Lake Amdaigin-Khol' 4 km W of Ak-Chyraa village (50°42'N, 93°16'E, 800 m), Ovyur Kozhuun, 14/15 vi, 10 viii 1963 (collector unknown), 22 viii 1971 (V. Nikolaev).
45. Marshes 40 km W of Oo-Shinaa settlement (50°47'N, 93°20'E, 770 m), Ovyur Kozhuun, 19 vii 1993 (A.V. Barkalov).
46. Lake Kara-Khool' (50°55'N, 94°18'E, 1,700 m) on the East Tannu-Ola Mts peneplain surface, Tes-Khem Kozhuun, 16 vii 1993 (A.V. Barkalov).
47. Khol'-Oozhu village (50°45'N, 94°25'E, 1,100 m), Tes-Khem Kozhuun, 16 vii 1960 (Cherepanov's expedition).

48. Shiveelig-Khem River valley (50°45'N, 94°33'E, 1,300 m), referred to as "Shivilig-Khem" by Zaika & Kosterin (1992), where it leaves the Tannu-Ola Mts, Tes-Khem Kozhuun, 07 vii 1990 (OK, VZ).
49. Khyralyg-Khem River valley, where it abandons the East Tannu-Ola Range (50°43'N, 94°40'E), 30 km NW of Samagaltai village, Tes-Khem Kozhuun, 23 vi 2001 (P.Ya. Ustjuzhanin).
50. Tes-Khem River, right bank between Shara-Sur and Ak-Erik villages (50°33'N, 94°30'E, 900 m), Tes-Khem Kozhuun, 04 vii 1990 (OK, VZ).
51. Small freshwater lake at southern bank of large bitter-salt Lake Shara-Nur (50°13'N, 94°32'E, 900 m): ca 100 m in diameter, with reed thickets, Tes-Khem Kozhuun, 07/10 vi 1995, 01 vi 2003 (VZ), 03/04 vi 2004 (A. Saaya).
52. Tes-Khem River floodplain (an uncertain locality), 25 viii 1962 (Cherepanov's expedition).
53. Erzin River floodplain at Erzin village (50°15'N, 95°10'E, 1,150 m), Erzin Kozhuun, 10-12 vii 2000 (OK).
54. Tes-Khem River right bank floodplain 5 km SW of Erzin village (50°15'N, 95°06'E, 1,150 m), Erzin Kozhuun, 11/13/16 vii 2000 (OK).
55. The NW bank of Lake Tore-Khol', on some maps Tere-Khol' (50°03'N, 95°00'E, 1,150 m), large, clear and warm freshwater (mineralisation 0.4 g/l) supplied by sand-filtered springs, firm sandy banks with sparse sedge, occasional small reed thickets; some shallow bays with a clayey bottom, submerged *Utricularia* and Charophyta at depth, surrounded by partly overgrown sand dunes, Erzin Kozhuun, 24 vi 1993 (VZ), 12 vii 1993 (A.V. Barkalov), 13/15 vii 1996, 13 vii 1999 (VZ), 15 vii 2000 (OK), 23 viii 2000, 04 vii 2004 (VZ).
56. Sharlan Bay of Lake Tore-Khol', with an aspen grove, surrounded by sands, the point from where the lake is fed by powerful springs, Erzin Kozhuun, 18 vi 1992, 24 viii 1994, 11/12/27 vi 1995, 24 vi, 11 viii 1995, 11 vii 1996, 13 vii 1999 (VZ).

Todzha depression, Todzha Kozhuun

57. "Todzha" (uncertain locality), vi-vii 1962 (collector unknown).
58. Lake Myun-Khol' (52°13'N, 96°00'E, 950 m), rather shallow, ca 3 km in diameter, 10 viii 1961 (Stepanchuk), 12 vii 1998 (VZ).
59. Toora-Khem village environs (52°28'N, 96°08'E, 850-900 m), banks of the Toora-Khem River: current 0.85-1.1 m/s, 10-15 m wide, stony bed, with spruce/larch taiga or grassy clearings, banks overgrown with sedges, 22 vi 1993 (VZ), 20/24/26 vii 2000 (OK); 31 vii 2002 (VZ); 09-11 vii, 02 viii 2004 (OK); 11-17 viii 2004 (A.V. Kuvaev).
60. Lake 4 km E of Adyr-Kezhig village (52°26'N, 96°18'E, 950 m): ca 100 m in diameter, with reed and sedge, 28 vi 1993, 31 vii 2002 (VZ), 09 vii 2004 (OK).

61. Azas tourist base (52°24'N, 96°28'E, 950 m) at Lake Azas (18 x 2 km), mostly 7-8 m deep, in places down to 30 m, mesotrophic, mineralisation by hydrocarbonates 70-80 mg/l, 10°C in May, up to 26°C in July, 27 vi 1987 (V.K. Zinchenko), 10 viii 2004 (A.V. Kuvaev).
62. Lake Nogaan-Khol' (52°25'N, 96°28'E, 950 m), ca 1 km^2, water of a saturated blue-green colour, bottom with a bright-white clay interspersed with broken mollusc shells, surrounded with dense larch taiga, water in late June ca 24°C, 21/24 vii 2000 (OK); 29 vii 2002 (VZ).
63. Krasnyi Kamen' cape environs (52°46'N, 96°33'E, 950 m) on northern bank of Lake Azas, 20/22/26-28 vii 2002 (VZ).
64. Small forest lake (52°27'N, 96°34'E, 950 m), 21 vii 2000 (OK).
65. N and E banks of Lake Azas at Ilgi-chul brook (52°46'N, 96°38'E, 950 m), 26 vi 2000 (A.V. Kuvaev), 21/22 vii 2000 (OK).
66. Swampy oxbow at mouth of Azas River (52°45'N, 96°36'E, 950 m): surrounded by larch taiga, 24 vii 2000 (OK).
67. Small lake at mouth of Azas River (52°44'N, 96°38'E, 950 m): surrounded by boggy *Pinus sibirica* and *Larix sibirica* taiga with *Sphagnum* spp., *Ledum palustre* and *Vaccinium uliginosum* dominating in the ground level, with a quaking bog along banks, 23 vii 2000 (OK).
68. Floodland meadow and taiga on the left bank of the Azas River at '1st hut' cordon (52°28'N, 96°52'E, 980 m), 30 vi 2000 (A.V. Kuvaev).
69. Iy-Khem River at Iy (Pervomaiskoe) village (52°34'N, 96°03'E, 800 m); current ca 0.85 m/s, rather warm, with stony bed and grassy or tussock banks with some willow bushes, 10 vii 2004 (OK), 18 viii 2004 (A.V. Kuvaev).
70. Lake Tonen'koe (52°33'N, 96°12'E, 1,000 m): ca 1.5 x 0.5 km, mesotrophic, with peaty quaking bog around banks,13 vii 2004 (OK).
71. Lake Dorug-Khol' (52°34'N, 96°14'E, 1,000 m): ca 5 x 1.5 km, clear, warm, mesotrophic with *Nuphar pumila*, *Persicaria amphibia*, *Potamogeton natans*; banks firm with some patches of quaking bogs with *Sphagnum* and sedge, 13 vii 2004 (OK).
72. Dus-Khem River between Toora-Khem village and Lake Borzu Khol' (52°38'N, 96°29'E, 1,000 m): 3-4 m wide, fast, with a shingle bed, a lot of *Sparganium* and moss in water, banks with sedge and abundant *Cicuta virosa*, 24/26 vi 1993 (VZ), 13 vii 2004 (OK).
73. Lake Borzu-Khol' (52°37'N, 96°46'E, 1,024 m): ca 2 x 3 km, up to 50 m deep, rather warm but with powerful ice-cold springs at banks, 13/14/17-19 vii 2004 (OK).
74. Lake Shuram-Khol' (52°49'N, 96°48'E, 1,049 m), 7.5 x 2 km, up to 100 m deep, banks with patches of reeds and *Naumburgia*, scarce floating *Persicaria amphibia*, 20 vii 2004 (OK).
75. Lake Izvestkovoe (52°43'N, 96°49'E, 1,049 m): 1.5 x 0.7 km, with limestone cliffs on its W bank, situated N of Lake Shuram-Khol' and connected with it by a river section, 20/21 vii 2004 (OK).

76. Small bog between Many-Khol' and Borzu-Khol' (52°37'N, 96°51'E, 1,071 m), 26 vi 1995 (VZ), 14-22 vii 2004 (OK).
77. Lake Many-Khol' or Manyg (52°33-37'N, 96°51-58'E, 1,071 m): 15 x 3 km, up to 100 m deep, water ca 12°C in late June, along bank some patches of reeds and *Naumburgia*, shallow bays with *Sphagnum* banks and *Potamogeton natans, P. lucens, P. pectinatus, Myriophyllum vulgaris* and *Batrachium* sp., 26 vi 1995; 14-22 vii 2004 (OK).
78. Lakes Ottug-Khol' (52°37-38'N, 96°47-48'E, 1,070 m): two small lakes (1.5 x 0.5 and 1 x 0.35 km) between Lake Many-Khol' and Er-Kara-Khol', with *Potamogeton perfoliatus, P. lucens, Myriophyllum vulgaris*, 16 vii 2004 (OK).
79. Lake Er-Kara-Khol' or Kilovastoe (52°39'N, 96°49'E, 1,067 m): 5 x 0.5-1.2 km, up to 20 m deep, with *Potamogeton perfoliatus, Ceratophyllum* sp., *Myriophyllum vulgaris*, a large patch of reeds at the western end, 18 vii 2004 (OK).
80. Lake Sailyg-Khol' (52°38'N, 96°54'E, 1,050 m): small (600 x 150 m), situated 1.5 km W of Lake Kadysh, brown water, rather stony bottom, although its name means 'Sandy Lake', banks with a border of *Carex* and *Calamagrostis* of varying width, *Persicaria amphibia, Potamogeton praelongus* abundant, *Lemna trisulca* and Charophyta present, *Gammarus* sp. present; without fish, adjacent to a quaking bog with *Carex rostrata* and *Comarum palustre*; 29 vii 2004 (OK).
81. Lake Kadysh (52°36-38'N, 96°56'-97°04'E, 1,050 m), 19 x 1.5 km, up to 120 m deep, studied at its shallow NW bank which has some hydrophytes, of which *Sagittaria natans, Potamogeton natans* and *Batrachium* sp. were most abundant, 25 vii - 01 viii 2004 (OK).
82. Chavash River (52°59'N, 95°52'E, 950 m) at Kyzyl-Khaya River mouth, 24/25 vi 1975 (collector unknown, additional label name "Ni-Bel'dyr" not recognizable), 19 vi 2010 (R. Dudko, I. Lyubechanskii).

Photography

Digital camera Olympus Camedia C8080 was used for the wing photos. Images of anal appendages were obtained with the stereomicroscope Stemi 2000-C and a digital camera AxioCam MRc5 (Zeiss). To improve the focus, serial photographs were treated with the program Helicon Focus 3.1 [http://helicon.com.ua/helicon-focus/].

Quantitative parametres for fauna analysis

Jaccard coefficient, *S*, was used as a measure of similarity of faunas. For the faunas of two regions, A and B, it is as follows:

$S = n\ (A^{\vee}B)\ /\ n\ (A^{\wedge}B)$

where n ($A^{\vee}B$) is the number of species found in both regions A and B and n ($A^{\wedge}B$) is the number of species found in any of the regions A and B.

Efficiency of biogeographical barriers between two adjacent faunas, in our case mountain systems, was measured as the efficiently coefficient $E = 1 - S$ (Sergeev 1986).

THE SPECIES

In total, 47 species were recorded. The flying season of each species is given after the localities. Anecdotal phenological data are presented in brackets.

ZYGOPTERA: CALOPTERYGIDAE

Calopteryx splendens (Harris, 1780)

Localities: 59, 69, 72, 74, 77; 26 June - 01 August.
Distribution and habitat: Only in Todzha depression; abundant on small rivers and the river section joining lakes Shuram-Khol' and Borzu-Khol' but never found at the major Biy-Khem River (Great Yenisey). Solitary individuals were rare at large lakes (locs 74, 77). On 12 vii 2004, at loc. 59, 42-46 males were counted at a 85 m long right bank section of Toora-Khem River (current ca 0.85 m/s), on 02 viii, only two males on this section.
Remarks: The populations in Todzha were remarkable for a discontinuous polymorphism in wing coloration (Fig. 3). For simplicity, the male and female morphs were designated with letters. About half the males (42 of 91 males collected; 46%) had a dark band occupying most of the wing area, starting at about midway between the arculus and nodus and leaving the tips transparent for 1.5-3 mm (morph A, Fig. 3a). In other males (49; 54%), the band was substantially extended at both sides, starting about the nodus and covering the wing tips, or leaving a hardly noticeable transparent zone at the fore wing tip as in the figured specimen (morph B, Figs 2a, 3b). Of 31 females collected, 17 (55%) had hyaline wings (morph C, Fig. 3c), while 14 were androchromic, with most of the wing area occupied by a smoky-brown band with the veins bluish iridescent, although more weakly so than in males. These androchromic females in turn were represented, in about equal proportions, by two distinct morphs: eight females (26%) had both fore wing and hind wing coloured to their apices (morph D, Figs 2b, 3d), and six (19%) had a gradual lightening of the fore wing to its apex (morph E, Fig. 3e). In male morph A, there was some variation in the width of the hyaline zone at the wing tip. In male morph B, a faint transparent border sometimes occurred at the fore wing apex: just 1-3 marginal rows of small cells were lighter so that it was hard to see if the tip had the transparent margin or not. In female morph E there was a slight variation in the degree of lightening in the fore wing. Nevertheless, all the morphs were distinct, so that each specimen could be classified unambiguous-

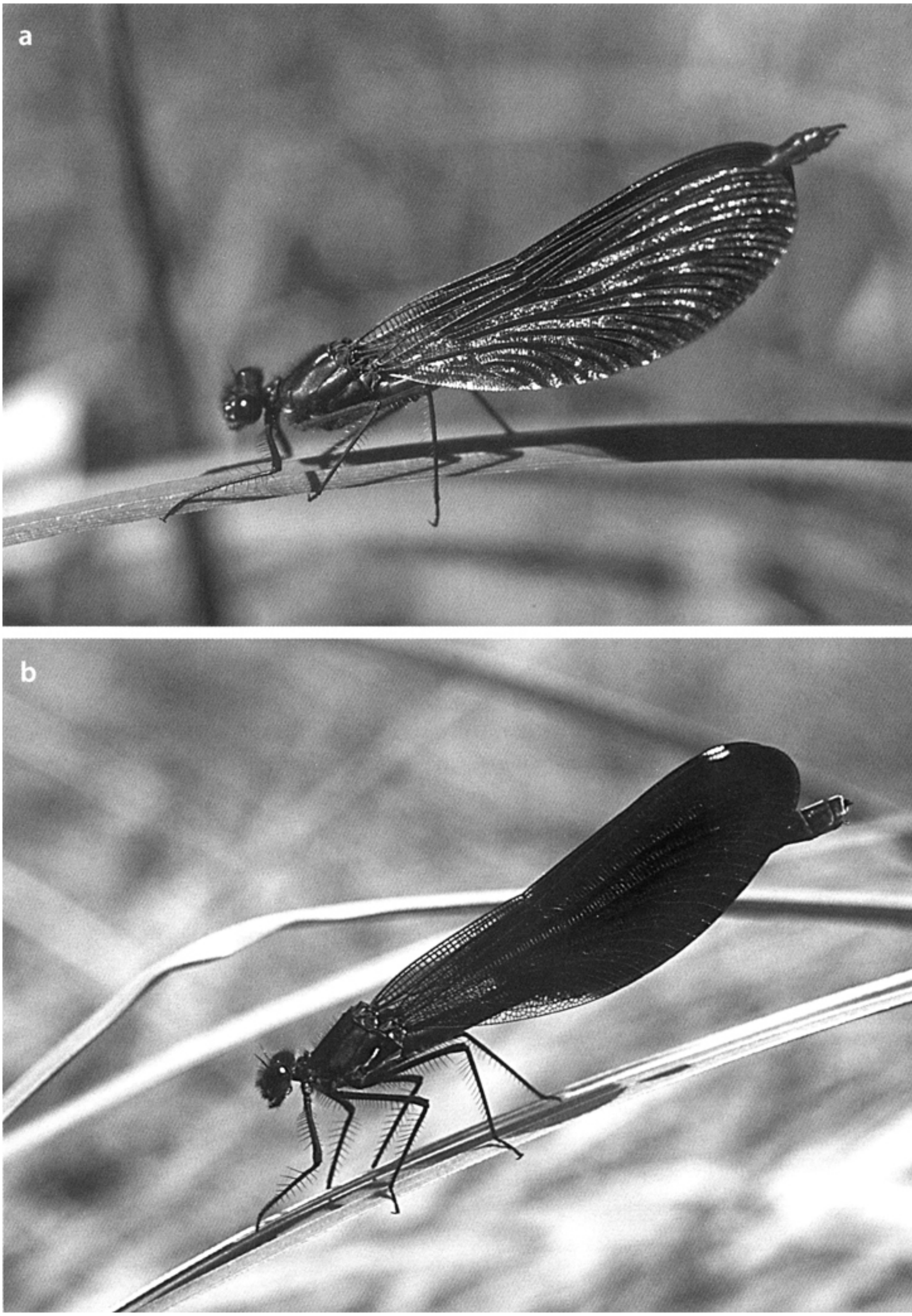

Figure 2. *Calopteryx splendens* — (a) ♂ of morph B, from the Toora-Khem River (loc. 59), 11 July 2004; (b) androchromic ♀ of morph D, from the Iy-Khem River (loc. 69), 10 July 2004. Photos by OK.

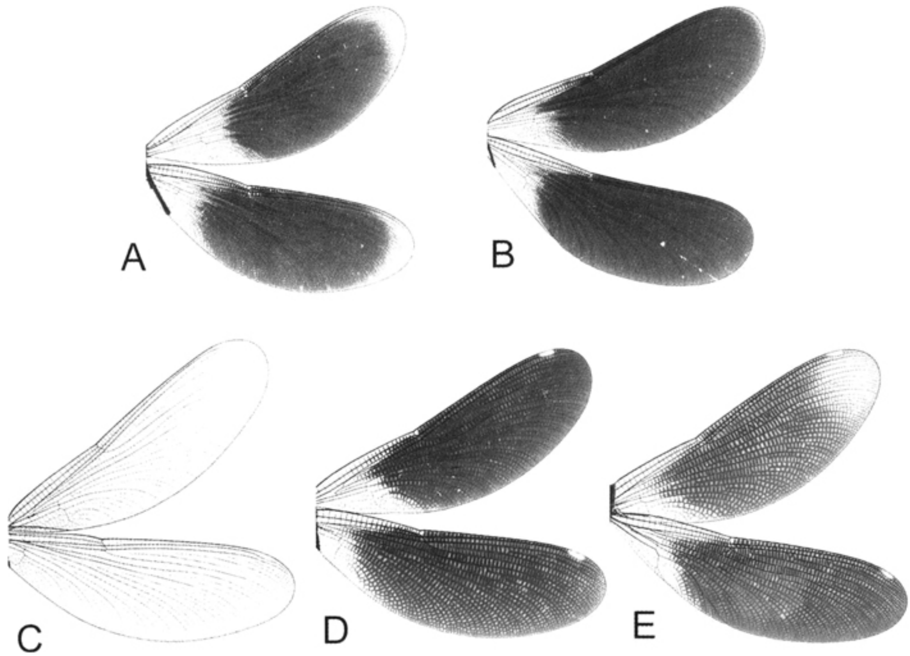

Figure 3: Polymorphism of wing coloration in the *Calopteryx splendens* population of the Iy-Khem River (loc. 69) — (a) male morph A; (b) male morph B; (c) female morph C; (d) female morph D; (e) female morph E.

ly. Visual observations of many more individuals in nature supported the distinctness of these two male and three female morphs, suggesting they are determined by alleles of one to three loci. All these morphs have been also recorded in West Siberia. The anomalous male morph B and female morphs D and E were found at comparably high frequencies in Bakchar District of Tomsk Province (Bernard & Kosterin 2010), at moderate frequencies in Omsk, and scattered in Altaiskiy Kray and Kemerovo Province but never at Novosibirsk (OK unpubl.). Distribution, frequencies and taxonomical history of wing coloration morphs of *C. splendens* in Siberia will be considered in detail elsewhere.

Lestidae

Lestes barbarus (Fabricius, 1798)

Localities and specimens: loc. 3: 22 vii 2004 – 1 ♀.
Distribution and habitat: The first published record for Tuva; probably a rare species confined to northern Tuva.

Lestes dryas Kirby, 1890

Localities: 3, 16, 23, 26, 33, 35, 45, 54, 58-60, 68, 73, 77, 78, 81; late June - mid August.

Lestes macrostigma (Eversmann, 1836)

Localities and specimens: LOC. 26: 02 ix 1999 – 1 individual observed by VZ on the eastern bank of Lake Khadyn.
Distribution and habitat: Recorded at mineralised water preferred by the species. A female was collected in Mongolia almost immediately south of Tuva, on Lake Ubsu-Nur southern bank, 17 vi 1995 by A.V. Zaika and VZ.

Lestes sponsa (Hansemann, 1823)

Localities: 1, 3, 8, 12, 16, 22, 23, 29, 32, 35, 43, 44, 48, 50, 51, 53-55, 59, 60, 64, 66, 71, 78, 80; late June - late August.

Sympecma paedisca (Brauer, 1877)

Localities: 1, 3, 5, 6, 7, 21, 22, 29, 44, 51, 54-56, 60; late April - late August.
Distribution and habitat: Common. Imagines appeared after hibernation in early spring, and occurred throughout the warm season; at loc. 22, earliest record of hibernated individuals on 23 iv 2001, latest record of individuals of the new generation on 24 viii 1994. In the Ubsu-Nur depression, earliest newly emerged individuals on 13 vii 2000 at loc. 54 and latest record on 22 viii 1971 at loc. 44.
Remarks: Our Tuvinian collection shows variation in integrity versus fragmentation of the bronze stripe of the 1st suture of the pterothorax. Preliminary data from loc. 22 pointed to strong fluctuation of frequency of its fragmentation in different generations, that may suggest dependency on conditions during larval development, but larger samples are to be analysed to prove these fluctuations.

COENAGRIONIDAE

Coenagrion armatum (Charpentier, 1840)

Localities: 23, 29, 55, 56, 59; mid June - late July.

Coenagrion ecornutum (Selys, 1872)

Localities: 14, 22, 23, 42, 43, 53, 54, 55, 56; 12 June - 29 July.
Distribution and habitat: More or less common on medium-sized, small stagnant waters in river floodplains but less frequent than *C. lanceolatum*. Quite abundant at small bogs of loc. 56 at large Lake Tere-Khol'. Not found in Todzha.

Coenagrion hastulatum (Charpentier, 1825)

Localities: 3, 33, 59, 67, 71, 77, 78; late June - early August.
Distribution and habitat: Found in Turan and Todzha depressions and at the Kaa-Khem sources (loc. 33), this species seems to be confined to taiga regions in Tuva. This suggests an ecological segregation with the closely allied species *C. lanceolatum*, which is confined to waters in steppe depressions.
Remarks: In one male from Todzha the lateral black streaks on S2 were fused with the mushroom-shaped spot.

Coenagrion hylas (Trybom, 1889)

Localities: 5, 53, 59, 82; 19 June - 28 July.
Distribution and habitat: Found in Turan, Todzha and Ubsu-Nur depressions, indicating a broad ecological tolerance; not found in the Central Tuvinian depression so far. In all cases it was recorded, quite abundantly, on oxbows and swamps at river banks, sometimes ice-cold owing to bottom springs, surrounded by arboreal vegetation: spruce/larch taiga in Todzha and Turan depression and poplar riparian wood in Ubsu-Nur depression. At loc. 59 a male was observed to attack a passing male *Calopteryx splendens*.
Remarks: The species was subdivided into a number of subspecies (see Belyshev & Haritonov 1974), which were synonymised by Lohmann (1992).

Coenagrion johanssoni (Wallengren, 1894)

Localities: 59, 67, 71, 72, 77, 78, 80, 82; 19 June - 29 July.
Distribution and habitat: This species, generally confined to the forest zone, was found only in Todzha, where it occurred at smaller lakes, bays of major lakes, mostly at *Sphagnum* and sedge bogs. Adults occurred at water and penetrate into open taiga and thickets of *Ledum palustre* and *Vaccinium uliginosum*. At the same time they were abundant around firm grassy lake banks at loc. 71.
Remarks: Belyshev (1955) described a subspecies *Agrion concinnum bartenevi*, with the lateral black streaks on S2 reaching its hind margin in males being the only diagnostic character. This subspecies was proposed to range "east of Altai and the Yenisey" (Belyshev 1973b: 539). In all but one of our males these streaks reached the hind margin of the tergite with a narrow anastomosis. However, this character, seemingly discontinuous, in fact just reflects extension of the black markings, which may exhibit a cline, with darker forms toward the east. Later Lohmann (1992) synonymised all the subspecies described within the species to restore its monotypical status, and this seems to be correct.

Coenagrion lanceolatum (Selys, 1872)

Localities: 16, 22, 29, 51, 54; late June - early August.

Distribution and habitat: Found in the Ubsu-Nur and Central Tuvinian depressions. Quite common on small and very small pools in river floodplains.
Remarks: Belyshev (1973b: 557) considered this species to range westwards to the Yenisey. Recently, it was reported from Guryevsk town in Kemerovo Province (Dronzikova 2000) and from a small lake in Artybash at the very bank Lake Teletksoe (M.V. Dronzikova pers. comm.). At the same time, Malikova (1995) has shown that the related *C. hastulatum* ranges eastwards to the Pacific and not to the Baikal - Zhigansk line, as Belyshev (1973b: 553) believed, although it is rare east of the Yenisey. Thus, these two related species tend to replace each other on opposite sides of the Yenisey but never completely. East of the river, *C. hastulatum* is more frequent in the north, e.g. in Yakutia. The localities considered here lie near the Yenisey, but all but one (loc. 3) localities where the 'western' *C. hastulatum* occurred are situated to the east of of all localities where the 'eastern' *C. lanceolatum* was found.

Coenagrion lunulatum (Charpentier, 1840)

Localities: 3, 5, 7, 9, 16, 23, 26, 45, 46, 51, 53, 55, 56, 59, 60, 71, 77; early June - late July.

Enallagma cyathigerum cyathigerum (Charpentier, 1840)

Localities and specimens: loc. 60: 09 vii 2004 – 2 ♂, 28 vii 1993 – 1 ♂ (teneral), 31 vii 2002 – 4 ♂ 1 ♀; loc. 62: 21 vii 2000 – 1 ♀; 29 vii 2002 – 6 ♂; loc. 63: 22 vii 2002 – 1 ♂; loc. 64: 21 vii 2000 - 1 ♂; loc. 68: 30 vi 2000 – 1 ♂; loc. 70: 13 vii 2004 – visual; loc. 71: 13 vii 2004 – 36 ♂, 4 ♀; loc. 73: 14 vii 2004 – visual; loc. 74: 20 vii 2004 – 5 ♂; loc. 75: 20 vii 2004 – visual; loc. 77: 14 vii 2004 – 3 ♂; loc. 78: 16 vii 2004 – 1 ♂; loc. 79: 18 vii 2004 – visual; loc. 80: 29 vii 2004 – 13 ♂, 3 ♀; loc. 81: 25 vii 2004 – 9 ♂, 2 ♀.
Specimens intermediate with *E. c. risi*: loc. 1: 25 vii 2004 – 5 ♂ like *E. c. cyathigerum*, 1 ♂ intermediate; loc. 3: 22 vii 2004 - 3 ♂ like *E. c. cyathigerum*, 4 ♂ intermediate; loc. 34: 27-28 vi 2004 – 1 ♂ intermediate, 4 ♀; 02 viii 2004 – 1 ♀; loc. 35: 30 vi 2003 – 2 ♂ like *E. c. risi*, 1 ♂ intermediate, 2 ♀; 29 vii 2008 – 10 ♂ intermediate, 1 ♀; loc. 36: 16 vi 2004 – 9 ♂ intermediate, 5 ♀.
Distribution and habitat: *E. c. cyathigerum* occurred in Todzha, a humid taiga region. The somewhat more arid Kaa-Khem upper basin (locs 34, 36) and the Turan depression were occupied by populations intermediate with subspecies *risi*.

In Todzha, *E. c. cyathigerum* occurred at rather small forest lakes and around banks of large lakes, where it was not abundant. In Tomsk Province (Bernard & Kosterin 2010), S Yakutia (Kosterin 2004b) and Kamchatka (Dumont et al. 2005), it also regularly inhabited small boggy pools or oxbows surrounded by forest, whereas subspecies *risi* prefers other habitats all over its range (see below).

Remarks: In all males from Todzha the structure of the superior appendages corresponded to that of the nominotypical subspecies: a yellow lobe is directed behind the black tooth (Fig. 4a) and, in lateral view, protrudes as a 'nose' (for SEM photos see Stoks et al. 2005). A proportion (five of 13; 40%) of males from Turan depression and most (21 of 23; 90%) from the upper Kaa-Khem basin had appendage morphology intermediate to *risi*, which has the yellow lobe protruding inwards beneath the black tooth (Fig. 4c; see also Seidenbusch 1997c; Kosterin 1999, 2004; Stoks et al. 2005). In these intermediate specimens, the lobe protruded somewhat behind the tooth and inward beneath it, best seen from above (Fig. 4b).

Specimens collected in Todzha demonstrated a variable expression of lateral melanisation of the abdomen. S3-S4 had long stripes, while on the following segments the black dorsal markings at their hind margins had acute forward-directed projections along the sides. On S2 and S9 were lateral streaks. This melanisation was in most cases very imperfect: the stripes and streaks often had indistinct margins and were brownish rather than black. Only in specimens with maximum melanisation, did the additional stripes and streaks appear as distinctly as the regular markings, which then resembled the pattern of *C. hylas*. Populations of *E. c. cyathigerum* with dark lateral stripes on the abdomen have a complicated taxonomic history in Russian literature, which will be outlined elsewhere, whereas in Europe, variability of black markings was never interpreted in terms of taxonomic differences (Dijkstra & Lewington 2006). Most probably, melanisation is a response to harsh climatic conditions, probably associated with prolonged larval development (Dumont et al. 2005). In Todzha, most of females were grey coloured, only at Lake Kadysh a female with some blue on the ground colour was collected.

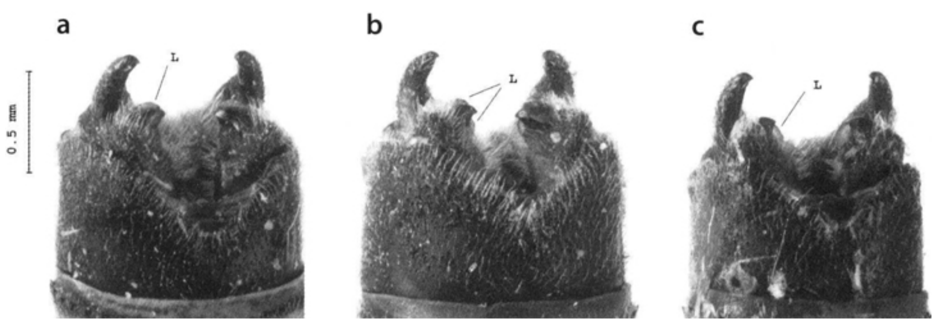

Figure 4: Structure of male anal appendages in *Enallagma cyathigerum*, dorso-lateral view — (a) *E. c. cyathigerum*, loc. 71, Todzha depression, 13 vii 2004 (OK leg.); (b) specimen intermediate between *E. c. cyathigerum* and *E. c. risi*, loc. 35, the Kaa-Khem River upper basin, 30 vi 2003 (I. Artemov leg.); (c) *E. c. risi*, loc. 26, Central Tuvinian depression, 25 vi 2004 (OK leg.). 'L' indicates the position of the yellow lobe on the superior appendages.

Enallagma cyathigerum risi Schmidt, 1961

Localities: 2, 16, 18, 22, 23, 25-31, 42-45, 54-56; 12 June - 24 August.
Distribution and habitat: The taxon *risi* was widespread in the Ubsu-Nur and Central Tuvinian depressions. It was also found in the Turan depression but was completely absent from the Todzha depression, where only ssp. *cyathigerum* occurred. *E. c. risi* inhabited rather large lakes with clear water surface and open banks, both freshwater and brackish. Among freshwater lakes, it appeared especially abundant at the large Lake Tore-Khol' (locs 55, 56) and oxbows of the Kaa-Khem River (loc. 22). However, in brackish lakes these damselflies attained enormous abundance, with several males perching on each stem of grass along the shoreline. This was also true in the less mineralized part of Lake Khadyn at the Khadyn River mouth (at loc. 26), where numerous larvae were found among reeds.

Curiously, a tandem in which a male *E. c. risi* grasped a male *E. najas* was observed at loc. 22.
Remarks: All specimens from the Central Tuvinian and Ubsu-Nur depressions had *risi*-typic superior appendages. Typical *risi* were found in the Turan depression at a salty lake of loc. 2, whereas at the freshwater lakes of locs 1 and 3 the males had the superior appendages either of the typical shape of *cyathigerum* or intermediate with *risi*. This pattern provides evidence that in Tuva, the two taxa differ not only morphologically but also in the extent of their ecological tolerances: *risi* is able to develop in both brackish and fresh water, whereas *cyathigerum* needs fresh water. So in the contact zone, brackish lakes are occupied by genetically pure *risi*, and in fresh water intergradation occurs. Occurrence of *E. c. risi* around large lakes, both brackish and freshwater, has been also recorded in the West Siberian Plain (Kosterin et al. 2001; Bernard & Kosterin 2010; OK unpubl.) and Transbaikalia (Kosterin 1999, 2004a). Ecological segregation in freshwater habitats between *E. c. cyathigerum* (small pools in *Sphagnum* bogs) and *E. c. risi* (large ponds) was recorded in Tomsk Province (Bernard & Kosterin 2010).

The existence of individuals intermediate with *cyathigerum* (Fig. 4b) in the Turan depression and their prevalence in the Kaa-Khem River upper basin tend to support the subspecific status of *risi* and not its status as full species, as suggested by Stocks et al. (2005). Such intermediate specimens are also known from wooded and rather humid mountain systems protruding into semiarid plains occupied by *risi*, namely Middle Ural, Altai, the mountainous regions of Irkutsk Province (Kosterin 1999, 2004a), and also from Amur and southern Khabarovskiy Kray Provinces (E.I. Malikova pers. comm.). Furthermore, intermediate specimens were also found in the vast bogs in Tomsk Province (Bernard & Kosterin 2010). Analysis of 18 S rDNA and intergenic spacers 1 and 2 by Samraoui et al. (2002) also suggests a subspecific status for *risi*. It was recently shown (Stoks et al. 2005) that the structure of the superior appendage, characteristic of sspp. *cyathigerum* and *risi* and also found in the North American species *E. annexum* (Hagen, 1861) and *E. vernale* Gloyd, 1943 (the '*cyathigerum*-type') and *E. boreale* Selys, 1876 (the '*risi*-type'), independently evolved at least twice, since the common ancestor of the Palaearctic and Nearctic lineages should have a different appendage shape. This striking fact suggests plasticity of certain of these structures, which may revert to some plesiomorphic states when specific genes are switched off. In this way both of these two structural types could appear in Eurasia in the pair of taxa, *cyathigerum* and *risi*, which had not yet diverged sufficiently to become full species. Structurally homogenous *risi* ranges in arid and semiarid zones of the Palaearctic from the Volga River to the Da Hinggan Ling Mts (Kosterin 1999, 2004a).

Erythromma najas humerale (Selys, 1887)

Localities: 22, 54; 16 June - 04 August.
Distribution and habitat: Occurs in the Central Tuvinian and Ubsu-Nur depressions. Habitat as in the nominotypical subspecies. Not found at Lake Tore-Khol' (locs 55, 56), most probably due to the scarce floating vegetation. It occurred in the floodplains of the major rivers Kaa-Khem (loc. 22) and Tes-Khem (loc. 54) at relatively large oxbow lakes fed with ice-cold ground springs.
Remarks: A majority of males from loc. 22 (32 of 41; 78%) and all four males from loc. 54 had light antehumeral stripes on the mesepisternum reaching ca 1/3 - 1/2 of its length. In five males from loc. 22, they occupied ca 1/4 of the mesepisternum length, in two less than 1/5, and in one they were totally missing. The inner sides of the femora and tibiae had yellow stripes extending for some distance but were interrupted in the distal part of the femora. This interruption was on average smaller than in specimens of *E. n. najas* from Todzha. In one male from loc. 54 the yellow stripes were wide and almost continuous. In females, the light antehumeral stripes on the pterothorax were present and complete in all specimens from loc. 22, in three specimens they were very wide, ca 2/3 of the width of the black stripes bordering them. In one of these females, there was also a pair of tiny, light, oval spots on the upperside of the head, as in *Paracercion calamorum* (Ris, 1916); analogous spots in *E. najas* were reported and figured from Amur Province by Malikova (2002). In 42 male specimens from loc. 22, the abdomen length varied within 24-29 mm but the values 24, 25 and 29 mm were exhibited by just one specimen each (mean 27.27, s.e. 0.24).

The taxon *humerale*, described as a species and thought to replace the typical *najas* east of the Lake Baikal area, has usually been considered as a subspecies of *E. najas*, but recently its species rank has been restored by Malikova (1995 and pers. comm.) and some Japanese authors (e.g. Inoue & Tani 2003). Malikova (1995) based her opinion on the presence of yellow antehumeral stripes in males (although variable in expression), a smaller size and, mostly, on differences of a quantitative nature in larval morphology. The antehumeral stripes and a greater expression of yellow colour on the legs were specified by Belyshev (1964a, 1973b: 583) as diagnostic features of ssp. *baicalense* Belyshev, 1964, described from Irkutsk Province (as *baicalensis*), with these diagnostic characters: "antehumeral stripes usually incomplete, quite a lot of yellow on inner surface of femora and tibia." In contrast, *humerale* sensu Belyshev (1964a: as *humeralis*) "stripes complete, inner surface of femur and tibia completely yellow" was considered by him to occur in the Far East. In fact, the name *baicalense* Belyshev is a synonym of *humerale* Selys, since the holotype of the latter originated from Irkutsk and not from the Far East, as Belyshev thought, so both taxa have not only a similar appearance, but also the same type locality (Malikova 1995). The reasons for separating *humerale* and *najas* at the species level are unconvincing. The range of these damselflies in Siberia is continuous and there is no report from anywhere in Central Siberia of a sympatric coexistence of two forms with any correlated characters. As far as imagines are concerned, there seems to be an easterly directed cline of expansion of the yellow colour on the legs, and of the frequency of occurrence and degree of development of the antehumeral stripe. Apparently, Belyshev (1964a) was aware of this trend, when he described *baicalense* as an "intermediate subspecies". Whether this expansion of yellow colour in males in more arid regions is genetically or environmentally determined is a matter for special investigation but since the general cline in Eurasia is mostly longitudinal rather than latitudinal, the former supposition seems more likely.

The antehumeral stripes were also variable in specimens from SE Transbaikalia: among 36 males examined, in eight they were present and continued throughout the length of the synthorax, in 26 they were expressed only in the first half of the front side of the synthorax, in one they were vestigal, in one absent, as in the typical *najas* (Kosterin 1999, 2004a). Specimens of *E. n. najas* from Todzha, mostly without antehumeral stripes, and those of *E. n. humerale* from loc. 22 in the Central Tuvinian depression, all but one with stripes, showed no sign of any significant difference in size; the samples are small but the ranges of variation in abdomen length almost entirely overlap. In general, the Central Tuvinian specimens of *E. n. humerale* were indistinguishable from the Transbaikalian ones. However, it is interesting to note that, again, Todzha appeared to shelter a population of *E. n. najas*, with a more 'western' appearance, while specimens from Central Tuva belong to the more 'eastern' subspecies *E. n. humerale*.

Erythromma najas najas (Hansemann, 1832)

Localities: 59, 60-62, 65, 68, 71, 72, 78; 24 June - 28 July.
Distribution and habitat: The nominotypical subspecies was found only in the Todzha depression. It was abundant at smaller lakes (locs 62, 78) and at the mesotrophic large lake Azas (locs 61, 65) but absent at oligotrophic large lakes (e.g. locs 73, 77, 81). Males were usually found on floating vegetation.

Remarks: 14 of 16 studied males had no light antehumeral stripes on mesepisternum, as it should be in the nominotypical subspecies, one had the stripes ca half the length of the mesepisternum and one ca one quarter the length. In 12 male specimens available for measurements abdomen length varied within 26-28 mm (mean 27.02, s.e. 0.15).

Ischnura elegans (Van der Linden, 1820)

Localities and specimens: loc. 43: 15 vi 1995 - 3 ♂; loc. 55: 15 vii 2000 – 1 ♂.
Distribution and habitat: A trans-Eurasian species becoming quite rare from Central Siberia and further east (Malikova 1995).

Ischnura pumilio (Charpentier, 1825)

Localities and specimens: loc. 10: 26 vi 2003 – 1 ♂ ; loc. 23: 29 vi 2004 – 1 ♀.
Distribution and habitat: The first reliable record for Tuva.The male was the only odonate collected on a damp meadow at loc. 10 as high as 950 m.
Remarks. This elusive species has so far been recorded from Siberia only in Altaiskiy Kray (Belyshev 1973b: 598), North Altai (Kosterin 1987) and at Novosibirsk (OK unpubl.).

ANISOPTERA: Aeshnidae

Aeshna affinis (Vander Linden, 1825)

Localities: 48, 54; (mid July).

Aeshna caerulea (Ström, 1783)

Localities: 38, 46, 76, 78, 81; late June - mid August.
Distribution and habitat: The first published record for Tuva. Recorded in a mountain taiga environment in the southern mountains (Mongun-Taiga massif and West Tannu-Ola Range) and found to be common in Todzha, where this environment predominates, inhabiting small pools (tens of metres) with *Sphagnum* banks (often quaking bog) surrounded by taiga; occurred also at sedge bogs in larger glades.

In contrast to larger aeshnid species, males of *A. caerulea* behaved as perchers rather than fliers: active individuals perched at sunshine on logs and tree trunks but did not exhibit perch fidelity (at a taiga pool near loc. 81). The same was observed by OK also in the Altai Mts in East Kazakhstan at an ancient moraine pool (49°06'N, 85°58'E, 2,050 m, 27 vii 2010): at high noon and in sunshine two males perched on a few large boulders at the pool bank, again showing no perch fidelity. Like a tyical percher, they took off when another male or other dragonfly passed by, then patrolled slowly over the water and along the banks for 0.5 - 1 min, finally landing on a boulder and perching until disturbed again. *A. caerulea* was repeatedly observed to perch readily (Dumont et al. 2005; Corbet & May 2008) but there were doubts if the observed individuals were active or resting (Corbet & May 2008). In this study, both in Tuva and Altai, perching behaviour was observed in active males. Being a percher was unexpected for an *Aeshna* (Corbet & May 2008), but is congruent with the facts that *A. caerulea* (1) is smaller than other northern Aeshnids, although retaining the *Aeshna* body build, and (2) lives in the coldest conditions. Thus it may face a problem of endogenic heating being insufficient for continuous flight, rather than of overheating.

Aeshna crenata Hagen, 1856

Localities: 54, 59, 63 (a small bay), 67, 69-71, 73, 75, 77, 79-82; late June - (early August).
Distribution and habitat: Abundant in a wooded floodplain of the Tes-Khem in the Ubsu-Nur depression, common in Todzha, bred at various lakes. Patrolling males and oviposition was also observed at the small Iy River (loc. 69) in Todzha. Both sexes may exhibit swarming feeding flights beyond the lakes. At loc. 77, a late teneral individual was seen on 14 vii 2004.
Remarks: The females collected were characterised by strongly developed infuscation of the wings, slight infuscation was also noticed on the wings of males from Todzha. This coloration become more pronounced in the eastern range of this species prompting Belyshev (1967) to describe ssp. *wnukowskii*, ranging, according to its author, east of the Yenisey. Belyshev (1967) stated that dark-winged individuals, mostly females, sometimes occur in the west as well, and light-winged ones, mostly males, in the east. It seems that the frequency and degree of development of the dark coloration gradually increase as an easterly cline so that it is impossible to define the border between the subspecies in either a geographical or taxonomic sense and that the subspecies name cannot be supported.

Aeshna grandis (Linnaeus, 1758)

Localities: 21, 22, 59, 60, 62, 65, 69, 72, 73, 75, 78-81; late June - mid September.

Aeshna juncea (Linnaeus, 1758)

Localities: 11, 17, 19, 21-24, 33, 35, 41, 43, 54, 55, 58, 62, 63, 65-67, 71, 77-81; mid June - early September.
Distribution and habitat: A common widespread species. On large lakes, as a rule, it is less abundant than *A. crenata* which excludes it (Belyshev 1973b: 421; Bernard & Kosterin 2010), however, in Todzha these two species were observed in about equal numbers at the large Lake Kadysh (loc. 81). In the large right bank of the Tes-Khem floodplain (loc. 54), which includes a variety of water bodies, both

species also occurred in abundance. In Todzha, the preferred habitats were *Carex rostrata* bogs, with *Comarum palustre* and/or *Menyanthes trifoliata*, where several patrolling males and some ovipositing females were invariably observed, but it occurred there also at pools of *Sphagnum* bogs and along the banks of major lakes. *A. juncea* may ascend the valleys of mountain rivers to their headwaters: at loc. 19 on 22 vii 1999, at 1,000 m, VZ observed a swarm of ca 20 individuals, mostly females, flying at the level of the top of a canyon 20 m wide and 20-30 m deep; they were feeding on emerging caddisflies. In a more open valley, 20-30 individuals flew ca 5-10 m above the water.
Remarks: The intraspecific taxonomy of this species needs revision. Recently Belevich (2005) synonymised all its subspecies. The light spots on the posterior of the head, which were formerly used for subspecific separation, are variably present in Tuva. In the Todzha specimens, all seven males studied had the spots, while three of four females studied lacked them. In the Central Tuvinian depression, among 10 males, five had spots, in two they were vestigal and in three absent; and among 22 females, 16 had spots, in one they were vestigal and in five absent. Two males from the Kaa-Khem upper basin had no spots. Among specimens studied from the Ubsu-Nur depression, three males had the spots and one male lacked them, while two females had the spots. Thus, the spots were more often lacking in females, and mostly so in those from Todzha.

Aeshna mixta Latreille, 1805

Localities: 26, 35, 48, 50; (early vii - late August).

Aeshna serrata Hagen, 1856

Localities: 22, 43, 53, 55, 56, 59, 60, 66, 80; (mid July - early September).
Distribution and habitat: This species prefers open, north Asian landscapes, especially steppe ones (Belyshev 1973b: 410). The related *A. crenata* tends to inhabit forest lakes, although the two species do not exclude one another and may co-occur (Kosterin et al. 2001; Dumont et al. 2005), hence we expected to see *A. serrata* more abundant in the Erzin environs. However, it was *A. crenata* which prevailed there, perhaps because the floodplain oxbows were surrounded by woody vegetation. On Lake Tore-Khol' with open banks (loc. 56) we met only with *A. serrata*, as would be expected. At the same time, *A. serrata* occurred in the wooded Todzha as well, at different localities but not at major lakes. Patrolling males of both *A. crenata* and *A. serrata* were present at loc. 80, the former being somewhat more abundant. Males of *A. crenata* were flying 1-2 m above the water while those of *A. serrata* flew low along the edge of the lake where it was fringed with *C. rostrata*. It was noteworthy that OK observed males of *A. serrata* in Omsk, West Siberia, where *A. crenata* is absent, flying as high as *A. crenata* on this lake. Hence we most probably are seeing a behavioural segregation forced by co-occurrence. Females

of *A. serrata* oviposited among *Carex rostrata*. What makes a habitat in Todzha suitable for *A. serrata* remained unclear. The only noticeable difference of Lake Sailyg-Khol' (loc. 80) from other lakes visited in Todzha was the absence of fish and abundance of *Gammarus*, but in West Siberia *A. serrata* successfully occupies habitats with numerous *Carassius* (OK unpubl.).

Aeshna subarctica elisabethae Djakonov, 1922

Localities: 57, 67, 71, 78-81; (late June - late July).
Distribution and habitat: This stenotopic inhabitant of *Sphagnum* habitats (Bernard & Kosterin 2010) was found only in the Todzha depression where it was quite common at lakes: the males flew above *Sphagnum* quaking mires.

Anax parthenope Selys, 1839

Localities and specimens: loc. 16: 05 vii 2004 – 1 ♂ visual; loc. 22: 05 vii 2004 – 1 ♀ visual, 07 vii 2004 – 1 ♂ visual; loc. 26: 26 vii 2004 – 2 ♂, 1 ♀; loc. 43: 26 vii 1970 – 1 ♀.
Distribution and habitat: The first published records for Tuva. Until recently, records of this species in Siberia were very scarce, e.g. Belyshev (1973b: 395) only once visually recorded it in western Transbaikalia. In the last two decades it has been recorded at several sites in Transbaikalia (Kosterin 1999), Kemerovo Province (Dronzikova 2000) and at Omsk, and so is supposed to be expanding its range (Kosterin 2007). However, the first specimen collected in Tuva was taken as long ago as 1970. Thirty-four years later, males were observed at loc. 26 patrolling banks (and attacked by *Motacilla citrinea*), and two tandems were observed to oviposit in reed thickets. Both lakes were large and brackish, with clear water and patches of reeds; occurrence of this species in salt water was also recorded by Kosterin (1999, 2004a) in southern Transbaikalia. However, observations of patrolling males and young females at locs 16 and 22 suggest this species was breeding in freshwater oxbows as well.

Gomphidae

Ophiogomphus obscurus Bartenev, 1909

Localities: 59, 69, 74, 75, 78; 10 July - 16 August; emergence at loc. 59 on 09-11 vii 2004.
Distribution and habitat: This species was met with only in Todzha where its typical taiga habitats occur. It bred abundantly in small and medium rivers connecting the large Todzha lakes between each other and the great Biy-Khem River (e.g. locs 59, 69); unfortunately, the Khamsyra River has remained unexplored. Although scarce individuals occurred also on the banks of large lakes and the mighty Biy-Khem River, no exuviae were found there.

Remarks: *O. obscurus*, described from Tomsk environs, ranges in general throughout the southern taiga zone east of the Ob' River. Full species rank of *O. cecilia* (Geoffroy in Fourcroy, 1785), *O. obscurus* and *O. reductus* Calvert, 1898 was challenged by Belyshev (1973b: 455-459) but supported by Asahina (1979) and Haritonov & Borisov (1990). All the known specimens demonstrate stability of the morphological characters and also coloration, described in detail by Bartenev (1930) and Asahina (1979). Throughout its vast range *O. obscurus* probably meets with just two congeners. First, in Tuva, southern Baikal region and Transbaikalia it may overlap with *O. spinicornis* (Kosterin 1999, 2004a). Such a case of sympatry at Kyra village in Chita Province was reported by Dubatolov et al. (2004). Secondly, *O. obscurus* should meet *O. cecilia*, ranging in Europe, the West Siberian Plain, N Kazakhstan and further eastwards, in a narrow stripe along the forest-steppe depressions: the Kuznetsk, Achinsk, Krasnoyarsk and Minusinsk depressions, up to Transbaikalia (Belyshev 1973b: 459-461). Two females collected in the Verkhnyaya Angara River basin (NE of Baikal) and examined by Kosterin (1999; 2004a) were identified as *O. cecilia* as well. Belyshev (1973b: 461) reported that he found specimens "intermediate between *cecilia* and *O. obscurus*" at lake Gusinoe in SW Transbaikalia, but we failed to find these specimens in his collection preserved in the SZMN. To date we know only one case of syntopy of these two species: in the SZMN there are five young females collected by Yu. Zapekina on the Mana River at Kandalak on the following dates: 2 ♀, 10 vii 1958; 1 ♀, 16 viii 1958; and 2 ♀, 20 viii 1958. Only the female from 16 viii is *O. cecilia*, the four others being *O. obscurus*, with all the diagnostic characters enumerated by Bartenev (1930) and Asahina (1979) clearly expressed. Noteworthy, both species were collected on the Isha River in North Altai: *O. cecilia* at Novaya Surtayka village (2 ♂, 1 ♀, 17 vii 1949) and *O. obscurus* at Choya village (1 ♂, 11 vi 1952); these localities are situated 42 km from each other but the former among meadow covered hills and the latter in taiga, conforming with the species' habitat preference. All four North Asian *Ophiogomphus* species prefer different landscapes: *O. cecilia* – forest-steppes; *O. obscurus* – taiga; *O. spinicornis* – steppes; *O. reductus* – deserts. However, there are no distinct borders and isolating barriers between these landscapes, so we may expect more cases of syntopic occurrence.

Ophiogomphus spinicornis Selys, 1878

Localities: 6, 13, 15, 22, 47-50, 54; 23 June - 1 August.
Distribution and habitat: Common in the Ubsu-Nur depression in the main Tes-Khem River floodplain (locs 50, 54) and valleys of rivers descending from the Tannu-Ola Mts. (locs 48, 49, 53) but only in the Tes-Khem River (loc. 50) was breeding proved by presence of numerous exuviae. This river had a moderately fast current, warm water and a sandy bed, whereas the ice-cold, turbulent mountain rivers were not suitable for larval development. Hence *O. spinicornis* most

probably reaches the valleys of the Tannu-Ola by adult dispersal. In the Turan depression the species bred in the Uyuk River (loc. 6) which was only 3-5 m wide, 0.5-1 m (to 2 m at floods) deep, and had a shingle bed with silt. Numerous individuals were observed on 01/02 vii 2004 at loc. 15 emerging from the swiftest reaches of the mighty Khemchik River where it flowed over its stone bed in a narrow gorge: here during eclosion the larvae clung to shingle banks and stone screes. This habitat resembled that in the Onon River in SE Transbaikalia (Kosterin 1999, 2004a). Hence, the species demonstrated its ability to breed in diverse, less cold rivers and was found around the Central Tuvinian depression. It is a striking fact that the species was almost absent in the Central Tuvinian depression per se, in spite of a rich diversity of riverine habitats. Only one teneral male was collected on 24 vii 2009 on a shingle bank of an island at the Kaa Khem and Biy Khem Rivers, next to loc. 22. This place has been being monitored by VZ for aquatic insects in mid-summer almost every day (except for trips and bad weather) since 1993.
Remarks: The "transitional form between *Ophiogomphus serpentinus* and *O. reductus*" earlier reported by us (Zaika & Kosterin 1992) for the Tes-Khem River and the Shiveelig-Khem River valley, as well as "*Ophiogomphus cecilia* Four." reported by Zaika (1996) for the eastern Ubsu-Nur depression appeared to be in fact the Chinese-Mongolian *O. spinicornis* (Kosterin 1999, 2004a). Most probably, it was this species which was reported by Valle (1942) as *O. reductus* for the Khemchik, since *O. reductus* and *O. spiniconis* have somewhat similar anal appendages and because it was *O. spinicornis* which we repeatedly found at the Khemchik River recently. In addition to Tuva, in the Russian territory this species is known for the Baikal southern bank and for the steppe Transbaikalia: the Onon River at Nizhniy Tsasuchey (Kosterin 1999, 2004a) and Kyra (Dubatolov et al. 2004) villages.

Corduliidae

Cordulia aenea (Linnaeus, 1758)

Localities: 36, 70, 71, 73, 75, 77-79; (mid July).
Distribution and habitat: The first reliable record for Tuva. Found only in taiga in NE and E parts of Tuva, the Todzha depression and the Kaa-Khem upper basin, respectively. In Todzha, males of this species were quite abundant flying around large and medium-sized lakes and more abundant at smaller ones, such as locs 70, 71, 73, where it prevailed over *Somatochlora graeseri* and *S. metallica*. In contrast to those species, patrolling males of *C. aenea* did not strictly follow the banks but also flew over open water. Females flew lower over the water surface than males.
Remarks: In the genus *Cordulia*, Jödicke et al. (2004) analysed variation of the DNA sequence of spacer ITS1 between rRNA genes, which is a non-coding region of a tandemly repeated nuclear sequence. They revealed substantial differences between (1) the European and West Siberian populations (samples from western

Europe and Novosibirsk), (2) the Far Eastern populations (samples from Yakutia, Amurland and Japan) and (3) the North American populations. They concluded that all populations are monophyletic and resulted from rapid recolonisation of the Holarctic in the Holocene from three refugia: a European, Far-Eastern and North American one, respectively. Good resolution of haplotypes specific to each of the three regions and absence of exchange of specific haplotypes between these regions have been revealed. This was interpreted as evidence of reproductive isolation rather than of isolation by distance. These three lineages were hence interpreted as separate taxa with full species rank, with the corresponding names *Cordulia aenea* (Linnaeus, 1758) (Europe and West Siberia), *C. amurensis* Selys, 1887 (Far East) and *C. shurtleffii* Scudder, 1866 (North America). While the reconstruction of the history of the studied populations is convincing, the taxonomic solution was obviously premature. Non-coding sequences evolve as a molecular clock, that is continuously and gradually accumulate nucleotide substitutions with time regardless the evolutionary fate of their carriers. This process is by no means connected with speciation, which is rather a discontinuous phenomenon, taking place in some isolated populations in certain favourable situations, driven by an intricate interaction of neutral and selective factors lasting for rather short periods of tens to hundreds thousand years and resulting in reproductive barriers between nascent species: this is the notorious punctuated equilibria pattern (Eldredge & Gould 1972), which is predominant in speciation (Coyne & Orr 2004; Stearns & Hoekstra 2005). Therefore the 'tree' of biological species is not necessarily congruent with the phylogenetic tree of populations, as Jödicke et al. (2004) assume: in some groups, some speciation event may have taken place, separating some clusters of populations while leaving the remaining populations of the paraphyletic ancestral species united by at least the potential of gene exchange. On a large time scale there is indeed a correlation between divergence of non-coding sequences and the rank of taxonomical differences. However, it is the discontinuity of speciation events, which depend on specific ecological situations and historical events, that makes the magnitude of divergence of DNA evolving as molecular clocks unacceptable as a basis for the resolution of two given populations as different species, although it resolves well the actual phylogeny of populations and may provide valuable hints as to species status of a popluation. In the case of "*C. aenea* s.str." vs "*C. amurensis*", there exist the following additional problems:

(1) Jödicke et al. (2004) found 20 haplotypes in 38 individuals analysed, that is a very high level of variation, if not an artifact. With such variation, almost all individuals are expected to be heterozygotes. At the same time the authors reported that only in five individuals did the sequencing profile contain ambiguous sites which might indicate heterozygosity. The authors suggest that the enigmatic 'mechanisms of concerted evolution' are able not only to homogenise tandem repeats within a cluster but also to turn heterozygotes for the cluster into homozygotes. Hovmöller & Johansson (2004) studied variability

in the same region of rDNA including ITS1, 5.8s rDNA and ITS2 region in *Leucorrhinia* by cloning individual copies, and registered intra-individual sequence variation in all investigated species (they designed a special test to prove that variation they revealed was not a polymerase artifact).

(2) No morphological differences are known between *C. aenea* s.str. and *C. amurensis*. Belyshev (1973b: 378) showed irrelevance of the absence of the amber basal wingspots in the latter but reported that *C. amurensis* is somewhat smaller. However, Dumont et al. (2005) reported data that the body size decrease clinally from west to east. These authors also found differences in the hamuli shape between specimens from Europe vs Kamchatka and Amurland, but they are too slight to be reliable. It should also be noted that the captions to figures 5 and 6 in Dumont et al. (2005), illustrating the hamuli differences, are erroneously transposed (E.I. Malikova pers. comm.; Kosterin & Dubatolov 2005).

(3) The genus *Cordulia* enjoys a continuous distribution from the Atlantic to Pacific, hence the two lineages must meet somewhere in Central Siberia. A further study of the patterns of molecular markers in the contact zone is necessary for the decision species vs subspecies, which would evaluate the degree of introgression of lineages by estimating frequencies of heterozygotes (if any) for lineage-specific haplotypes and testing their deviation from equilibrium. The geographical location of the putative contact zone is unknown, but it may just be in Tuva.

Epitheca bimaculata (Charpentier, 1825)

Localities: 63, 67, 72, 73, 77, 79, 81; 23 June - 22 July.
Distribution and habitat: So far found only in Todzha. Present on clear lakes as well as at small boggy lakes; one female captured on a small river between lakes (loc. 72). Exuviae were occasionally found at the lakes of Many-Khol' and Kadysh and were found surprisingly numerous at some points of banks of medium size lakes (locs 73, 79; 18 vii 2004). Males flew along lake banks or taiga edges.
Remarks: The Hw length was 38 mm in two males and 39 mm in one male. In a female from loc. 77, the amber between C and Sc reached to the base of R2 while the basal spot on the Hw occupied the triangle. In specimens from loc. 64, the basal amber was absent, the dark basal spots reached the middle of the triangles in the two males collected in 2000 and did not reach triangles in the one collected in 2002. According to the diagnostic characters by Belyshev (1973b: 341-342), the two former specimens combined those of ssp. *altaica* Belyshev, 1951 (the basal spots reaching the triangles) and ssp. *sibirica* (Selys, 1887) (the amber absent), the latter specimen corresponded to *sibirica*, while the specimen from Lake Many-Khol' corresponded to *altaica*. However, subspecific taxa within *E. bimaculata* can not be supported, hence all subspecies have been synonymised by Kosterin (2004a).

Somatochlora alpestris (Selys, 1840)

Localities: 61, 76, 77; (late June - mid July).
Distribution and habitat: The first published record for Tuva. Found in Todzha, invariably at small (1-2 m) pools with black water among boggy, peaty taiga, often close to bays of major lakes. The males flew partly over the water, partly over the surrounding *Sphagnum*/*Carex rostrata* bogs, partly among dead tree trunks and branches. Females were observed ovipositjng into *Sphagnum* between stems of *C. rostrata*.
Remarks: Belyshev (1973b: 348) considered the presence of two anal-cubital veins on the Fw as a diagnostic feature of this species. In one of our females, there was only one of this vein on the left Fw.

Somatochlora arctica (Zetterstedt, 1865)

Localities and specimens: loc. 78: 16 vii 2004 – 1 ♂; 18 vii 2004 – 2 ♂.
Distribution and habitat: The first published record for Tuva. Found only in one locality in Todzha: at a series of non-tussock sedge bogs among open taiga, with *Carex lasiocarpa*, *Comarum palustre* and *Menyanthes trifoliata*, forming a quaking mat above the water. Males were widely patrolling ca 1.5 m above the sedge carpet.

Somatochlora exuberata Bartenev, 1911 – bona species

Localities: 59, 69, 72; (early July) - early August.
Distribution and habitat: Males patrolled along sedge banks of small and medium-sized rivers with shingle beds. Females oviposited onto mud at the water edge under the sedge, among dead branches or openly (02 viii 2004 at loc. 59). Current speed of these rivers varied from 0.35-1.1 m/s. On the great Biy-Khem River the species was not seen. In Tuva, habitat segregation between *S. exuberata* and *S. metallica abocanica* was very strict. *S. exuberata* occurred only at rivers (in total 52 ♂, 3 ♀ captured) and *S. m. abocanica* at lakes (in total 39 ♂, 14 ♀ captured at lakes and only 1 ♀ at the medium-sized river at loc. 59).
Remarks: This taxon demonstrated all the diagnostic characters given by Bartenev (1911): absence of even traces of a yellow stripe between the yellow spots on the frons; absence of yellow on fore femora; black hairs in the upper part of the head; black Pt; very dark body. The wings were hyaline, in one male with a hardly noticeable darkening of a yellow-brownish tint. Thorax dark-bronze-green, rather dull; abdomen glossy-black, with faintest bronze sheen. Additionally, the projection bearing male accessory genitalia was entirely black, anterior to it was a large whitish triangular spot on either side of S2. These traits of male S2 strongly differed from those of *S. metallica* (rear half of the projection bearing the accessory genitalia yellow; spots yellow and oval). In *S. exuberata*, the epiproct length was 2/3 of that of cerci, or even shorter. No specimen looked intermediate between *metallica* and *exuberata*.

Therefore, the specific integrity of *S. exuberata* and *S. metallica* is now corroborated by their sympatry with strict habitat segregation. Todzha is the only hitherto known place of their sympatry, *S. exuberata* ranging east and *S. metallica* west from there. In regions with only one species present, both occur at lakes and rivers, although *S. metallica* is in general more lentic and *S. exuberata* more lotic. Thus co-occurrence reinforces habitat segregation between the species.

There is some confusion concerning the date of Bartenev's names *S. exuberata* and also *Leucorrhinia intermedia* (see below). Both names are commonly referred to as Bartenev (1912) – a German translation of a paper previously published in Russian. As Malikova (2006) pointed out, Bartenev himself used to assign his original descriptions to 1910, a practise partially adopted by other authors. The Russian journal containing the original descriptions is very rare but Malikova (2006) reported on her discovery of a copy held in the library of the Zoological Institute in St Petersburg. She found the cover of the relevant issue dated 1911. Bartenev's paper was accepted on 27 February 1910 but others were not accepted until April 1911, confirming that the issue was not published before 1911. Hence, the correct names are *Somatochlora exuberata* Bartenev, 1911 and *Leucorrhinia intermedia* Bartenev, 1911.

Recently Malikova (2006), in a short abstract paper, supported Asahina's (1938) and Lohmann's (1994) view on the conspecificity of *S. exuberata* and *S. japonica* Matsumura, 1911. She claimed that the latter name has at least one month priority and hence is valid. Here we retain the name *S. exuberata* until the problem is formally resolved.

Somatochlora graeseri Selys, 1887

Localities: 22, 54, 59, 65, 67, 77, 78, 81; 26 June - 4 August.
Distribution and habitat: The most widespread *Somatochlora* in Tuva, occurring in both humid and arid areas but with abundance increasing northwards. At loc. 54 this species was scarce: males were observed slowly patrolling at a large oxbow with ice-cold water due to bottom sources: perhaps the only suitable habitat in the steppe Ubsu-Nur depression. In loc. 22 in the Central Tuvinian depression we found it also at oxbows where it was much more abundant. In the Todzha depression it was not abundant on the banks of major lakes – at loc. 81 four patrolling males of *S. graeseri* were recorded compared with 18 males of *S. metallica abocanica* – but was abundant at lesser swampy lakes and at medium-sized rivers where, however, it preferred oligotrophic temporary oxbows. Everywhere the species was mostly associated with rather deep and cold water and numerous inundated logs. Oviposition at loc. 81 was also observed near a half-inundated log.
Remarks: A female from loc. 54 completely lacked an amber tint to the wing bases. One of the two females collected at loc. 22 had only traces of it, while in another specimen it was well developed. In the Todzha depression, all females had

well-expressed basal amber, except in one of them the colour was very pale but the patch still extended to the triangle. Belyshev (1973b: 362) wrote that the degree of amber tinting varies greatly, including its complete absence. It may be possible that in the arid intermontane depressions of Tuva the reduction in the amber tint is a common feature. In males from loc. 22 the wings were noticeably darkened.

Somatochlora metallica abocanica Belyshev, 1955.

Localities: 59, 60, 63, 65, 67, 70, 73-75, 77-81; (mid - late July).
Distribution and habitat: Found only in the Todzha depression, where it was quite abundant along the banks of all major lakes studied and also at small lakes, with only the above mentioned female collected at a river (loc. 59). At loc. 77 some females had such great infestations of water mites on their sternites that the mass of mites spread apart the lower edges of the tergites so that the distal part of the abdomen was flattened above.
Remarks: A female from loc.60 lacked one diagnostic character of *S. metallica*, as there was no yellow on the fore femora, but it had all other characters well expressed: a wide yellow stripe on the frons, bright body coloration, light hairs on the head and strongly darkened wings. All collected specimens corresponded to the description of ssp. *abocanica* (Belyshev 1955), except for the brown infuscation of the wings, which was weak in majority of specimens.

Somatochlora sahlbergi Trybom, 1889

Localities and specimens: loc. 33: 13 vii 2008 – 1 ♂.
Distribution and habitat: The first published record for Tuva. The male flew over a pool 6 m in diametre and 2 m deep situated among spruce taiga. In recent decades this species has been revealed to range widely in the mountains of South and East Siberia and northern Far East (Kosterin 1992, 2004b; Dumont et al. 2005; Dubatolov et al. 2004; Kosterin & Lyubechanskii 2009), where it is invariably associated with taiga, in mountains often near the tree-line. The southernmost known sites, at 1,600-1,800 m on the Sokhondo mountain in southern Chita Province, are situated at 49°40-50'N (Dubatolov et al. 2004).

LIBELLULIDAE

Leucorrhinia dubia orientalis Selys, 1887

Localities: 26, 35, 36, 54, 59, 70, 71, 77, 78, 80, 81; 16 June - 29 July.
Distribution and habitat: Found in all principal parts of Tuva except the Khemchik and Turan depressions. Two preferred habitat types were recorded: shallow bays, bordered with *Sphagnum* bogs, of major lakes of Todzha and large oxbow lakes with ice-cold water resulting from ground springs. These dragonflies were

especially abundant at a large oxbow at loc. 59, with *Utricularia vulgaris* and *Hippuris vulgaris*, and in a bay with *Potamogeton pectinatum* at the northern bank of Lake Many Khol' (loc. 77).

Remarks: In all males collected, the spots on S4-5 were missing, which is considered diagnostic for the race *orientalis* (Belyshev 1973a: 294). In 31 out of 55 males the spot on S6 was also missing and in 20 males this spot was represented by a barely noticeable longitudinal trace on the dorsal carina of the tergite; three males had a small spot and one male (loc. 36) had short and very narrow yellow streaks along the dorsal carina of S4-6. In contrast to the spots on S1-2, which were red, the spots on S7 and (if present) S6 were yellow even in fully mature males. This feature is present in *orientalis* over all its range (OK unpubl.); only a slight orange tint appears in old individuals, while in *dubia* s.str. all spots become red with maturity.

The dark basal spot on the hind wing was nearly triangular, which is diagnostic for *orientalis*, while in *dubia* s.str. the spot is larger and has a clearly convex outer margin (E.I. Malikova pers. comm.). In females, the spot part above vein CuA was missing or vestigal, which is diagnostic for *orientalis* vs *dubia* s.str. according to Belyshev (1973a: 295-296). The inferior appendage in our male series had a triangular and rather deep notch, which corresponded with the characters of *orientalis*, whereas *dubia* s.str. has a shallow notch (Sjöstedt 1927; Seidenbusch 1997b).

The labrum was white in males and generally black in females. In all females collected beyond Todzha there were two small, pale spots laterally at the base of the labrum. In one of them (loc. 54), in addition to these two spots, there was a narrow, pale mark centrally at the base of the labrum as well as a pair of small pale marks at its anterior margin. Among females from Todzha (n = 25), in five the pale spots were absent, in eight there were only traces of the latero-basal spots, in 10 these spots were well expressed, in one there were additional paired light streaks at the outer margins of the labrum, and in one the coloration was the same but the lateral spots were connected with a light streak along the labrum base. Belyshev (1973a: 296) considered the female labrum coloration to be diagnostic: entirely black in *dubia* s.str. and light with a black outer margin and a black spot at the base in *orientalis*. This appears to be incorrect: a series of 96 *orientalis* females from different sites in SZMN, collected by Belyshev himself, suggests that the labrum is predominantly black with lateral white spots. Only three females missed these spots, while in 49 females (ca 50%) additional white coloration was present as small patches at the anterior and/or posterior margin of the labrum, and only in two females was the labrum white with a black spot in its centre. No geographical trend was evident.

Hence the Tuvinian specimens demonstrated all known diagnostic characters of the taxon *orientalis*, the status of which, however, remains problematic. Two species groups within *Leucorrhinia*, the *dubia*-group and *rubicunda*-group, demonstrate a strikingly similar taxonomic pattern. Both groups enjoy a continuous transpalaearctic distribution, each represented by a western/eastern pair of taxa: *dubia*/*orientalis* and *rubicunda*/*intermedia*, respectively, but within each pair little is known what happens at the meeting of their ranges. Both eastern taxa were introduced as full species (Selys 1887: *L. orientalis*; Bartenev 1911: *L. intermedia*) but were formerly considered as subspecies by most subsequent authors, including Belyshev in early years (e.g. 1964b). Then Belyshev (1964c) discovered that *orientalis* has much more developed larval spines than *dubia* s.str. and upgraded the status of these taxa to species. Indeed, larvae of East Siberian *orientalis* have strong curved spines on S4-7 (S8) and very long lateral spines (Belyshev 1973a: fig. 101; Seidenbusch 1997b). However, it is well known that there is great variation in the spine development in *dubia* s.str. (Belyshev 1973a: fig. 103; Seidenbusch 1997a), while in Japan, *orientalis* larvae have moderately developed spines (Hovmöller & Johansson 2004). Therefore the extent of the larval spine development would seem to have no taxonomical value. Johansson (2002) showed that presence of fish induces longer spines in larvae of *L. dubia*. Other environmental factors may also be involved. It is noteworthy that in the *rubicunda*-group, *rubicunda* s.str. has much less developed larval spines than Siberian *intermedia* (Belyshev 1973a). We see that in both species groups the spines are more developed in the 'East Siberian' taxon. We therefore suppose that living in a severe continental climate, often in elevated habitats, somehow promotes the development of larval spines.

The above mentioned differences between imaginal *dubia* s.str. and *orientalis* are rather slight and quantitative and seem therefore insufficient for a separation at the species level. Following Inoue & Tani (2003), Hovmöller & Johansson (2004) and Dumont et al. (2005), we therefore consider *orientalis* as a subspecies of *L. dubia*.

According to Belyshev (1973a: figs 102, 104), the West Siberian Plain, which spreads west of the Yenisey (at 58°N), is inhabited by *L. dubia* s.str., while *orientalis* ranges in the mountains of South Siberia (Altai and eastwards) and everywhere east of the Yenisey. Examination of Belyshev's collection in SZMN by OK supported this view. Hence, our findings of the latter in Tuva were in agreement with Belyshev's maps.

Recently Malikova (2004) claimed that the ranges of *dubia* s.str. and *orientalis* as well as the ranges of *rubicunda* s.str. and *intermedia* overlap in Siberia, that could suggest a full species status of all these taxa. In fact, this claim was based on a male of *dubia* s.str. and a female of *rubicunda* s.str. with the same label (here translated from Russian), "Mel'nikovo village, Irkutsk Province, Maksimovich, Society of Researchers of Siberia, 10.06.1912", found in the collection of the Zoological Institute in St Petersburg (E.I. Malikova pers. comm.). Irkutsk is actually deep inside the ranges of *orientalis* and *intermedia*, but the Irkutsk Province was greatly extended around that time and villages called Mel'nikovo are scattered all over Russia, so the labels of those two old specimens are doubtful.

Leucorrhinia rubicunda (Linnaeus, 1758)

Localities: 4, 22, 29, 30, 33, 35, 36, 51, 55, 56, 59, 70-72, 77, 78, 81; 25 May at Kyzyl - 27 July in Todzha.

Distribution and habitat: This species also occurred at oxbow lakes, including large ones, together with *L. dubia*, but often at small ones and also small floodplain bogs with sedge swamp. On loc. 29 the species was very common on small bays among bushes, mostly at the outflow of the Mazhalyk brook. Most probably in Todzha the flight period is delayed as compared to warmer regions of Tuva. These dragonflies generally perched on dry branches.

Remarks: In all our females, the lobes of the vulvar scale were short, as should be in *rubicunda* s.str. (Bartenef 1933; Belyshev 1973a: fig. 108); in males the hamuli shape corresponded to this taxon as well (Belyshev 1973a: fig. 108). All males have distinct longitudinal ridges laterally on S4-8; in females the ridges are noticeable on S5-8.

Belyshev (1973a: 294-297) did not gave reliable characters to discriminate the taxa *rubicunda* and *intermedia* Bartenev, 1911, which he considered as subspecies in earlier works (e.g. Belyshev 1964b, 1966) but raised to full species in his monograph (Belyshev 1973a: 320-324) without a clear explanation. He had problems reliably identifying them in the adult stage, exemplified by the following citation (translated by OK): "by the structure of the genital hooks our specimen somewhat differs from the typical form, inclining towards the eastern subspecies *L. rubicunda intermedia* Bart.; this is seen, although to less extent, also in the female which has a dark-brown, almost black pterostigma" (Belyshev 1964b: 61). Later, in his monograph (Belyshev 1973a: 320), he wrote: "in the final analysis, it absolutely does not matter how they should be treated: either as well differentiated subspecies or weakly formed close species with predominately quantitative variations distinguishing them" (translated by OK). In his key, Belyshev (1973a: 294-297) provided the following imaginal character: in *rubicunda* the lateral ridges should be present on (S2) S4-8, while in *intermedia* on (S5) S6-7 in males and on (S6) S7 or absent in females. Besides, the 'typical' *intermedia* was shown to have more slender and more hooked hamuli. The shape of hamuli was thought to differ qualitatively (Belyshev 1973a: fig. 106; Dumont et al. 2005: figs 8, 10). Notwithstanding this, Belyshev (1973a) noted that the Hokkaidian subspecies *ijimai* Asahina, 1961, traditionally attributed to *intermedia*, has the hamuli similar to that in *rubicunda* s.str.

The imaginal diagnostic characters above, given by Belyshev (1973a: 294-297), seem unconvincing, although specimens from SE Transbaikalia, that is from the centre of the presumed range of the taxon *intermedia*, indeed have weak ridges only on S6-7 or none (Kosterin 1999; 2004a). However, Belyshev seems to have not been aware of the only alternative and hence reliable character for the differentiation between both taxa: the lobes of the valvular vulva, which are quite long in *intermedia* and very short in *rubicunda*. However, he depicted them correctly (Belyshev 1973a: figs 106, 108; see also Bartenef 1933: fig. 40). With such a character present, we cannot reject the status of these two taxa as full species, but they might equally be conspecific, in the event of there being a single dimorphic character controlled by alleles of one gene.

The geographical ranges of *L. intermedia* and *L. rubicunda* are problematic since Belyshev had no means to reliably differentiate them. According to him, the pattern of distribution of this pair almost mirrors that of the pair *dubia/orientalis*, with the difference that *rubicunda* does not extend as easterly as to the Yenisey at 58-60°N (Belyshev 1973a: figs 107, 109). OK checked the females in Belyshev's collection and found exclusively and undoutedly *L. intermedia* females from Irkutsk Province, Noril'sk environments, Transbaikalia, Amur Province, Primorye, Yakutia and eastern Mongolia (the Tola and Onon River basins). At the same time, there is not a single female of the *rubicunda*-group from the areas of the presumed western border within 85-95°E, that is from the Yenisey basin west of Irkutsk, the Tom' River basin and Altai. Thus, all 10 dots from these areas on the map for *L. intermedia* (Belyshev 1973a: fig. 107) remain dubious. They could be based on his earlier collections, e.g. in the Kashtak valley and at the Bazaikha River at Krasnoyarsk, reported (still as *L. rubicunda rubicunda*) in Belyshev (1964b) but since lost.

Curiously, Belyshev & Korshunov (1976) mentioned one 'quite typical' female of *L. rubicunda* collected by Y.P. Korshunov on 28 vii 1968 at the Tanlovaya River, the left tributary of the Shchuchya River on the Yamal Peninsula (ca 67°N, 67°E). In the SZMN collection, OK found three males and two females with the same label; one female had the long *intermedia* lobes of the valvular vulva, while in the other the lobes were completely missing.

Thus the border or contact zone between *L. intermedia* and *L. rubicunda* is still to be found. It was expected not far from the Yenisey River within 85-95°E. However, our specimens suggest that Tuva at least, encompassing the Yenisey headwaters and situated within 90-100°E, is inhabited solely by *L. rubicunda*.

Libellula quadrimaculata Linnaeus, 1758

Localities: 16, 20, 22, 23, 29, 34-36, 51, 54, 59, 61, 66, 70, 73-75, 77, 78, 82; mid May - early August.

Orthetrum cancellatum (Linnaeus, 1758)

Localities: 43, 55, 56, 62, 71; mid June - early August.
Distribution and habitat: The species inhabits large lakes with open, not boggy banks. At Lake Tore-Khol' (locs 55-56), with its sandy banks, the species occurred in great abundance. Finding it in taiga in Todzha was surprising: a dead male found in a cobweb within dense larch taiga at loc. 62 and four females in a dry open valley surrounded by taiga north of loc. 71.
Remarks: As anywhere in West Siberia, the males were pruinosed with blue not only on all of the abdomen but also over the thorax.

Sympetrum danae (Sulzer, 1776)

Localities: 1, 3, 8, 16, 18, 22, 23, 35, 40, 43, 44, 48, 52, 54, 55, 56, 59, 61, 63, 65, 66, 71, 77, 78, 80; early July - mid September.

Sympetrum depressiusculum (Selys, 1841)

Localities: 16, 22, 23, 31; early July - early September.

Sympetrum flaveolum (Linnaeus, 1758)

Localities: 3, 5, 8, 15, 16, 22-24, 26, 30, 35, 37, 38, 43, 48-50, 54, 56, 58, 59, 65, 71, 75, 78, 81; late June - mid August.

Sympetrum pedemontanum (Müller in Allioni, 1766)

Localities: 22, 23, 43, 44, 69; late July - mid September.

Sympetrum sanguineum (Müller, 1768)

Localities: 22; (late July).

Sympetrum tibiale (Ris, 1897)

Localities and specimens: loc. 18: 09 vii 1994 - 1 ♂; loc. 43: 18 vii 1993 - 1 ♂, 1 ♀; loc. 44: 22 viii 1971 – 1 ♂, 1♀.
Distribution and habitat: This generally Central Asian species ranging from Mongolia and Kashgharia in the east to the North Caucasus in the west and reaching Afghanistan in the south (Belyshev 1973a: 261), reaches its northern limit in Tuva. Here it was rare in the Ubsu-Nur and Central Tuvinian depressions. One female was also collected on the southern bank of Lake Ubsu-Nur in Mongolia on 17 viii 1995 by A.V. Zaika and VZ.

Sympetrum vulgatum (Linnaeus, 1758)

Localities: 8, 18, 19, 22, 26, 31, 33, 41, 44, 48, 53, 55; early July - early October.
Remarks: The length of the abdomen (excl. appendages) varied from 22-27 mm in males and 24-28 mm in females, that of the Hw from 26-31 mm in males and 28-30 mm in females. The Pt was 2.6-3 mm long. Wing venation was pale and there was no amber in the wing membrane behind the costa. Thus, all specimens from Tuva have the characters of the nominotypical subspecies and do not demonstrate any tendencies towards the Transbaikalian and Far Eastern subspecies *S. vulgatum imitans* Selys, 1886. The latter is bigger, with dark venation and amber in the costal space, especially in females (Belyshev 1973a: 267).

Comparative analysis of the fauna

The 47 species recorded in Tuva belong to 17 genera in seven families. A maximum number of 11 species (23.4%) was recorded in Coenagrionidae and Libellulidae (four genera in both). Also found were nine species (19.2%) of Aeshnidae (two genera), eight species (17.0%) of Corduliidae (three genera), five species (10.6%) of Lestidae (two genera), two species (4.3%) of Gomphidae (one genus) and one species (2.1%) of Calopterygidae (one genus).

Of these 47 species, six (12.8%) have a Holarctic distribution: *Lestes dryas, Aeshna juncea, A. subarctica, Somatochlora sahlbergi, Libellula quadrimaculata, Sympetrum danae.* Six species (12.8%) are confined to the East Palaearctic: *Coenagrion ecornutum, C. lanceolatum, Ophiogomphus obscurus, O. spinicornis, Somatochlora exuberata, S. graeseri.* Two, *O. spinicornis* and *S. exuberata*, reach their westernmost limit in Tuva. Nine species (19.1%) are West Palaearctic but range eastward to Siberia: *Calopteryx splendens, Lestes barbarus, L. macrostigma, Ischnura pumilio, Aeshna affinis, A. grandis, Somatochlora metallica, Leucorrhinia rubicunda* and *Sympetrum sanguineum*; for six, *L. macrostigma, L. barbarus, I. pumilio, S. metallica, L. rubicunda* and *S. sanguineum*, their easternmost limits are most probably in Tuva. The remaining 26 species (55.3%) are transpalaearctic and range from Europe to the Far East. In this rough analysis, both taxa of *Enallagma* are considered two subspecies of one species and *L. dubia* is considered to include ssp. *orientalis.*

With respect to the latitude, most species (37; 78.7%) may be considered boreal and widely ranging in the taiga zone of Eurasia. Only eight species (17.0%) have their northern limits in Tuva and may be called temperate, namely: *L. barbarus, L. macrostigma, I. pumilio, A. affinis, A. mixta, Anax parthenope, O. spinicornis* and *S. tibiale.*

Twenty-nine species were recorded in the Ubsu-Nur depression, 34 in Central Tuva in a broad sense, including the Turanian depression and the Khemchik and Kaa-Khem River basin, and 32 species in Todzha Depression (Table 1). *Ischnura elegans* and *A. affinis* were met only in the Ubsu-Nur depression; *L. barbarus, L. macrostigma, I. pumilio, S. sahlbergi, S. depressiusculum* and *S. sanguineum* only in Central Tuva, and *C. splendens, C. johanssoni, A. subarctica, O. obscurus, Epitheca bimaculata, Somatochlora alpestris, S. arctica, S. exuberata* and *S. metallica* were recorded only in the Todzha depression. *Aeshna grandis* was not recorded in the Ubsu-Nur depression, while *A. crenata* and *Orthetrum cancellatum* were not recorded in the Central Tuva. *Coenagrion ecornutum, C. lanceolatum, E. cyathigerum risi, A. mixta, A. parthenope, O. spinicornis, S. tibiale* and *S. vulgatum* were not found in Todzha.

Due to a short summer, the flight periods of all species converged in mid-summer around July. Early species, e.g. *L. rubicunda* and *L. quadrimaculata*, appeared later than, for instance, in Europe, so they occurred until late July. Only several

Sympetrum spp. and single individuals of *Aeshna* spp. were found on the wing until September. The only species hibernating as an imago, *Sympecma paedisca*, occurred throughout the season: mature individuals were recorded until early July and immature individuals from mid July, so the generations may overlap.

A quantitative comparison of the faunas of the three main parts of Tuva, listed in Table 1, has been estimated using Jaccard coefficient values, *S*, which are as follows: 0.66 for the pair Ubsu-Nur / Central; 0.47 for Central / Todzha; 0.50 for Ubsu-Nur / Todzha.

Table 1 also presents lists of odonate species found in four adjacent regions: (4) Mongolia in the south, considered here as the land within the state borders of Mongolian People's Republic excepting Bulgan Somon, which is situated west of the Mongolian Altai Mts and geographically belongs to Dzhungaria; (5) the Altai Mts in the west, considered within Russia and Kazakhstan but excluding the Mongolian Altai and Gobi Altai; (6) the Yenisey River basin north of the Sayans, territory of Khakas Republic and Krasnoyarskiy Kray Province, with the Angara River basin excluded; (7) Buryatia (Buryat Republic) in the east, considered here with adjacent regions of Irkutsk Province including the Irkutsk environs.

Compiling Table 1 we faced some taxonomic problems. It is still unclear which *Leucorrhinia* taxa of the two pairs of vicariants actually occur in Mongolia. Belyshev & Doshidorzhi (1960) reported *L. intermedia* for Central Aimak, whereas Krylova (1974) listed that record under the name *L. rubicunda*, stating that the previous identification was incorrect. We included both species, for *L. rubicunda* must exist in the Mongolian part of the Ubsu-Nur depression and *L. intermedia* in eastern Mongolia adjacent to the Daurskiy Nature Reserve (Kosterin 1999, 2004a). *L. dubia dubia* has never been recorded from Mongolia but Peters (1985) reported *L. orientalis*. Again, we must expect the latter in the Mongolian part of the Ubsu-Nur depression. In any case, we consider these two taxa conspecific. Existence of intermediate specimens between *Enallagma c. cyathigerum* and *E. c. risi* in the Altai Mts and Irkutsk Province (Kosterin 1999, 2004a) and Tuva (this paper) prompted us to list them together as *E. cyathigerum*.

The main mountain chains of Tuva were evaluated as biogeographical barriers with the efficiency coefficient, *E*. The *E* value for the chain Taskyl Range + Academician Obruchev Mts, which separates Todzha from Central Tuva was 0.53, and 0.34 for the southern chain of Tuvinian mountains (Tsagan-Shibetu – Tannu-Ola – Khorumnug Taiga – Sangilen Mts), which separates Central Tuva from the Ubsu-Nur depression. The *E* value for the East Sayan Mts, which separate Buryatia + Irkutsk Province from the Todzha + Central Tuva, was 0.33. The West Sayan Mts separate the Yenisey basin north of them from both Central Tuva and Todzha, and evaluation of their barrier efficiency dealing with these two parts of Tuva in toto provided the *E* value 0.37. The Altai Mts separate the West Siberian Plain and East Kazakhstan from Central Tuva and Ubsu-Nur depression with the efficiency of $E = 0.66$.

Table 1. Odonate species recorded in Tuva (1-3) and adjacent regions (4-7) — **1**: Central Tuva, incl. Turan and Khemchik depressions and Kaa-Khem basin (locs 1-36); **2**: Ubsu-Nur depression (locs 37-56); **3**: Todzha depression (locs 57-82); **4**: Mongolia, without Bulgan Somon; **5**: Altai Mountains; **6**: Yenisey basin N of Sayans, without Angara basin; **7**: Buryatia and Irkutsk Provinces. — Information for Mongolia (4) was taken from Dumont (2003) and Kosterin (2004a); for Altai (5) from Belyshev (1973a, b), Kosterin (1987, 1989, 2005), Dronzikova (2000) and Chaplina et al. (2007); for the Yenisey basin (6) from Belyshev (1973a, b) and Malikova (1995); for Buryatia and Irkutsk Provinces (7) from Belyshev (1973a, b). For notes on subspecific taxa, see text.

	Tuva			Adjacent regions			
	1	2	3	4	5	6	7
Calopteryx japonica Selys, 1869	-	-	-	-	+	+	+[2]
Calopteryx splendens (Harris, 1870)	-	-	+	+	+	+	+[2]
Calopteryx virgo (Linnaeus, 1758)	-	-	-	+	-	+	-
Lestes barbarus (Fabricius, 1798)	+	-	-	+	+	-	-
Lestes dryas Kirby, 1890	+	+	+	+	+	+	+
Lestes macrostigma (Eversmann, 1836)	+	-	-	+	+	-	-
Lestes sponsa (Hansemann, 1823)	+	+	+	+	+	+	+
Lestes virens (Charpentier, 1825)	-	-	-	+	+	-	-
Sympecma paedisca (Brauer, 1877)	+	+	+	+	+	+	+
Coenagrion armatum (Charpentier, 1840)	+	+	+	+	+	+	+
Coenagrion ecornutum (Selys, 1872)	+	+	-	+	+	+	+
Coenagrion glaciale (Selys, 1872)	-	-	-	-	-	-	+
Coenagrion hastulatum (Charpentier, 1825)	+	-	+	-	+	+	+
Coenagrion hylas (Trybom, 1889)	+	+	+	+	+	+	+
Coenagrion johanssoni (Wallengren, 1894)	-	-	+	+	+	+	+
Coenagrion lanceolatum (Selys, 1872)	+	+	-	+	+	+	+
Coenagrion lunulatum (Charpentier, 1840)	+	+	+	+	+	+	+
Coenagrion puella (Linnaeus, 1758)	-	-	-	-	+	-	-
Coenagrion pulchellum (Vander Linden, 1825)	-	-	-	-	+	-	-
Enallagma cyathigerum (Charpentier, 1840)	+	+	+	+	+	+	+
Erythromma najas (Hansemann, 1823)	+	+	+	+	+	+	+
Ischnura aralensis Haritonov, 1979	-	-	-	-	+[1]	-	-
Ischnura elegans (Van der Linden, 1820)	-	+	-	+	+	-	+
Ischnura pumilio (Charpentier, 1825)	+	-	-	+	+	-	-
Nehalennia speciosa (Charpentier, 1840)	-	-	-	-	+	+	-
Platycnemis pennipes (Pallas, 1771)	-	-	-	-	+	+	-
Aeshna affinis Vander Linden, 1825	-	+	-	+	+	-	-
Aeshna caerulea Ström, 1873	+	+	+	+	+	+	+
Aeshna crenata Hagen, 1856	-	+	+	+	+	+	+
Aeshna grandis (Linnaeus, 1758)	+	-	+	-	+	+	+
Aeshna juncea (Linnaeus, 1758)	+	+	+	+	+	+	+
Aeshna mixta Latreille, 1805	+	+	-	+	+	-	-
Aeshna serrata Hagen, 1856	+	+	+	+	+	-	+
Aeshna subarctica Walker, 1908	-	-	+	-	+	-	+
Aeshna viridis Eversmann, 1836	-	-	-	-	+	-	-

	Tuva			Adjacent regions			
	1	2	3	4	5	6	7
Anax ephippiger (Burmeister, 1839)	-	-	-	-	+	-	-
Anax imperator Leach, 1815	-	-	-	-	+[1]	-	-
Anax parthenope Selys, 1839	+	+	-	+	+	-	+
Macromia amphigena Selys, 1871	-	-	-	-	+	+	-
Nihonogomphus ruptus (Selys, 1857)	-	-	-	-	+	+	+
Ophiogomphus cecilia (Geoffroy in Fourcroy, 1785)	-	-	-	-	+	+	-
Ophiogomphus obscurus Bartenev, 1909	-	-	+	-	+	+	+
Ophiogomphus spinicornis Selys, 1878	+	+	-	+	-	-	+
Shaogomphus postocularis (Selys, 1869)	-	-	-	-	+	+	-
Stylurus flavipes (Charpentier, 1825)	-	-	-	-	+	-	+
Cordulia aenea (Linnaeus, 1758)	+	-	+	-	+	+	+
Epitheca bimaculata (Charpentier, 1825)	-	-	+	-	+	+	+
Somatochlora alpestris (Selys, 1840)	-	-	+	-	+	+	+
Somatochlora arctica (Zetterstedt, 1840)	-	-	+	-	+	+	+
Somatochlora exuberata Bartenev, 1911	-	-	+	-	-	?	+
Somatochlora flavomaculata (Vander Linden, 1825)	-	-	-	-	+	-	-
Somatochlora graeseri Selys, 1887	+	+	+	+	+	+	+
Somatochlora metallica (Vander Linden, 1825)	-	-	+	-	+	+	-
Somatochlora sahlbergi Trybom, 1889	+	-	-	-	+	+	+
Leucorrhinia albifrons (Burmeister, 1839)	-	-	-	-	+	-	-
Leucorrhinia caudalis (Charpentier, 1840)	-	-	-	-	+	-	+[2]
Leucorrhinia dubia (Vander Linden, 1825) s. l.	+	+	+	+	+	+	+
Leucorrhinia intermedia Bartenev, 1910	-	-	-	+	+	+	+
Leucorrhinia pectoralis (Charpentier, 1825)	-	-	-	-	+	-	-
Leucorrhinia rubicunda (Linnaeus, 1758)	+	+	+	+	+	-	-
Libellula depressa Linnaeus, 1758	-	-	-	-	+[1]	-	-
Libellula quadrimaculata Linnaeus, 1758	+	+	+	+	+	+	+
Orthetrum albistylum (Selys, 1842)	-	-	-	-	+[1]	-	+
Orthetrum brunneum (Fonscolombe, 1837)	-	-	-	+	+[1]	-	-
Orthetrum cancellatum (Linnaeus, 1758)	-	+	+	+	+	+	-
Sympetrum croceolum (Selys, 1883)	-	-	-	-	+	-	-
Sympetrum danae (Sulzer, 1776)	+	+	+	+	+	+	+
Sympetrum depressiusculum (Selys, 1841)	+	-	-	+	+[1]	+	-
Sympetrum flaveolum (Linnaeus, 1758)	+	+	+	+	+	+	+
Sympetrum fonscolombii (Selys, 1840)	-	-	-	+	+[1]	-	-
Sympetrum meridionale (Selys, 1841)	-	-	-	+	+	-	-
Sympetrum pedemontanum (Müller in Allioni, 1766)	+	+	+	+	+	+	+
Sympetrum sanguineum (Müller, 1768)	+	-	-	+	+	+	-
Sympetrum striolatum (Charpentier, 1840)	-	-	-	+	-	-	-
Sympetrum tibiale (Ris, 1897)	+	+	-	+	+[1]	-	-
Sympetrum vulgatum (Linnaeus, 1758)	+	+	-	+	+	+	+
Total species	34	29	32	43	71	43	43

[1)] Recorded only from Altai within Kazakhstan, absent from Russian part of Altai.
[2)] Recorded only from Irkutsk Province, not yet found in Buryatia.

Discussion

With 47 species recorded the faunal list is still likely to be incomplete. The eastern *Coenagrion glaciale* (Selys, 1872), flying at the beginning of the warm season, might be found anywhere, first of all in the Todzha depression. On the rivers of Todzha and the wooded piedmonts of the West Sayan, some rheophilic species, known from the Kemerovo Province and northern Altai, are not excluded if they cross the Sayans, e.g. *Calopteryx japonica, Macromia amphigena, Nihonogomphus ruptus, Shaogomphus postocularis* and *Stylurus flavipes*. Southern species of *Sympetrum*, known from Mongolia, might also be met with, i.e. *S. fonscolombii, S. meridionale* and *S. striolatum*. The latter was collected by VZ on 17 viii 1995 at the southern bank of Lake Ubsu-Nur, which is situated in Mongolia but nearby the border to southern Tuva. It is surprising that we found only two species of Gomphidae, both belonging to the genus *Ophiogomphus*.

Most of the species recorded in Tuva are also found in Europe (87%; plus two more species, *Coenagrion ecornutum* and *Somatochlora graeseri*, reaching the eastern border of Europe in the Ural Mts). The proportion of species reaching the Pacific coast is only slightly less (79%); for details of the longitudinal limits see Kosterin (2005). It may be concluded that Tuva, the centre of Asia, is exclusively inhabited by widely ranging allochtonous species. In the Tuvinian fauna 79% of species are boreal.

From the values of the Jaccard coefficient (*S*) and notes on certain species it is clear that Todzha differs strongly in its odonate fauna from the rest of Tuva. This is also consistent with the different ecological conditions and general landscape features in Todzha. Moreover, the Taskyl and Obrucheva Mts are more ancient than the West Sayan and Tannu-Ola Mts. One may conclude that Todzha is only artificially (administratively) attributed to Tuva, and the natural histories of Todzha and the main Tuva have been independent for a very long time.

Among the three main depressions of Tuva, the Todzha depression has the greatest number of species found in or absent from this depression only. Firstly we should mention the presence of species characteristic of wooded habitats: *Coenagrion johanssoni, Ophiogomphus obscurus, S. exuberata* and *S. metallica abocanica*. The sympatry observed of the two latter taxa has finally provided a sound argument for their species status. *Enallagma c. cyathigerum* in Siberia is characteristic of the taiga zone, hence it inhabits Todzha and scarcely penetrates beyond it to the Turan depression and the Kaa-Khem upper basin. At the same time nearby, in the Central Tuvinian and Ubsu-Nur depressions, only *E. c. risi* occurs, a taxon confined to the forest-steppe and steppe zones of Asia (Kosterin 1999, 2004a). Only in Todzha is the genus *Calopteryx* present. At the same time, in certain respects the fauna of the north-eastern Todzha depression looks more western than that of the more southerly lying steppe depressions. In Todzha *Coenagrion hastulatum* has been found, which generally predominates in Siberia west of the Yenisey, while in the Central Tuvinian depression the closely related *C. lanceolatum* prevails, which in Siberia is generally abundant east of the Yenisey. Again, Todzha is presently the easternmost known habitat of a generally western species *S. metallica*. The appearance of most male specimens of *E. najas* from Todzha corresponds to the western nominotypical subspecies, while in the rest of Tuva is inhabited by *E. n. humerale*.

It should be noted that the fauna of the forest and steppe depressions did not fully correspond with our a priori expectations. According to our experience in West Siberia, the two related *Aeshna* species, *A. crenata* and *A. serrata*, partly displace each other ecologically: the former prefers lakes in more or less wooded landscapes, while the latter prefers open landscapes and is most abundant at often brackish steppe and forest-steppe lakes, although it extends far to the north within the forest zone. However, in Todzha *A. crenata* coexists at a number of localities with *A. serrata*. *A. crenata* also flew abundantly in the floodplains of the Tes-Khem and Erzin River in the Ubsu-Nur depression, which were surrounded with floodplain forests neighbouring patches of sand desert, but only a few individuals of *A. serrata* were seen in the Erzin floodplain. Moreover, in Todzha *Orthetrum cancellatum* was found, although known to prefer lakes in open steppe and forest-steppe landscapes.

As to the neighbouring regions, the greatest number of species (71) has been recorded in the Altai Mts. This mountainous country is in general very unsuitable for odonates, and its rich fauna occurs mostly in its western and northern foothills. The short Tuvinian slope of Altai is still unexplored and must be very poor in Odonata, so all species included in Table 1 are found beyond (from the Tuvinian point of view) the highest mountains of Altai. It is noteworthy that the fauna of the Altai Mts includes all species recorded in the entire West Siberian Plain. In each of the three other adjacent regions considered in Table 1, 43 species were recorded, which is only slightly less than 47 in Tuva.

It was interesting to evaluate the efficiency of the main mountain chains, which border or subdivide Tuva, as biogeographical barriers. The efficiency (*E*) of the Taskyl and Academician Obruchev Mts, which separate Todzha from Central Tuva, although broken by the Biy-Khem River valley, is much greater (0.52) than of the contiguous and unbroken southern chain of Tuvinian Mts, which separate Central Tuva from the Ubsu-Nur Depression (0.32). This is not surprising since the former mountains are much more ancient than the latter, and they separate the intermontane depressions with drastically differing climatic and ecological conditions. The efficiency of the East Sayan Mts, which separate the Buryatia and Irkutsk Provinces from Todzha and Central Tuva, is low (0.33), while that of the huge mountain mass of Altai, separating the West Siberian Plain and East Kazakhstan from Central Tuva and Ubsu-Nur Depression and being most hostile to odonate life, has the highest efficiency (0.66) of all the barriers compared.

Tuva turns out to be the hub of several problems in the taxonomy of Palaearctic dragonflies, in spite of its rather poor fauna and the absence of endemics. It is a crucial place to investigate the relationship of several pairs of vicariant taxa, which most probably came into secondary contact there after a period of isolation and divergence. Most probably, divergence took place during the last (or some earlier) cooling of the Pleistocene, while the new contact happened in the Holocene (Kosterin 2005). In the present study we resolved such a relationship for the *S. metallica* / *S. exuberata* pair, which proved to consist of good species with ecological segregation in the zone of sympatry. The pair *E. najas najas* / *E. n. humerale* is here separated geographically (Todzha/Central Tuva and Ubsu-Nur Depression). Our specimens of the *Leucorrhinia rubicunda*-group represent true *L. rubicunda*, although *L. intermedia* was expected here from the maps in Belyshev (1973a: figs 107, 109). So, a solution to the puzzle of their relationship should be sought for the east of Tuva. The *L. dubia*-group is represented in Tuva by *L. dubia orientalis*, as expected. Lack of reliable morphological differences does not allow a clear attribution of the Tuvinian *Cordulia aenea* specimens to either *C. aenea* s.str. or *C. amurensis*, but these two lineages may co-occur in Tuva as well. Besides these western/eastern pairs of taxa, in Tuva also northern/southern pairs of taxa meet. Tuva is a potential zone of sympatry of *Ophiogomphus obscurus* and *O. spinicornis*. *Enallagma cyathigerum cyathigerum* and *E. c. risi* meet in the Kaa-Khem River basin and the Turan Depression, where they partly segregate into different habitats and partly intergrade with each other.

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References

Asahina, S., 1938. Odonata of Hokkaido. Tenthredo 2: 149-172.

Asahina, S., 1979. Notes on Chinese Odonata. XI. On two North Chinese gomphids, with special reference to Palaearctic *Ophiogomphus* species. Tombo 22: 2-11.

Bartenev, A.N., 1911. [Contributions towards a dragonfly fauna of Siberia 15]. Raboty iz Laboratorii Zoologicheskago Kabineta Imperatorskago Varshavskogo Universiteta 6/7: 1-78. [In Russian].

Bartenef [Bartenev], A.N., 1912. Materialen zur Odonatenfauna Sibiriens. 15. Odonaten aus Transbaikalien. Zoologische Jahrbücher (Systematik) 32: 221-284.

Bartenev, A.N., 1930. Sur une collection des Odonates de la Sibérie orientale et du Turkestan et sur le genre *Ophiogomphus* Sel. dans la région paléarctique. Revue Russe d'Entomologie 24: 115-127. [In Russian; French title]

Bartenef [Bartenev], A.N., 1933. Übersicht der *Leucorrhinia* (Britt., 1850) -Arten und -Varietäten. Archiv für Naturgeschichte (N.F.) 2: 1-53.

Belevich, O.E., 2005: [Dragonflies of the genus *Aeshna* (Odonata, Anisoptera) of the Palaearctic.] Dissertation, Institute of Systematics and Ecology of Animals, Novosibirsk. [In Russian].

Belyshev, B.F., 1955. [Unknown forms and stages of dragonflies from Siberia.]. Zametki po Faunei Flore Sibiri (Tomsk State University) 18: 27-29. [In Russian].

Belyshev, B.F., 1964a. [A new species and subspecies of dragonflies (Odonata, Insecta) from the Southern Baikal Region.]. Izvestiya Vostochno-Sibirskogo Otdeleniya Geograficheskogo Obshchestva SSSR 62: 7-10. [In Russian].

Belyshev, B.F., 1964b. Contributions to the knowledge of fauna of dragonflies (Odonata) of Siberia. I. Fragmenta Faunistica 11: 53-74. [In Russian; English summary].

Belyshev, B.F., 1964c. [The larva of *Leucorrhinia orientalis* Selys and some issues of systematics and genesis of the species.]. Izvestiya Vostochno-Sibirskogo Otdeleniya Geograficheskogo Obshchestva SSSR 62: 3-7. [In Russian].

Belyshev, B.F., 1966. Contributions to the knowledge of fauna of dragonflies (Odonata) of Siberia. II. Materials concerning the fauna and ecology of dragonclies of the Tunka valley in the southern Baikal region. Fragmenta Faunistica 12: 385-411. [In Russian; English summary].

Belyshev, B.F., 1973a. Dragonflies (Odonata) of Siberia. Volume 1, part 1. Nauka, Siberian Branch, Novosibirsk. [In Russian; English title].

Belyshev, B.F., 1973b. Dragonflies (Odonata) of Siberia. Volume 1, part 2. Nauka – Siberian Branch, Novosibirsk. [In Russian; English title].

Belyshev, B.F. & A.K Doshidorzhi, 1960. [Contributions towards the knowledge of the odonate fauna of Mongolia.]. In: "Biologicheskii sbornik". Vostochno-Sibirskoe Otdelenie Geograficheskogo Obshchestva SSSR & Protivochumnyi Institut Sibiri i Dal'nego Vostoka, Irkutsk, pp. 217-221. [In Russian].

Belyshev, B.F. & A.Yu. Haritonov, 1974. [*Agrion hylas* Trybom (Insecta, Odonata), its subspecies and related species in Siberia.]. In: Cherepanov, A.I. (ed.) "Morfologiya i biologiya novykh i maloizvestnykh vidov fauny Sibiri". Novye i maloizvestnye vidy fauny Sibiri 8. Nauka, Siberian Branch, Novosibirsk, pp. 21-29. [In Russian].

Belyshev, B.F. & Y.P. Korshunov, 1976. [New materials for comprehension of the dragonfly fauna (Insecta, Odonata) of transpolar Siberia.]. In: Zolotarenko, G.S. (ed.) "Fauna gel'mintov i chlenistonogikh Sibiri. Fauna Sibiri." Trudy Biologicheskogo Instituta 18. Nauka, Novosibirsk, pp. 151-156. [In Russian].

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

Chaplina, I.A., H.J. Dumont, A. Yu. Haritonov & O.N. Popova. 2007. A review of Odonata of Kazakhstan. Odonatologica 36: 349-364.

Corbet, P.S. & M.L. May, 2008. Fliers and perchers among Odonata: dichotomy or multidimensiotal continuum? A provisional reappraisal. International Journal of Odonatology 11: 173-183.

Coyne, J.A. & H.A. Orr, 2004. Speciation. Sinauer Associates, Sunderland.

Dijkstra, K.-D.B. & R. Lewington, 2006. Field guide to the dragonflies of Britain and Europe., British Wildlife Publishing, Gillingham.

Dronzikova, M.V., 2000. [Odonata of the Tom River basin (fauna and distribution, ecological and ethological characteristics of species)]. Dissertation, Institute of Systematics and Ecology of Animals, Novosibirsk. [In Russian].

Dubatolov, V.V., R.Yu. Dudko, V.G. Mordkovich, O.B. Korsun, S.E. Chernyshev, D.V. Logunov, Yu.M. Marusik, A.A. Legalov, S.V. Vasilenko, L.G. Grishina, G.S. Zolotarenko, A.V. Barkalov, V.P. Petrova, P.Ya. Ustjuzhanin, S.Yu. Gordeev, V.K. Zinchenko, M.G. Ponomarenko, I.I. Lyubechanskii, N.N. Vinokurov, O.E. Kosterin, E.I. Malikova, A.L. L'vovskii, E.A. Maksimenko, E.E. Malkov, A.N. Streltzov, S.G. Rudykh & D.A. Mil'ko, 2004. Biodiversity of the Sokhondo Nature Reserve. Arthropoda. Sokhondo Nature Reserve, Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences, Novosibirsk & Chita. [In Russian].

Dumont, H.J., 2003. Odonata from the Republic of Mongolia and from the Autonomous Region of Inner Mongolia. International Journal of Odonatology 6: 127-146.

Dumont, H.J., A.Yu. Haritonov, O.E. Kosterin, E.I. Malikova & O.G. Popova. 2005. A review of the Odonata of Kamchatka Peninsula, Russia. Odonatologica 34: 131-153.

Eldredge, N. & S.L. Gould, 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M. (ed.) "Models in palaeobiology". Freeman, Cooper & Co., San Francisco, pp. 82-115.

Haritonov, A.Yu. & S.N. Borisov, 1990. Eurasian species of the genus *Ophiogomphus* (Odonata, Gomphidae). In: Zolotarenko, G.S. (ed.) "Redkie gel'minty, kleshchi i nasekomye". Novye i maloizvestnye vidy fauny Sibiri 21). Nauka, Siberian Branch, Novosibirsk, pp. 43-51. [In Russian; English summary].

Hovmöller, R. & F. Johansson, 2004. A phylogenetic perspective on larval spine morphology in *Leucorrhinia* (Odonata: Libellulidae) based on ITS1, 5.8s and ITS2 rDNA sequences. Molecular Phylogenetics and Evolution 30: 653-662.

Inoue, K. & K. Tani, 2003. All about dragonflies. Revised edition. Tombow Shuppan Co., Osaka [In Japanese and English].

Johansson, F., 2002. Reaction norms and production costs of predator-induced morphological defences in a larval dragonfly (*Leucorrhinia dubia*: Odonata). Canadian Journal of Zoology 80: 944-950.

Jödicke, R., P. Langhoff & B. Misof, 2004. The species group taxa in the Holarctic genus *Cordulia*: a study in nomenclature and genetic differentiation (Odonata: Corduliidae). International Journal of Odonatology 7: 37-52.

Kosterin, O.E, 1987. [The dragonfly community of Lake Manzherok.] In: Tambovtsev, A.N. (ed.) "Problemy formorovanitya zhivotnogo naseleniya nazemnykh i vodnykh biotsenozov", A.M. Gorky Omsk State Pedagogical Institute, Omsk, pp. 76-92. [In Russian].

Kosterin, O.E., 1989. [On the dragonfly fauna of the mountainous Altai.]. In: "Problemy ekologii gornykh regionov (sektsiya odonatologii)". Vsesoyuznaya Nauchno-Prakticheskaya Konferentsiya, 9-13 October 1989, Dushanbe, pp. 6-10. [In Russian].

Kosterin, O.E., 1992. New distribution records of *Somatochlora sahlbergi* Trybom (Odonata, Corduliidae). Acta Hydroentomologica Latvica 2: 22-26.

Kosterin, O.E., 1999. Dragonflies (Odonata) of the Daurskii State Nature Reserve and its surroundings. In: Dubatolov, V.V. (ed.) "Nasekomye Daurii i sopredel'nykh territorii. Sbornik nauchnykh trudov. Vypusk 2", Privatly publ., Novosibirsk, pp. 5-40. [In Russian; English summary].

Kosterin, O.E., 2002. [*Ophiogomphus spinicornis* Sel.]. In: Putintsev, N.I., L.K. Arakchaa, V.I. Zabelin & V.V. Zaika (eds) "Krasnaya Kniga Respubliki Tyva. Zhivotnye". Izdatel'stvo Sibirskogo Otdeleniya Rossiiskoi Akademii Nauk, Filial "Geo", Novosibirsk, p. 14. [In Russian].

Kosterin, O.E., 2004a. Odonata of the Daurskiy State Nature Reserve area, Transbaikalia, Russia. Odonatologica 33: 41-71.

Kosterin, O.E., 2004b. Some Odonata collected in Aldan Ulus of Sakha (Yakutia) Republic in Late June 2002. Notulae Odonatologicae 6: 27-31.

Kosterin, O.E., 2005. Western range borders of eastern odonate species in Siberia and their putative origin. Odonatologica 34: 219-242.

Kosterin, O.E., 2007. The first record of *Anax* on the West Siberian Plain: *A. p. parthenope* Selys in Omsk (Anisoptera: Aeshnidae). Notulae Odonatologicae 6: 112-115.

Kosterin, O.E. & V.V. Dubatolov, 2005. A dragonfly (Odonata) collection from the Bol'shekhekhtsirskii State Nature Reserve (Khabarovskii Krai, Russia). In: Streltzov, A.N. (ed.) "Fauna Dal'nego Vostoka Rossii: Sbornik Nauchnykh Trudov", Blagoveshchensk State Pedagogical University, Blagoveshchensk, pp. 9-14.

Kosterin, O.E. & I.I. Lyubechanskii, 2009. Odonata collection from the Bureinskii State Nature Reserve, Khabarovskii Krai, Russia. Notulae Odonatologicae 7: 25-36.

Kosterin, O.E. & V.V. Zaika, 2001. Odonate fauna of the Tyva Republic, or Tuva (Central Siberia). Abstracts of papers of XV International Symposium of Odonatology, Novosibirsk, pp. 10-11.

Kosterin, O.E. & V.V. Zaika, 2003. Odonatological expeditions to the Tyva republic (Tuva) in 2000-2002. IDF-Report 5: 1-32.

Kosterin, O.E., A.Yu. Haritonov & K. Inoue, 2001. Dragonflies of the part of Novosibirsk Province east of the Ob' River, Russia. Sympetrum Hyogo 7/8: 24-49. [In English and Japanese].

Krylova, V.N., 1974. Dragonflies (Odonata) of the Mongolian People's Republic. In: "Nasekomye Mongolii. Tom IV (2)", Nauka, Leningrad, pp. 14-22 [In Russian; English title].

Lohmann, H., 1992. Ein Beitrag zum Status von *Coenagrion freyi* (Bilek, 1954) und zur subspezifischen Differenzierung von *C. hylas* (Trybom, 1889), *C. johanssoni* (Wallengren, 1894) und *C. glaciale* (Selys, 1872), mit Bemerkungen zur postglazialen Ausbreitung ostpaläarktischer Libellen (Zygoptera: Coenagrionidae). Odonatologica 21: 421-442.

Lohmann, H., 1994. *Somatochlora metallica abocanica* Belyshev, 1955, a new member of the European dragonfly fauna (Anisoptera: Corduliidae). Notulae Odonatologicae 4: 39-40.

Malikova, E.I., 1995. [Dragonflies (Odonata, Insecta) of the Far East of Russia.]. Dissertation, Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk. [In Russian].

Malikova, E.I., 2002. The dragonflies (Insecta, Odonata) of the Khingansky State Nature Reserve and its vicinities: In. Streltzov, A.N. (ed.) "Zhivotnyi mir Dal'nego Vostoka 4", Blagoveshchensk State Pedagogical University, Blagoveshchensk, pp. 61-78. [In Russian, English summary].

Malikova, E.I., 2004. On the taxonomic status of Far Eastern *Leucorrhinia*. Abstracts of Papers of XVI International Symposium of Odonatology, Schwerin, pp. 14-15.

Malikova, E.I., 2006. Synonymy of *Somatochlora japonica* Matsumura, 1911 and *S. exuberata* Bartenev, 1911, with the priority of the former. Abstracts of Papers of XVII International Symposium of Odonatology, Hong Kong, p. 33.

Maskaev, Yu.M., B.B. Namzalov & V.P. Sedel'nikov, 1985. [Geobotanical zoning.]. In: Koropachinskii, I.Yu. (ed.) "Rastitel'nyi pokrov i estestvennye kormovye ugodya Tuvinskoi ASSR", Nauka, Siberian Branch, Novosibirsk, pp. 210-247. [In Russian].

Molokova, N.I. & N.D. Kartashev, 1999. [The Azas Nature Reserve.]. In: Pavlov, D.S., V.E. Sokolov, E.E. Syroechkovskii (eds) "Zapovedniki Sibiri", Logata, Moscow, pp. 128-126. [In Russian].

Peters, G., 1985. Die Libellenfauna der westlichen und nördlichen Mongolei und einige Phänomene ihrer intrakontinentalen Isolation. Mitteilungen des Zoologischen Museums Berlin 61: 11-42.

Samraoui, B., P.H. H.Weekers & H.J. Dumont, 2002. The *Enallagma* of the western and central Palaearctic (Zygoptera: Conenagrionidae). Odonatologica 31: 345-434.

Schiel, F.-J., 1998. Zur Habitatbindung des Großen Granatauges (*Erythromma najas* Hansemann, 1823) (Odonata: Zygoptera) am südlichen Oberrhein. Naturschutz am Südlichen Oberrhein 2: 129-138.

Seidenbusch, R., 1997a. Comparison: variability in the occurence of dorsl spines in larvae of *Leucorrhinia dubia* Vanderlinden 1825 and *Leucorrhinia rubicunda* Linnaeus 1758. Sulzbach-Rosenberger Libellenrundbrief 4: 2 pp.

Seidenbusch, R. 1997b. Need in solving taxonomic puzzles: *Leucorrhinia orientalis* Selys, 1887 versus *Leucorrhinia dubia orientalis* Selys, 1887, *Sympetrum imitans* Selys, 1886 versus *Sympetrum vulgatum imitans* Selys, 1886, *Sympetrum sinaiticum arenicolor* Jödicke, 1994 versus *Sympetrum deserti arenicolor* Jödicke, 1994 (= *decoloratum* Selys, 1884 sensu Bartenef (1915)). Sulzbach-Rosenberger Libellenrundbrief 6: 3 pp.

Seidenbusch, R., 1997c. Morphological imaginal comparison in the *Enallagma deserti*-complex: *Enallagma deserti* Selys, 1871, *Enallagma boreale* Selys, 1875, *Enallagma circulatum* Selys, 1883, *Enallagma belyshevi* Haritonov, 1975, *Enallagma risi* Schmidt, 1961. Sulzbach-Rosenberger Libellenrundbrief 6: 6 pp.

Selys-Longchamps, E. de, 1887. Odonates de l'Asie mineure et revision de ceux des autres parties de la faune paléarctique (dite Européenne). Annales de la Société Entomologique de Belgique 31: 1-85.

Sergeev, M.G., 1986. [Regularities of distribution of orthopteran insects of North Asia]. Nauka, Novosibirsk. [In Russian].

Shaktarzhik, K.A., 1993. [Geography of Tuva Republic]. Tuvinskoe Knizhnoe Izdatel'stvo, Kyzyl. [In Russian].

Sjöstedt, Y., 1927. Entomologische Ergebnisse der schwedischen Kamtchatka-Expedition 1920-1922. 13. Odonata. Arkiv för Zoologi 19A (16): 1-5.

Stearns, S.C. & R.F. Hoekstra, 2005. Evolution: an introduction. Second edition. Oxford University Press, Oxford.

Stoks, R., J.L. Nystrom, M.L. May & M.A. McPeek 2005. Parellel evolution of ecological and reproductive traits to produce cryptic dragonfly species across the Holarctic. Evolution 59: 1976-1988.

Suslov, S.P., 1954. [Physical geography of the USSR. Asian Part.]. Gosudarstvennoe Tekhnicheski-Pedagogicheskoe Izdatel'stvo Ministerstva Obrazovaniya RSFSR, Moscow. [In Russian].

Valle, K.J., 1942. Odonaten aus dem westlichen Zentralasien. Annales Entomologici Fennici 8: 114-126.

Zaika, V.V., 1996. [Amphibiotic insects (Insecta) of the Ubsu-Nur Depression.]. In: "Global monitoring and the Ubsu-Nur Depression". Proceedings of IV International Symposium on the results of International Program of Biospheral Monitoring 'The Ubsu-Nur Depression experiment', Intellekt, Moscow, pp. 62-66. [In Russian].

Zaika, V.V., 1999. [Hydrobionts of Lake Tore-Khol' (central part of the Ubsu-Nur Depression, Tuva).]. In: Abstracts of IV International Scientific Conference "Natural conditions, history and culture of West Mongolia and adjacent regions", Tomsk, April 20-24 1999, Tomsk State University, Tomsk, pp. 46-47. [In Russian].

Zaika, V.V., 2003. [Amphibiotic insects of lakes of Todzha (North-East Tuva).] In: "Biodiversity and preservation of the gene fund of flora, fauna and people of the Central Asian Region". Proceedings of 1st International Scientific and Practical Conference (Kyzyl, 23-28 September 2002), TuvIKOPR SO RAN, Kyzyl, p. 36. [In Russian].

Zaika, V.V., 2005. [Aquatic ecosystems of South Siberia and North-West Mongolia and their entomofauna.] In: "Natural conditions, history and culture of West Mongolia and the adjacent regions". Proceedings of VII International Conference, (19-23 September 2005, Kyzyl), TuvIKOPR SO RAN, Kyzyl, pp. 154-159. [In Russian].

Zaika, V.V. & O.E. Kosterin, 1992. Some interesting findings of dragonflies (Odonata) in South Tuva. Acta Hydroentomologica Latvica 2: 81-84.