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First data on dragonflies (Odonata) of Dagestan highlands, Russia

Первые данные о стрекозах (Odonata) высокогорий Дагестана

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Key words: Odonata, dragonflies, damselflies, *Aeshna juncea*, Russia, Caucasus, Dagestan, highlands, lakes, vertical migrations.

Ключевые слова: Odonata, стрекозы, *Aeshna juncea*, Россия, Кавказ, Дагестан, высокогорья, озёра, вертикальные миграции.

Abstract. Published data on Odonata of Dagestan in highland habitats, that is situated above the tree line, were confined to registration in 1924–1926 of *Aeshna juncea* (Linnaeus, 1758) at Kurush village (the southernmost settlement of Russia). During the focused studies on the dragonflies of Dagestan in 2021–2023, we accumulated data on those of seven highland habitats situated in six districts at elevations of 2000–2800 m a.s.l., five of which are lakes or lake groups. Thirteen species from five families were revealed, including *Cordulia aenea* (Linnaeus, 1758) recorded in Dagestan for the first time, its habitat at 2525 m a.s.l. at Lake Bezdonnoe appearing the most elevated of those known for this species in the world. Elevation limits of other dragonflies of Dagestan are discussed. The huge population of *A. juncea crenatoides* Bartenef, 1925 of Lake Debrishara (2816 m a.s.l.) is unique in many respects: (1) the emerged dragonflies commence a downward vertical migration to the valley situated ca 400 m below; (2) about one quarter of specimens have an unusual pattern of the synthorax sides, with the additional pale stripe merging with the fore main stripe (the same morph was revealed in all specimens in populations in Armenia and South-eastern Turkey); (3) females thrice exceed males in number. Possible causes of these peculiarities are discussed.

Резюме. Литературные данные о стрекозах Дагестана, населяющих высокогорные, то есть расположенные выше границы леса, местообитания сводились к фиксации в 1924–1926 гг. *Aeshna juncea* (Linnaeus, 1758) у с. Куруш (самый южный населённый пункт России). В ходе целенаправленных исследований стрекоз Дагестана в 2021–2023 гг. получены данные о стрекозах семи изолированных высокогорных местообитаний в шести районах, расположенных на высотах 2000–2800 м н.у.м., из которых пять являются озёрами или озёрными группами. Выявлено 13 видов стрекоз пяти семейств, в том числе *Cordulia aenea* (Linnaeus, 1758) была найдена в Дагестане впервые, причём её местообитание на высоте 2525 м н.у.м. на оз. Бездонное оказывается самым высоко расположенным из известных для этого вида в мире. Обсуждаются высотные пределы других видов стрекоз Дагестана. Огромная популяция *A. juncea crenatoides* Bartenef, 1925 озера Дебришара (2816 м н.у.м.) уникальна во многих отношениях: (1) выплодившиеся на нём стрекозы совершают вертикальную миграцию вниз, в долину, расположенную на приблизительно 400 м ниже; (2) около четверти особей имеют необычный рисунок боков синторакса, с дополнительной светлой полоской, сливающейся с первой основной полосой (такая же морфа выявлена в Армении и ЮВ Турции, где к ней относятся все особи популяций); (3) по численности самки втрое преобладают над самцами. Обсуждаются возможные причины таких особенностей.

Introduction

Dragonflies and damselflies (further on just «dragonflies») are amphibiotic insects with the larvae developing in water. Compared to other groups of such insects, mayflies, stone flies and caddis flies, they are quite thermophilous, so that with latitude, limnophylic species became more and more predominating over rheophylic ones, while highlands of the temperate zone, here assumed as altitudinal belts over the tree line, appear in general uncomfortable for dragonflies, even in the extreme south of this country. Highland dragonfly assemblages were to some extent studied in the course of general investigations of Odonata fauna of the Russian part of the Caucasus in the beginning of the XX by A.N. Bartenev [Bartenef, 1929a, 1930], and recently

[Ketenchiev, Haritonov, 1998, 1999; Skvortsov, 2010; Kosterin, 2023]. At the same time the fauna of Dagestan remained quite underexplored: there was just an old special paper by Artobolevskij [1929] and a number of short reports most recently [Ilyina et al., 2014, 2022; Ilyina, Aliev, 2017; Onishko, Dunaev, 2017]. To fill this gap, in 2021–2023 the authors undertook a focused study of dragonflies of Republic of Dagestan, during which a number of highland habitats was studied, only for one of which, the environs of Kurush village, just one species, *Aeshna juncea* (Linnaeus, 1758) has been previously reported in literature [Artobolevslky, 1929]. Besides, some data by the first author for previous years were taken into account.

The mountains occupy a bit more than half of the area of Dagestan. Although broad plateaux with levelled surfaces are numerous in their relief, there are very few lakes which could serve as dragonfly habitats [Akhmedkhanov et al., 1996]. This is not surprising since those plateaux are formed by limestone, sensitive to water erosion and so not holding water on its surface. Limestone ranges occupy most of the mountain area of Dagestan forming the so-called Limestone Region. Only the Watershed Range, along which the border of Russia and Georgia goes, and the parallel to it Lateral Range are formed by shale and comprise the Shale Region. Lakes are frequent on the latter two high ranges but are situated mostly in the nival zone, over 3000 m a.s.l. [Akhmedkhanov et al., 1996] and hence unfit dragonfly development.

We examined dragonflies of six lakes, lake groups or other habitats, including the majority of relatively easily accessible highland lakes of Dagestan, situated, in its different administrative districts, at the levels of 2000–3000 m a.s.l. Being so rare in Dagestan, all highland dragonfly habitats appeared quite unique both in their natural conditions and their dragonfly assemblages, not representing anything 'typical'. Therefore this communication is of rather ecological than faunistic nature, so in 'Results' below we consider the localities separately, simultaneously characterising the their habitats and dragonflies, and then provide a general annotated checklist of collected specimens and photographic observations.

Materials and Methods

Observing and photographing of dragonflies and their collecting with an entomological net were made on walk routes, in some cases involving ascend by feet to lakes for 700–1000 m. The collected specimens were immersed in acetone overnight, then dried out and placed to cotton layers, with final storing in individual cellophane envelopes at the Institute of Cytology & Genetics of the Siberian Branch of the Russian Academy of Sciences.

The data up to 2021 were represented by collected specimens only. Since 2022, much attention was paid to photographic registration of dragonflies, which allowed us to restrict collecting and hence damage to fragile highland populations to the necessary minimum. For this the camera Sony Cyber-shot DSC-RX10 was used. The track backlogs of all routes were put down with the use of GPS-navigator GARMIN Dacota 20, and the photographs were synchronised with them for geolocation using the Adobe Photoshop Lightroom Classic software, with visual checking of geolocation correctness. All photographic registrations of dragonflies were uploaded as observations to the internet-platform iNaturalist [2023] where they got individual numbers (x) being an integer value of nine (in our case) digits. These observation numbers are provided in parenthesis in the annotated list below, in subsections «Photographic records», or «Collected specimens» if exactly the collected specimens were photographed. These observations are available by substituting x with their numbers in the following URL form: https://inaturalist.org/observations/x.

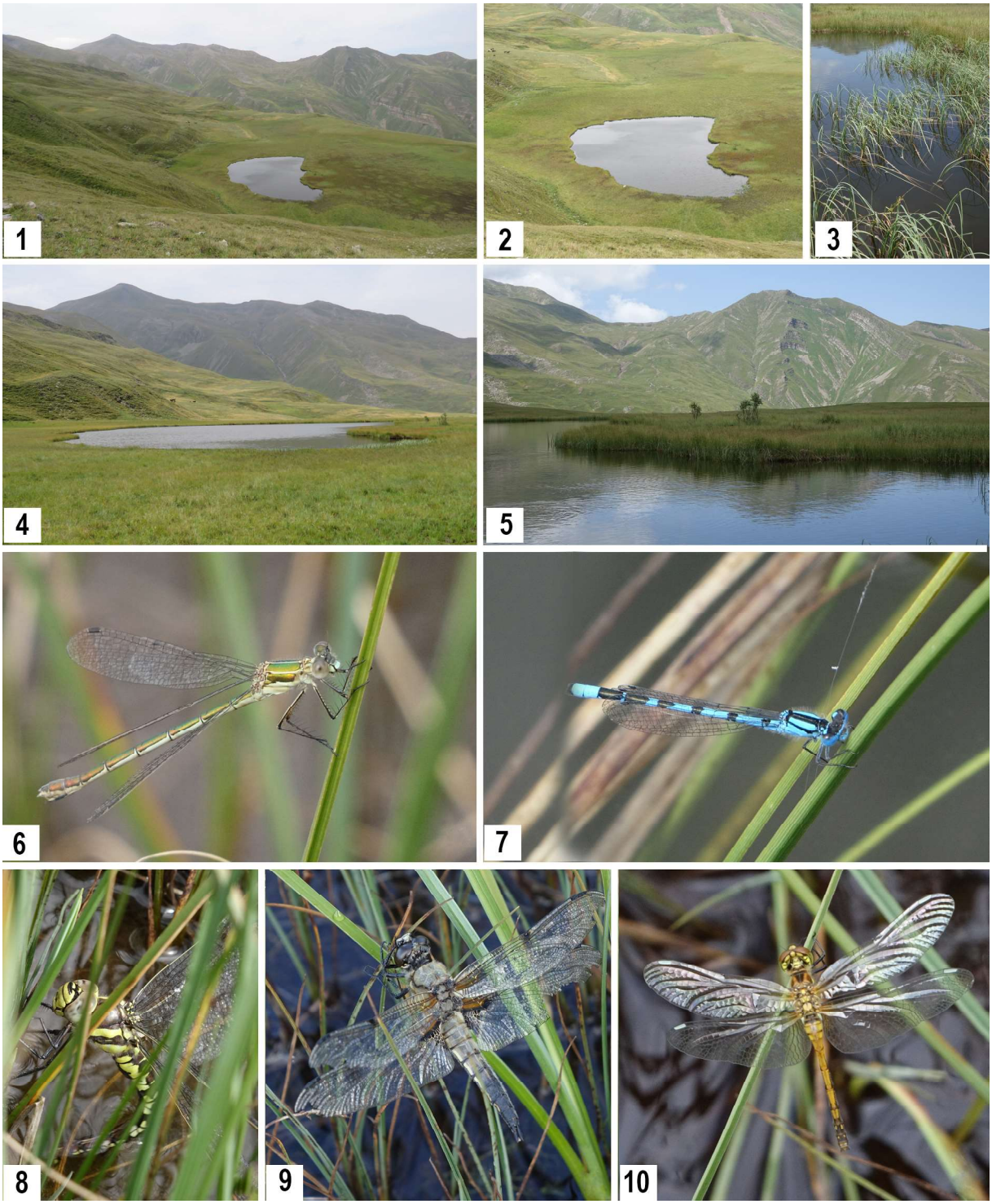
They can serve as numerous external geolocated illustrations to this paper. Also the observations confirmed in iNaturalist as of 'research grade' are adopted by Global Biodiversity Information Facility [iNaturalist contributors, iNaturalist, 2023].

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:C32D5200-7E55-4F41-9B4F-CB6F1B0E49E7.

Localities examined

Lake Bezdonnoe (Ag'il' Ig'ra) is situated in Tsumada District, 3 km NW of Upper Gakvari village, on the Snegovoy (Snowy) Mt. Range, on a ledge of a NNE slope of a spur going from the Zainkort Mt (3308 m a.s.l.) in 3.9 km WNW, on the right board of the Gaderi River valley, at 2525 m a.s.l., 42.570–42.571° N, 46.015–46.018° E (Figs 1–6). The open water surface is 95×50 m, while the lake lies in a depression 250×180 m filled with hanging. yet walkable sedge (2–3 species, mostly *Carex rostrata* Stokes) floating bog, the area of which is four times as large as that of open water (Figs 1–5), with patches of sparser sedge or *Aulacomnium* sp. moss soaking with water, but without additional 'windows' of open water. The ridge rises up to 50–100 m above the lake, at its side the floating bog narrows to 5–10 m. On the opposite side, the depression, with the floating bog up to 120 m broad, is bordered by just a negligible gentle relief elevation, which separates it from the Gaderi River valley. The lake is fed with springs descending from the ridge and a larger brook entering the lake from NWN, with an own short valley also clad with sedge floating bog, with participation of *Eriophorum vaginatum* L. The lake has no surface outlet. On the bog, flowering *Epilobium* sp. and rare *Swertia iberica* Fisch. & C.A. Mey. occur, near the water edge few saplings of birch (*Betula litwinovii* Doluch.) and one of pine (*Pinus sylvestris* L. var. *hamata* (Steven) Fomin) were met with. The water edge is the hanging margin of the floating bog formed by *Carex rostrata* Stokes, the water is immediately deep. Between 2021 and 2023, trout was introduced into the lake, so on the 2023 visit we permanently observed fishes jumping out of the water, perhaps because hydrogen shortage. There are few *Rana macrocnemis* Boulinger, 1885. The

lake environs are clad with short subalpine meadows, on the ridge N slope with frutescent and fruticulose plants such as *Rhododendron caucasicum* Pall., *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Empetrum nigrum* L. s.l. The closest forest vegetation is 2.8 km apart in the NE direction, where reaches about 2400 m a.s.l.



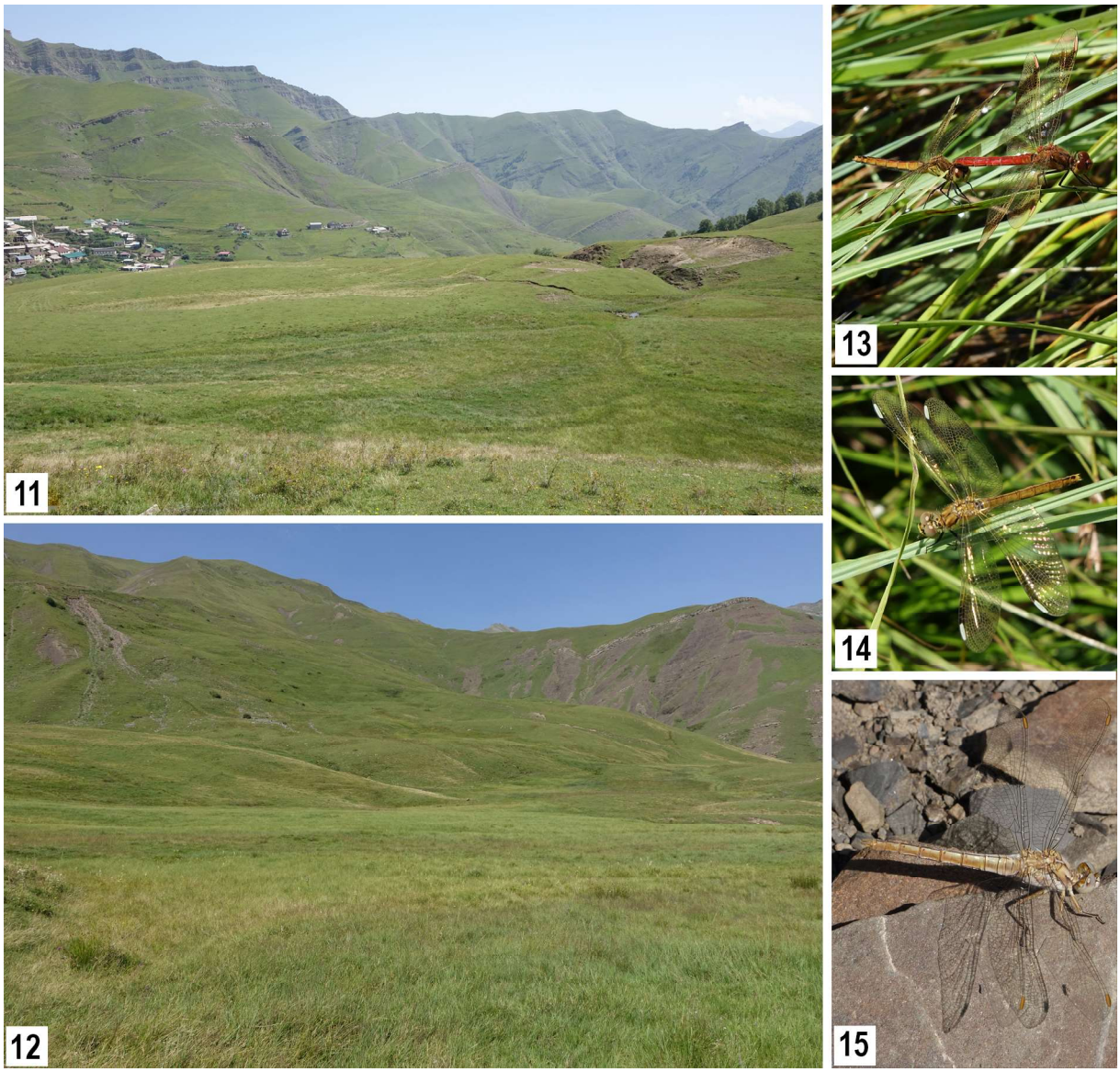
Figs 1–10. Dragonflies photographed on 5.VIII.2023 at Lake Bezdonnoe (Ag'il' Ig'ra); males (7.9) and females (6, 8, 10): 1–5 — views of the lake; 6 — *Lestes sponsa* (Hans.); 7 — *Enallagma cyathigerum cyathigerum* (Charp.); 8 — oviposition of *Aeshna juncea crenatoides* Bart.; 9 — *Libellula quadrimaculata* L.; 10 — teneral *Sympetrum danae* (Sulz.).

Рис. 1–10. Стрекозы, сфотографированные 5.VIII.2023 у озера Бездонное (Агьилъ Игьра); самцы (7, 9) и самки (6, 8, 10): 1–5 — вид озера; 6 — *Lestes sponsa* (Hans.); 7 — *Enallagma cyathigerum cyathigerum* (Charp.); 8 — *Aeshna juncea crenatoides* Bart., откладка яиц; 9 — *Libellula quadrimaculata* L.; 10 — неокрепшая *Sympetrum danae* (Sulz.).

Studied on 11.VIII.2021 by E.I. and, more thoroughly, on 5.IX.2021 jointly by E.I. and O.K. The observations for the latter visit are provided below.

Highland bog in the Gakvari River valley **(**Figs 11–15) is situated in Tsumada District, 0.8 km SW of Upper Gakvari village (and 3.4 km SSE of Lake Bezdonnoe), on the right board of the Gakvari River valley, in a shallow depression (ca 650×500 m) of the NE slope of a SE spur of the Zainkort Mt (neighbouring to the above considered spur), at 2000–2070 m a.s.l., 42.536–42.543° N, 46.023–46.027° E. The bottom of this large sedge bog (Figs 11–12) is slightly slanting so its water, varying in amount, is entirely semicurrent and the bog is crossed by several brooks; no signs of cattle grazing. The following flowering plants were frequent: *Parnassia palustris* L., *Geranium palustre* L., also *S. iberica* Fisch. & Mey. close to the firm slope and *Lythrum salicaria* L., *Cardamine uliginosa* M. Bieb., *Epilobium algidum* M. Bieb., *Mentha longifolia* L. etc. by the brooks. The bog outlet is a considerable brook flowing over a steeper slope in a small valley with stony banks and small patches of bog vegetation, with abundant *Juncus effusus* L. The last outposts of forest vegetation are in 300–400 m to SE, almost reaching 2000 a.s.l. Examined on 6.VIII.2023 by E.I. and O.K.

Tlyanub Lakes (Figs 16–18A) is a group of six (earlier seven) lakes in Shamil' District, 5–6 km WNW of Tlyanub village, situated in the Shale Region but close to its bodrer with the limestone Region. These terrace-type lakes are disposed on a small grassy plateau (formed as a dead glacier moraine), 3.5×2.7 km, on the NW prin-

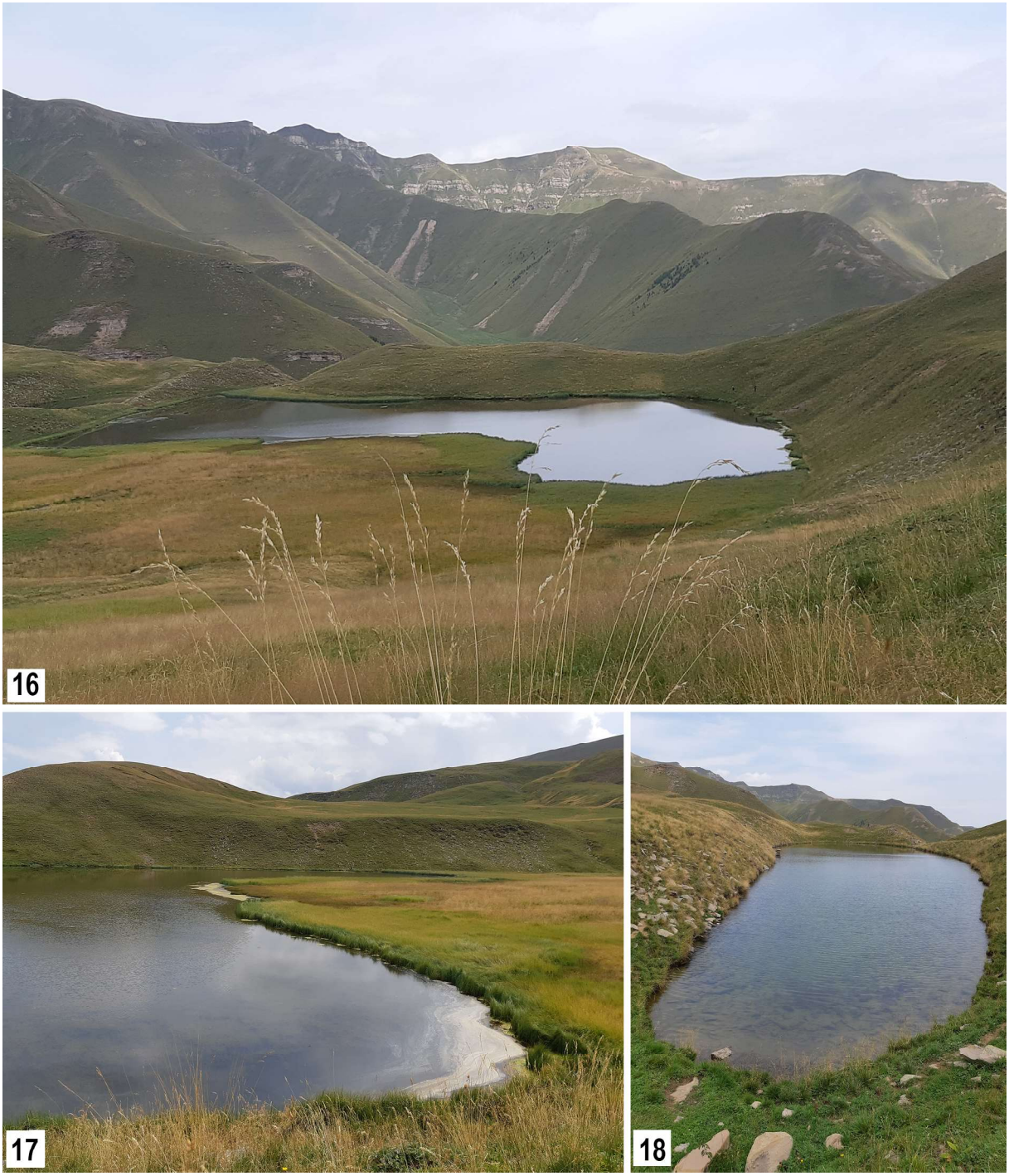


Figs 11–15. Dragonflies photographed on 6.VIII.2023 at a sedgy, flowing water bog at Upper Gakvari village: tandem (13), teneral female (14) and young male (15). 11–12 — views of the bog; 13–14 — *Sympetrum pedemontanum pedemontanum* (Müll.); 15 – *Orthetrum brunneum* (Fons.).

Рис. 11–15. Стрекозы, сфотографированные 5.VIII.2023 на проточном осоковом болоте в окрестностях с. Верхнее Гаквари: тандем (13), свежевыплодившаяся самка (14) и молодой самец (15). 11–12 — вид болота; 13–14 — *Sympetrum pedemontanum pedemontanum* (Müll.); 15 — *Orthetrum brunneum* (Fons.).

ciple slope of Bogos Mt. Range, at 2417–2537 m a.s.l., 42.452–42.455° N, 46.394–46.396° E. The largest is Lake Ruchchabazulkhor [Руччабазулхор] (Figs 16–17) is 250×165 m, with sedge thickets of varying breadth along the banks and some small thread algae matts in water at the banks. At slightly higher level, in an erosion depression, a somewhat smaller Lake Khurzukhukhkhor [Хурзухуххор] lies (Fig. 18), missing aquatic and semiaquatic vegetation, with grassy (Poaceae) banks. The rest four lakes are small and nameless, also missing aquatic and semiaquatic vegetation. As compared to the description of these lakes by K. Akhmedkhanov [1998], for the last quarter of century the area of the lakes shrank substantially and the seventh lake disappeared and got overgrown with grass. The lakes are used for sheep drinking. Studied on 22.VIII.2021 by E.I.

Lake Mochokh (Fig. 19) is situated in Khuznakh District, in the valley between two parallel limestone



Figs 16–18. Tlyanubskie Lakes views. 16–17 — Lake Ruchchabasulkhor; 18 — Lake Khurzukhukhkhor.
Рис. 16–18. Вид на Тлянубские озёра. 16–17 — оз. Руччабазулхор; 18 — оз. Хурзухуххор.

mountain ranges Tanusdiril and Kachta (Ochlinskiy), north of Mochokh village, at 1633 m a.s.l., 42.624–42.532° N, 46.619–46.629° E, The lake is of the landslide-dam type as formed by the landslide of 1963, which dammed the Mochokhtlyar River mouth [Idrisov, 2014]. The largest of the examined water bodirs, 1250×500 m (Fig. 19), with the maximum depth of 60 m; the water is clear and deep. The banks are stony, mostly gentle, locally with small thickets of *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha* sp. There are *Rana ridibunda* Pallas, 1771 and *R. macrocnemis* Boulinger, the trout was introduced. The lake is surrounded by subalpine meadows, the closet outpost of pine/birch forest are found 0.5 upstream of the valley at ca 1600 m a.s.l., also there are small willow thickets along the river at the lake upstream end, and the landslide dam is also being overgrown with forest. Examined on 8.VII.2023 by E.I.

Takhor Lakes are situated in the Shale Region of Dagestan. A group of seven lakes and smaller pools, also called Slantsevye (Shale) Lakes, situated in Tlyarata District 7–10 km SE of Tokhota village, on the NE principal Slope of the Watershed (Great Caucasus) Mt. Range, in the Takhor River headwaters at elevations of 2906–3151 m a.s.l. The closest pine/birch forests are 4.5 km down the valley, at 2200 m a.s.l. Two lakes were examined. The lake 9 km SE of Tokhota village is situated at 3044 m a.s.l., 41.939–41.941° N, 46.411–46.413° E. It has neither surface influx nor outlet, a shale stony bottom and not so cold water but lacks any aquatic and semiaquatic vegetation. Numerous Tipulidae (many mating) were observed at its banks. It is surrounded by alpine meadows, degraded through heavy sheep grazing and stone screes. The lake 7 km SE of Tokhota is at 2906 m a.s.l., 41.948–41.949° N, 46.423–46.425° E. It also lacks any water vegetation but tadpoles of *R. macrocnemis* Boulinger were abundant in water. It has two outlet brooks, separated with a grassy bog with the cottongrass *Eriophorum vaginatum* L. Also surrounded by the same degraded alpine meadows, with presence of the thistle *Cirsium obvallatum* (M. Bieb.) Fisch. Studied on 16.VIII.2016 by E.I. and on 24.VII.2022 by E.I. and O.K.

Lake Debrishara (Figs 20–31) is situated in Agul District 4.5 km SW of Chirag village and 5.2 km ENE of the Alakhundag Mt. (3830 m a.s.l.), in a small cup-like depression of a SE spur of the Kokma Mt. Range, at 41.799–41.800° N, 47.407–47.409° E, 2816 m a.s.l. Its size is 175×171 m, but the open water area is only ca 72×70 m while the rest water area is occupied by thick emerging sedge (*Carex rostrata* Stokes Stokes) (Figs 20–22). The lake is fed by several springs (with flowering *Epilobium algidum* M. Bieb., *Cardamine uliginosa* M. Bieb. etc.) flowing from the adjacent NW ridge slope, and has an outlet as a small brook crossing an earthy natural dam of a negligible height, which separates the lake from the quite steep slope. About a half of the depression, mostly from the side opposite to the outlet, is occupied by sedge floating bog, mostly of *C. rostrata* Stokes, while the broad thickets of the same sedge species emerging from the lake at its outlet side grow from the firm bottom. The lake is mostly ca 1 m deep but deeper at its centre, the water is very cold. The inner side of the sedge thickets is rimmed by a broad floating strip of flowering *Persicaria amphibia* (L.) Delarbre. The bottom is covered with a carpet of *Myriophyllum verticillatum* L.; at the shallow water along the firm bank there is a strip of submerged *Potanogeton alpinus* Balb. No frogs, but a *Neomys schelkovnikovi* Satunin, 1913 was noticed. The lake and floating bog are surrounded by a strip of damp meadow with flowering *Saxifraga hirculus* L., *Trifolium spadiceum* L., the ridge slope is clad with alpine meadows and screes. The closest outposts of birch (*B. litwinovii* Doluch.) forest are 1.2 km apart, on north-exposed slopes at ca 2500 m a.s.l. Exained on 18.VII.2021 by E.I. and on 9.VIII.2023 by E.I. and O.K.

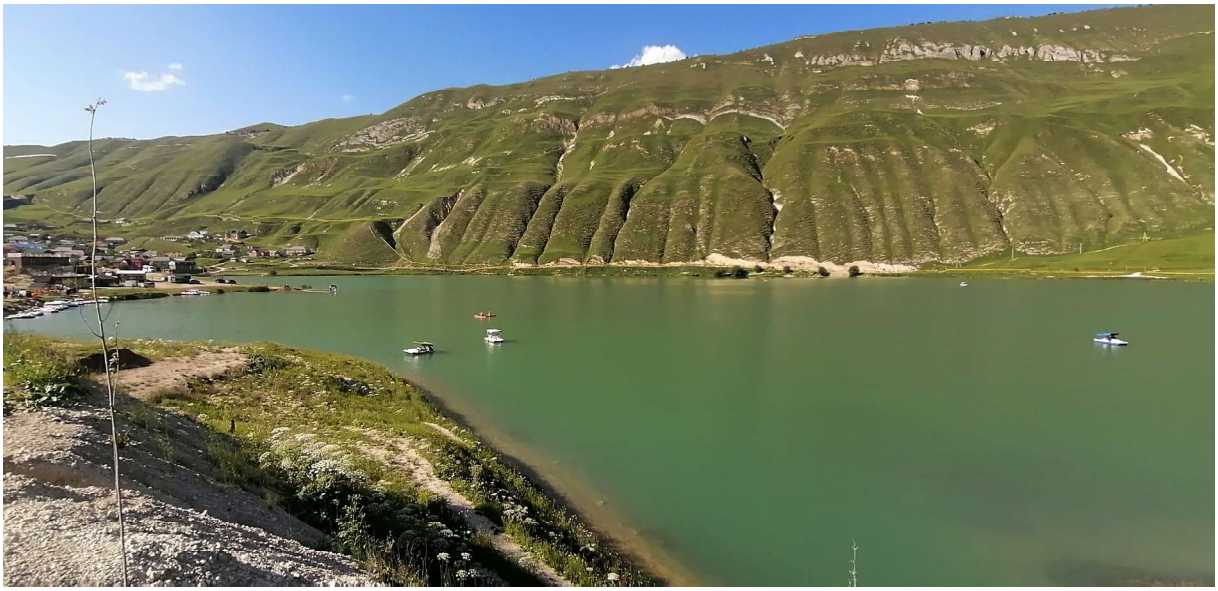


Fig. 19. Lake Mochokh view.
Рис. 19. Вид на озеро Мочох.

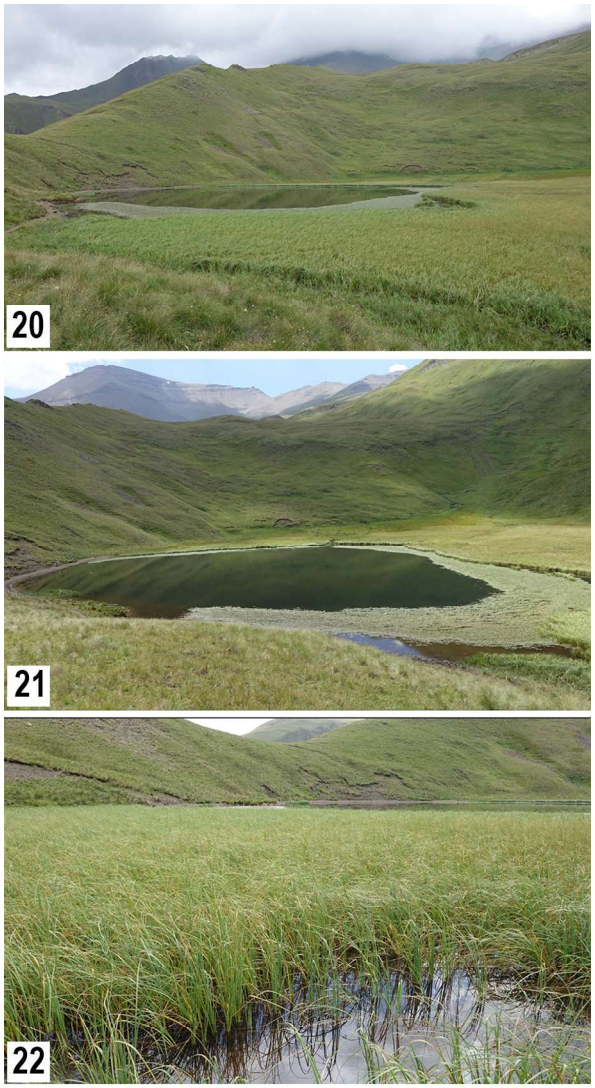
Rivulet at Kurush (Figs 32–34) is a shallow rivulet 1 km NE of Kurish village, Dokuzparinskiy District, in a fold of the Shalbuzdag Mt. (4142 a.s.l.) SW slope, at 2469 m a.s.l., 41.2883° N, 47.8379° E. It flows through a small grassy (Poaceae, *Tussilago farfara* L., *Cephalaria gigantea* (Ledeb.) Bobrov etc.) valley, then among large boulders at a steeper slope (Fig. 33). Surrounding slopes are clad with high herbage subalpine meadows, used for hey. Examined on 14.VIII.2022 by E.I.

Of the seven examined habitats, two (the Takhor Lakes and Tlyanub Lakes) were situated in the Shale Region of the mountainous Dagestan, while the five others — in the Limesone Region.

Results of the localities study

Observations on visits to the Lake Bezdonnoe (Ag'il' Ig'ra). The water edge formed by the margin of the floating bog of *C. rostrata* Stokes was patrolled by males of *Aeshna juncea crenatoides* Bartenef, 1925 (which flied not as low above the water as in the European Part and Siberia [Bernard, Kosterin, 2010], where they are under pressure of competing other *Aeshna* Fabricius, 1775 species). Two ovipositing females were observed, one at the water edge of a tiny bay, the other in about 1 m from its bank (Fig. 8), both were not at all cautious and were collected by hand. Also the water edge was patrolled by males of *Cordulia aenea* (Linnaeus, 1758), which passed by the same point of the bank with an interval of ca 5 minutes; a copula was observed. In the water edge sedge (*C. rostrata* Stokes), males of *Enallagma cyathigerum cyathigerum* (Charpentier, 1840) (Fig. 7) were quite numerous, among which the only male of *Coenagrion puella* (Linnaeus, 1758) was found. *Sympetrum danae* (Sulzer, 1776), mostly just hatched (Fig. 10), abounded on the floating bog, especially at patches with sparser sedge and more water; few mature, already black males were observed among them, but no copulae. Among them, four individuals of *Sympetrum flaveolum* (Linnaeus, 1758) were found. Just hatched, still grey *E. cyathigerum* (Charp.) were also numerous there. The only female of *Lestes sponsa* (Hansemann, 1823) (Fig. 6) was found in sparse sedge near the water edge, but persistent search for more individuals failed. Old individuals of *Libellula quadrimaculata* Linnaeus, 1758 (Fig. 9) were also quite frequent on the floating bog but not at the water. They were aggressive towards each other but lost any activity when the sun hid behind a cloud — being disturbed they just fell down. At such moments no any *S. danae* (Sulz.) could also be startled from sedge. At the ridge slope base, a very cautious male of *Libellula depressa* (Linnaeus, 1758) appeared for a while.

Observations on the Highland bog in the Gakvari River valley examination. In the sedge bog patches seeping with water, there were a huge number of just hatched *Sympetrum pedemontanum pedemontanum* (Müller in Allioni, 1766) (Fig. 14) they were present also at the banks of the brooks flowing through, but in less numbers. Solitary mature individuals and ovipositing tandems (Fig. 13) of the same species occurred among them, and also two mature males *S. flaveolum* (L.) were met with. No damselflies. In the outlet brook valley below the bog, a young male (Fig. 15) and female of *Orthetrum brunneum* (Fonscolombe, 1837) were found (resting exclusively on stones), and several individuals of *S. pedemontanum* (Müll.).



Figs 20–22. Lake Debrishara with broad thickets of *Carex rostrata* Stokes.

Рис. 20–22. Вид на озеро оз. Дебришара с обширными зарослями *Carex rostrata* Stokes.

Observations on the visit to the Tlyanub Lakes. The dragonflies were found mostly at the largest lake, in riparian and floating vegetation. Of Zygoptera, there were numerous *E. cyathigerum cyathigerum* (Charp.) and the only male of *L. sponsa* (Hans.); of Anisoptera, *A. juncea crenatoides* Bart. and *S. danae* (Sulz.) were quite abundant. Besides, two specimens of *Sympetrum vulgatum vulgatum* (Linnaeus, 1758) were collected, one of which just after hatching.

Observations on the visit to the Lake Mochokh. The patches of riparian vegetation harboured numerous *E. c. cyathigerum* (Charp.) and *Ischnura elegans elegans*

Figs 23–31. Photographs of dragonflies near Lake Debrishara: *Aeshna juncea crenatoides* Bart. (23–28, 31), *Sympetrum flaveolum* (L.) (29) and *S. danae* (Sulz.) (30), at Lake Debrishara (23–39) and in a 400 valley m below the Lake (31). 23–25 — teneral males; 26–28 — teneral females; 29–30 — mature males; 31 — young male.

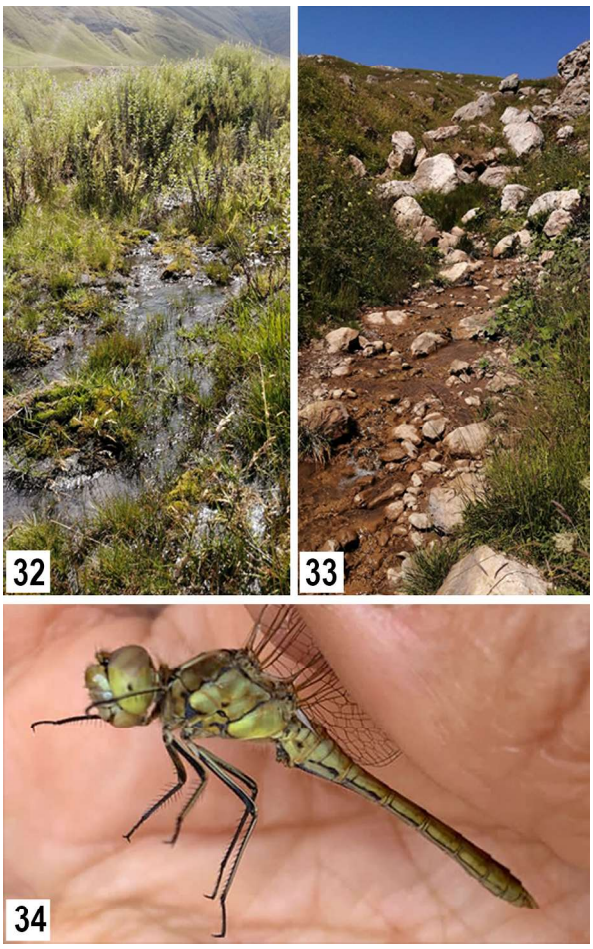
Рис. 23–31. Фотографии стрекоз у озера Дебришара: *Aeshna juncea crenatoides* Bart. (23–28, 31), *Sympetrum flaveolum* (L.) (29) и *S. danae* (Sulz.) (30), у оз. Дебришара (23–39) и в долине 400 м ниже оз. Дебришара (31). 23–25 — свежевыплодившиеся самцы; 26–28 — свежевыплодившиеся самки; 29–30 —зрелые самцы; 31 — молодой самец.

(Vander Linden, 1820), among which a single (again) male of *C. puella* L. was found; *L. quadrimaculata* L. was also registered.

Observations on the visits to the Takhor Lakes. A male and female of *A. juncea crenatoides* Bart. were observed and caught at the upper of the studied lakes on 16.VIII.2016. No any dragonfly was observed at any lake on 24.VII.2022, in spite of excellent weather. Most probably all Takhor Lakes, situating too high and missing any aquatic vegetation, unfit dragonfly development, while the above dragonflies arrived there on dispersal from their breeding places at some lower levels.

An example of such place can be a pool ca 4×2 m found in the pine forest belt at 1820 m a.s.l. on the Dzhoakhor River right bank (41.969N, 46.508E), 9–9.5 km ENE of Takhor Lakes and 1100–1300 m below them, examined on 16.VIII.2016 by E.I. and on 26.VII.2022 by E.I. and O.K. E. It is situated on a small bank terrace in a relatively narrow gorge, shaded by mixed forest. On the latter date, there were numerous *R. macrocnemis* Boulinger tadpoles, few *Notonecta glauca* Linnaeus, 1758 and Gerridae sp. in the water, and three *Aeshna* Fabr. larvae of different ages were also found. The largest one was identifiable as *A. juncea* (L.), while the ringed femora and the mentum proportions of the medium and early instar larvae could suggest *A. cyanea* (Müll.), but not for sure. Nearby some *Aeshna* sp. was observed passing by over a shingle river bank, but was not caught.

Observations on the visits to the Lake Debrishara. On 18.VII.2021, intensive emerging of *A. juncea crenatoides* Bart., was observed on the lake; also several males of *E. cyathigerum cyathigerum* (Charp.) and a female of *S. flaveolum* (L.) were collected. For the three hours of examination on 9.VIII.2023 (12 a.m.–3 p.m.), no Zygoptera were fund, while mass emerging of *A. juncea crenatoides* Bart. took place (Figs 23–28) in the broad *C. rostrata* Stokes thickets at the outlet side of the lake and along the outer margin of the open water (but not on the dense floating bog missing any water surface). They were most numerous at both outer (the bank side) and inner (the water side) margin of the outlet side sedge thicket. At the outer margin of the latter, hatching individuals were hanging on average in half a metre from each other, and sometime less. Seven individuals were counted in the area of 4 m^2, that provided the estimation of their density of ca 2 per m^2. As it usually observed during mass emerging, some individuals were hatched incorrectly: either started to harden and get coloured not completing hatching, or fell into the water. Permanently individuals were observed on their maiden flights out of the lake along obliquely rising trajectories (A teneral female was noticed at 11 a.m. in grass on the ridge crest 400 km SE and 114 m below the lake, at 41.8031° N, 47.4111° E, one more was observed passing by). Sometimes solitary mature males were seen patrolling the sedge inner margin along the water edge, but they were obviously few (maybe one) and not too active, so the main part of the population still did not start reproduction activity.



Figs 32–34. Photographs of dragonfly *Sympetrum vulgatum vulgatum* (L.) and its habitats at the environce of Kurush village. 32 — a swamplet by the Chekhychay River; 33 — a swamped brook; 34 — a male at the swamped brook.

Рис. 32–34. Фотографии стрекозы *Sympetrum vulgatum vulgatum* (L.) и её местообитаний в окрестностях с. Куруш. 32 — болотце возле р. Чехычай; 33 — болотистый ручей; 34 — самец, собранный на болотистом ручье.

A mature male of *S. flaveolum* (L.) (Fig. 29) kept to the grass along the firm bank, while on a damp meadowy bank between two springs a very cautious mature male of *S. danae* (Sulz.) (Fig. 30) was observed.

Next day morning (9–11 a.m.), 10.VIII.2023, the valley of the Chiragchay River right tributary 1.5–1.8 km E of Lake Debrishara was also examined, at the elevations of 2320–2400 m a.s.l. This was a fast river with shingle banks with *Myricaria bracteata* Royle bushes; it flowed among moist, at some places bogged subalpine meadows with fragments of willow thickets (including *Salix caprea* L.), there was a slope overgrown with birch forest at the right bank. Numerous individuals of *A. juncea crenatoides* Bart. were found resting on bushes (Fig. 31); they were startled literally with every step, and many of them landed again very soon. Some ranged in trophic flight over glades between bushes and trees, and even immediately over the raffle river. All these dragonflies were young, not yet intensively coloured, but already not teneral as their wings did not or slightly glitter. No doubt

all them bred in Lake Debrishara, which lied 400 higher and ca 2 km apart from this location.

Observations on the visit to the Rivulet at Kurush. A single male of *S. vulgatum vulgatum* (L.) (Fig. 34) was flying at the banks and rested on high grasses. Also few *Aeshna* Fabr., most probably *A. juncea* (L.), were ranging above the rivulet and a nearby boglet. Similar darners were sometimes seen at the Chekhychay River downstream of the village (41.2883° N, 47.8379° E), as flying along *M. bracteata* Royle bushes on a small mossy boglet formed by a slow brook (Fig. 32).

Annotated list of dragonfly species collected in Dagestan highlands

Lestes sponsa (Hansemann, 1823)

Fig. 6.

Material. ***Lake Bezdonnoe:*** 5.VIII.2023, E. Ilyina, O. Kosterin leg. — 1♀ (Fig. 6) (189380113); ***Tlyanub Lakes:*** 22.VIII.2021, E. Ilyina leg. — 1♂ (191782715).

Coenagrion puella (Linnaeus, 1758)

Material. ***Lake Bezdonnoe:*** 5.VIII.2023, E. Ilyina, O. Kosterin — 1♂ (177991051); ***Lake Mochokh:*** 8.VII.2023, E. Ilyina leg. — 1♂.

Enallagma cyathigerum cyathigerum (Charpentier, 1840)

Fig. 7.

Material. ***Lake Bezdonnoe:*** 5.VIII.2023, E. Ilyina, O. Kosterin leg. — 9♂♂ (3 teneral) (Fig. 7), 6♀♀ (2 teneral); ***Tlyanub Lakes:*** 22.VIII.2021, E. Ilyina leg. — 7♂♂, 3♀♀; ***Lake Mochokh:*** 8.VII.2023, E. Ilyina leg. — 6♂♂; ***Lake Debrishara:*** 18.VII.2021, E. Ilyina leg. — 3♂♂.

Photographic records. Lake Bezdonnoe: 5.VIII.2023, O. Kosterin — 2♂♂ (189307653, 189348256), 1 copula (189314026).

Ischnura elegans elegans (Vander Linden, 1820)

Material. ***Lake Mochokh:*** 8.VII.2023, E. Ilyina leg. — 5♂♂.

Aeshna juncea crenatoides Bartenef, 1925

Figs. 8, 23–28, 31, 35–38, 40–41.

Material. ***Lake Bezdonnoe:*** 11.VIII.2021, E. Ilyina leg. — 1♀, 2 larvae (middle stages); the same place, 5.VIII.2023, E. Ilyina, O. Kosterin, — 2♂♂ (189332791, 189353182), 2♀♀ (Figs 8, 40–41) (189350999, 189432165); ***Tlyanub Lakes:*** 22.VIII.2021, E. Ilyina leg. — 1♂ (191782815), 1♀; ***Lake Takhor:*** 16.VIII.2016, E. Ilyina leg. — 1♂, 1♀ (200369768); ***Lake Debrishara:*** 18.VII.2021, E. Ilyina leg. — 4♀♀ (teneral); the same place, 9.VIII.2023, O. Kosterin, E. Ilyina leg. — 4♂♂, 6♀♀ (all but 1 ♂ teneral); the valley 1.5 km E Lake Debrishara, 10.VIII.2023, O. Kosterin, E. Ilyina leg. — 1♀.

Photographic records. Lake Debrishara: 9.VIII.2023, O. Kosterin — 12♂♂ (189535230, 189580299, 189583865, 189587478, 189589003, 189626183, 189674968, 189674969, 189675533, 189677018, 189677376, 189678419), 32♀♀ (189530458, 189531119, 189531407, 189531666, 189534065, 189534691, 189534909, 189535227, 189580300, 189580517, 189581143, 189581675, 189581897, 189583156, 189585543, 189586212, 189588022, 189588379, 189588688, 189625914, 189626013, 189626907, 189627592, 189627715, 189628111, 189628755, 189628757, 189673980, 189676163, 189676164, 189678168, 189678169) (all just hatched but the male 189587478 mature) (Figs 23–28, 35–38, 1 larva (189679880); the ridge 114 m NE of Lake Debrishara, 9.VIII.2023, O. Kosterin — 1 teneral ♀♀ (189489555); the valley 1.5 km E Lake Debrishara, 10.VIII.2023, O. Kosterin — 3♂♂ (189862009, 189863023, 189863487), 2♀♀ (189860986, 189864474).

Remarks. All collected specimens from Lakes Bezdonnoe and Takhor had the synthorax coloration as described for *Aeshna juncea crenatoides* Bartenef, 1925 with the pale stripes, especially the main lateral ones on the mesepimeron and metepimeron, very broad. There is also a small additional streak on the metepisternum, between the 1st and 2nd main stripes on the mesepimeron and metepimeron, plus two pale marks behind and below the spiracle [Bartenef, 1929a, b, 1930; Kosterin, 2023]. Let us designate this as «morph A». Both specimens from Tlyanub Lakes were the same.

At the same time, in part of specimens from Lake Debrishara the additional streak on the metepisternum is enlarged and at its upper end merges to the first main stripe on the mesepimeron (Figs 37–38). Let us call this variant of the synthorax pattern «morph B». The rest specimens from Lake Debrishara represented morph A of (Figs 35–36). The morphs A and B were distinct (Figs 35–36), without any synthorax pattern version transitional between them.

On 9.VIII.2023, a sample of 43 just hatched individuals at Lake Debrishara was examined in hand (including 8 of 10 specimens collected on this day) and was found to be comprised by 32 females and only 11 males. Adding to this sample the mature male ranging along the sedge and the above mentioned teneral female found on the ridge just below the lake (both also collected), we have a sample of 45 individuals examined on this day. The unusual morph B was represented by 8 individuals (5 females and 3 males), morph A by 37 individuals (28 females and 9 males) (among the specimens collected on this day, there were 2 males and 4 females of morph A and 2 males and 2 females of morph B). Next day, 3 males and 2 females (one of them collected) were randomly (regardless the synthorax pattern and sex) photographed in the valley below the lake so that the synthorax pattern was well seen. Among them, morph A was represented by 2 males and morph B by 1 male and 2 females. Among 4 females randomly collected at Lake Debrishara on 18.VII.2021, 2 represented morph A and 2 morph B.

So, in total a sample of 54 individuals from Lake Debrishara was analysed, of which 39 (72.2 %) appeared females and 15 (27.8 %) males. As to the synthorax pattern, 41 individual (75.9 %) was morph A and 13 (24.1 %) morph B, no correlation of the frequency of morphs A and B being traced.

One of the two females from Lake Bezdonnoe obtained on 5.VIII.2023 had vestigial «lateral genital plates» (Fig. 40); the other did not have them (Fig. 41) (see *Discussion*).

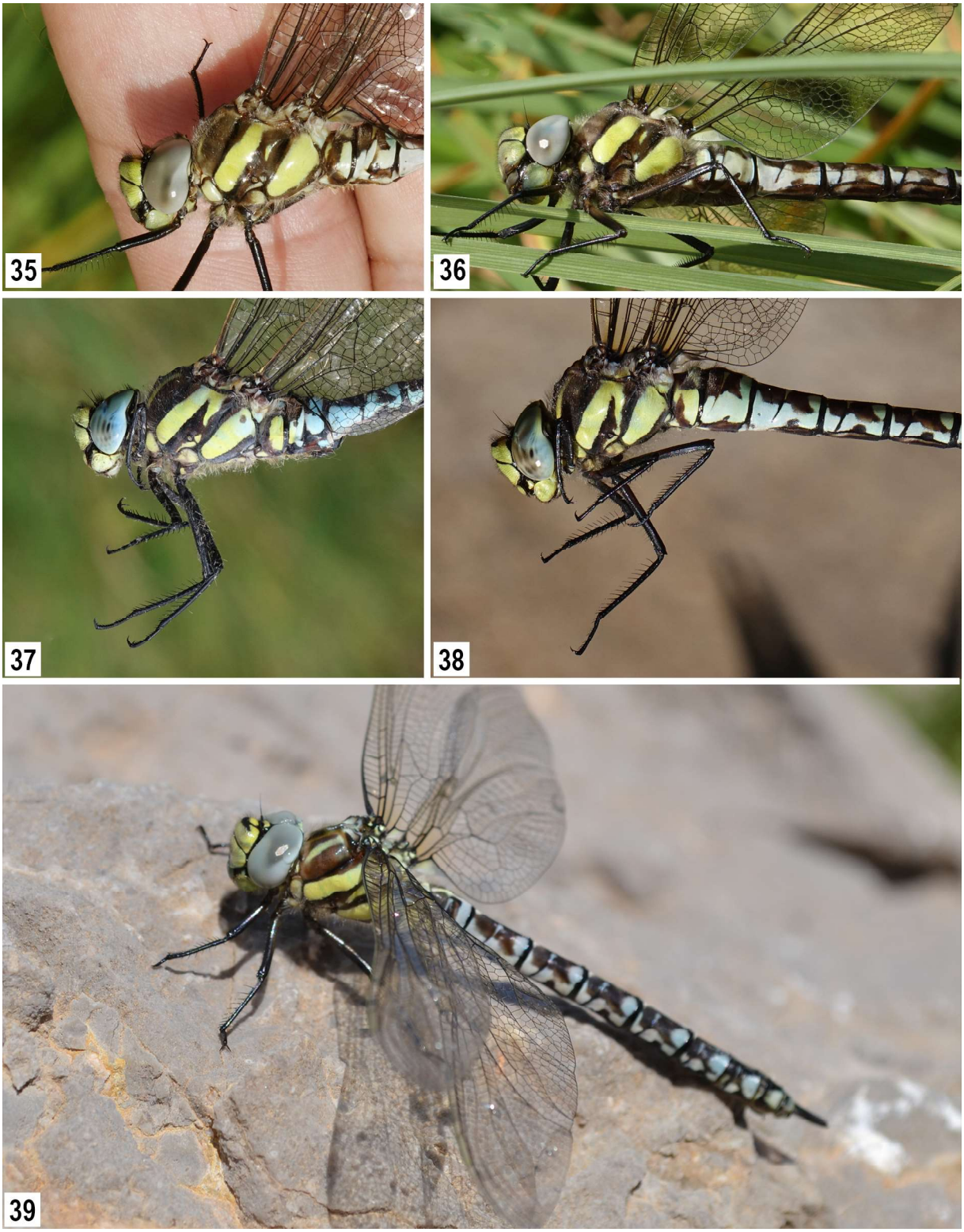
Cordulia aenea aenea (Linnaeus, 1758)

Material. ***Lake Bezdonnoe:*** 5.VIII.2023, E. Ilyina, O. Kosterin — 3♂♂ (189316082, 189347654).

Libellula quadrimaculata Linnaeus, 1758

Fig. 9.

Material. ***Lake Bezdonnoe:*** 11.VIII.2021, E. Ilyina leg. — 1♂; the same place, 5.VIII.2023, E. Ilyina, O. Kosterin — 2♂♂, 1♀; ***Lake Mochokh:*** 8.VII.2023, E. Ilyina leg. — 1♂.



Figs 35–39. The synthorax pattern of *Aeshna juncea crenatoides* Bart.: morphs A (35–36) and B (37–39), males (35, 37) and females (36, 38–39). 35–38 — at Lake Debrishara; 39 — at Munzur Mountain in SE Turkey. Photo 39 by S. Deleva.

Рис. 35–39. Окраска синторакса *Aeshna juncea crenatoides* Bart.: морфы A (35–36) и B (37–39), самцы (35, 37) и самки (36, 38–39). 35–38 — на оз. Дебришара; 39 — на г. Мунзур, СВ Турция. Фото 39 — С. Делевой.

Photographic records. *Lake Bezdonnoe:* 5.VIII.2023, O. Kosterin — 1♂ (Fig. 9) (189376772), 1♀ (189433792).

Libellula depressa
Linnaeus, 1758

Visual registration. Lake Bezdonnoe: 5.VIII.2023, E. Ilyina — 1♂.

Orthetrum brunneum (Fonscolombe, 1837)

Fig. 15.

Material. *Bog at Upper Gakvari:* 6.VIII.2023, O. Kosterin, E. Ilyina leg. — 1 teneral ♂ (Fig. 15) (189873676).

Photographic records. The same place, O. Kosterin — 2♀♀ (190035749).

Sympetrum danae
(Sulzer, 1776)

Figs 10, 30.

Material. *Lake Bezdonnoe:* 11.VIII.2021, E. Ilyina leg. — 1♂, 1♀; the same place, 5.VIII.2023, E. Ilyina, O. Kosterin leg. — 2♂♂, 1♀; *Tlyanub Lakes:* 22.VIII.2021, E. Ilyina leg. — 1♂, 2♀♀ (191782602).

Photographic records. *Lake Bezdonnoe:* 5.VIII.2023, O. Kosterin — 1♂ (189432751), 7♀♀ (Fig. 10) (189305685, 189306468, 189308253, 189308254, 189353803, 189377885); *Lake Debrishara:* 9.VIII.2023, O. Kosterin — 1♂ (Fig. 30) (189818405).

Sympetrum flaveolum
(Linnaeus, 1758)

Fig. 29.

Material. *Lake Bezdonnoe:* 5.VIII.2023, E. Ilyina, O. Kosterin leg. — 2♂♂; *Bog at Upper Gakvari:* 6.VIII.2023, O. Kosterin, E. Ilyina leg. — 1♀; *Lake Debrishara:* 18.VII.2021, E. Ilyina leg. — 1♂.

Photographic records. *Lake Bezdonnoe:* 5.VIII.2023, O. Kosterin — 1♂ (189316604); *Bog at Upper Gakvari:* 6.VIII.2023, O. Kosterin — 1♂ (189923572); *Lake Debrishara:* 9.VIII.2023, O. Kosterin — 1♂ (Fig. 29) (189725025).

Sympetrum vulgatum vulgatum
(Linnaeus, 1758)

Fig. 34.

Material. *Tlyanub Lakes:* 22.VIII.2021, E. Ilyina leg. — 2♂♂ (1 teneral); *Kurush:* 14.VIII.2022, E. Ilyina leg. — 1♂ (191783168) (Fig. 34).

Remarks. The specimens exhibit the characters of the nominotypical subspecies, in particular the black colour predominates over the yellow one in their femora and tibia (Fig. 34). At the same time in Rutul and Gergebil Districts of Dagestan at lower elevations of 1370 and 800 a.s.l., respectively, we found already the subspecies *S. vulgatum decoloratum* Selys, 1884 (= *S. vulgatum flavum* Bartenev, 1915) (to be published elsewhere).

Sympetrum pedemontanum pedemontanum
(Müller in Allioni, 1766)

Figs 13–14.

Material. *Bog at Upper Gakvari:* 6.VIII.2023, O. Kosterin, E. Ilyina — 2♂♂, 3♀♀.

Photographic records. *Bog at Upper Gakvari:* 6.VIII.2023, O. Kosterin — 1♂ (189872417), 3♀♀ (Fig. 13) (189925089, 189925090, 189922557), tandem (Fig. 14) (189922300).

Discussion

Species composition of dragonflies of Dagestan highlands

So, 13 species of Odonata have been so far registered above the tree line in Dagestan. *C. aenea* is for the first time reported for the fauna, its presence in Dagestan being predicted still by Artoboklevskij [1929]. This set of species comprises just 22 % of the so far revealed fauna of Dagestan including 60 species (unpubished), however, taking into account the hostility of highlands in the temperate zone for Odonata in general and rarity of their suitable habitats in Dagestan in particular, this figure is quite substantial. It is noteworthy that *O. brunneum* (Fons.) and *S. pedemontanum* (Müll.) were found only in the Upper Gakvari village environs on a semicurrent sedge bog and its outlet spring valley, and so only quite conventionally can be attributed as highland dragonflies. That habitat and also the brook near Kurush are the only lotic of the highland dragonfly habitats examined, and there is no surprise that the four species found there (*S. flaveolum* (L.)*, S. vulgatum* (L.)*, S. pedemontanum* (Müll.)*, O. brunneum* (Fons.)) scarcely overlap (the two former species) with those found at lakes (all other species). The species assemblages found at particular lakes suggest existence of some highland lake dragonfly fauna, the core of which is comprised by *E. cyathigerum* (Charp.)*, A. juncea* (L.), *L. quadrimaculata* L.*, S. danae* (Sulz.) and *S. flaveolum* (L.), with each lake missing some of these species (or we failed to register them), because far remoteness of these lakes from each other strongly hamper species exchange.

So far only *A. juncea* (L.) was reported for the highlands of Dagestan, as follows (translated from Russian): «2♂♂, Kurush, in a ravine at southern slope, 26.VIII.1926, R; 1♂ and 1♀, Kurush, seepages among subalpine meadow, 8300–8400 f[eet], 24.VII.1926, R; 1♂, Kurush, seepages among subalpine meadow, northern slope, 23.VIII.1924, R.; 1♀, Shalbuz-Dag Mt, northern slope from Kurush to Akhty, 5000 f[eet], 5.IX.1926, R. In all specimens, the yellow stripes of the thorax lateral sides and anterior sides are developed much stronger than in typical ones, the membranula is paler» [Artobolevskij, 1929: 231]. These elevations, provided in feet, corresponded to 2530–2560 and 1524 m a.s.l. Actually the reports from Kurush referred to approximately the same locality where the male of *S. vulgatum vulgatum* (L.) was collected and some darners observed by us.

As most of the Odonata fauna of Dagestan, all species met with in highlands, except for *O. brunneum* (Fons.), either belong to the Boreal fauna of Europe or penetrate there from the nemoral zone. Of other species found by us at lower elevations in Dagestan, judging by their ecological characteristics, we could expect to meet in highlands also *Lestes dryas* Kirby, 1890. Beyond Dagestan, only one highland dragonfly habitat was examined in the Russian part of the Caucasus, which is the Lagonaki Plateau in the Republic of Adygea, where only *A. juncea crenatoides*

Bart. [Kosterin, 2023] and *L. depressa* L. (unpubl.) were found. Besides, Khmelevskie Lakes in Krasnodarskiy Kray, disposed exactly at the tree line, at 1703–1875 m a.s.l., were studied by A.N. Bartenev in 1926–1929 [Batenef, 1930], O.K. in 2006 and A.N. Medvedev in 2013 [Kosterin, 2023]. In addition to the above mentioned *L. quadrimaculata* L. and *E. cyathigerum* (Charp.) (represented there by another subspecies, *E. cyathigerum rotundatum* Bartenef, 1929)), two more species were found there: *Coenagrion lunulatum* (Charpentier, 1840) (only by A.N. Bartenev) and *Leucorrhinia dubia* (Vander Linden, 1825) [Batenef 1930; Kosterin 2023]. It is these two Boreal species which we expected to find in Dagestan highlands but these expectations failed and instead we found *C. aenea* (L.), quite unexpectedly.

It is noteworthy that we did not met in the Dagestan highlands any migratory species, such as *Aeshna affinis* Vander Linden, 1820, *A. mixta* (Latreille, 1805), *Anax ephippiger* (Burmeister, 1839), *Anax parthenope* (Selys, 1839), *Pantala flavescens* (Fabricius, 1798), *Sympetrum fonscolombii* (Selys, 1840), although at least the four latter ones are known to cross high mountain ranges on their seasonal migrations [Borisov, 2015]. It is not excluded that they could be met in the Dagestan highlands in other seasons.

Elevation limits

The Dagestan territory as a whole lies to the north of the Watershed Range (Great Caucasus), along which its south-western border goes, so is entirely in Europe (up to its most widespread conventional southern border also along the Great Caucasus). In this respect it is of interest to compare our data with information of upper limits of occurrence of the same species in Europe. This information is partly provided in the «Atlas of the European Dragonflies and Damselflies» [Boudot et al., 2015]. The upper limits indicated for *L. sponsa* (Hans.) [Boudot, Raab, 2015] and *C. puella* L. [Boudot, Nelson, 2015] are 2500 m a.s.l., which is almost exactly the elevation of Lake Bezdonnoe where they were found in Dagestan. The upper limit of *I. elegans* (V. Lind.) is reported as 1600 m [Boudot, Šalamun, 2015], which again corresponds to the elevation of Lake Mochokh, 1632 m, where it was found by us. For *L. depressa* L., the limit of 1400 m a.s.l. was indicated [Kalkman, Chelmik, 2015], while we found it at 2500 m a.s.l. The upper limits of *S. vulgatum* (L.) were indicated as 1400 m in the Alps and 2100 m in the Pyrenees [Kalkman et al., 2015]; the elevation of Lake Mochokh is between these values but the finding at Kurush appeared almost 400 m higher than the European record. The information provided for three species is vague: for *E. cyathigerum* (Charp.) «well over 2000 m» [Kalkman, Kitanova, 2015] (that formally corresponds to our data), for *S. pedemontanum* (Müll.) «not rare up to 1000 m» [Kalkman, 2015] (that could mean that it occurs also at higher levels but rarely). That Atlas [Boudot et al., 2015] did not communicate the upper limits for *A. juncea* (L.), *C. aenea* (L.), *L. quadrimaculata* L., *O. brunneum* (Fons.), *S. danae* (Sulz.), *S. flaveolum* (L.).

The two papers on the Odonata fauna of the adjacent Georgia [Schröter et al., 2015; Seehausen et al., 2016] do not provide elevation limits explicitly but the detailed information on the localities studied allowed us to infer them. Let us do this for species for which the European information was absent or vague.

The upper limit of *A. juncea* (L.) in Georgia appeared to be 2430 m a.s.l. This is just 95 m lower than Lake Bezdonnoe, but a huge population of this species exists at Lake Debrishara at a 386 m higher level. However, on the Amuslar Mt in Armenia this species breeds in water bodies up to 2560 a.s.l. and recorded up to 2988 m (copula) [Ananian, Schröeter, 2020], while in Tadjikistan it breeds in the mountains up to 3120 a.s.l. [Schröter, 2012].

Up to the available information, the upper limit of *E. cyathigerum* (Charp.), *S. flaveolum* (L.) and *L. quadrimaculata* L. in Georgia is 2115 m a.s.l. [Schröter et al., 2015; Seehausen et al., 2016]. This is 700 m below Lake Debrishara, where populations of the two former species were found, and 405 m below Lake Bezdonnoe where the population of the latter exists. The only habitat of *S. danae* (Sulz.) known from Georgia is at 2081 m a.s.l., which is 735 m below Lake Debrishara where it was found. However already in the Central Asian mountains *L. quadrimaculata* L. occurs up to 2800 m a.s.l., *S. flaveolum* (L.) and *S. danae* (Sulz.) up to 3000 m, while *E. cyathigerum* (Charp.) up to 3550 m a.s.l. [Borisov, 2006; Borisov, Haritonov, 2007], although the latter is represented there by another subspecies, *E. cyathigerum rotundatum* Bart. (= *E. risi* Schmidt, 1964 [Kosterin, 2023]).

The known upper limit of *S. vulgatum* (L.) in Georgia is 2065 m a.s.l., of *S. pedemontanum* (Müll.) 1450 m and *L. depressa* L. 2105 m a.s.l. [Schröter et al., 2015; Seehausen et al., 2016]; in the first case this is above and in the second and third cases below our Dagestanean records. In the mountains of Central Asia *S. pedemontanum* (Müll.) occurs up to 2000 m a.s.l. [Borisov, 2006]

The upper limit of *C. aenea* (L.) is 1083 m a.s.l. in Georgia, where it was found on a small lake east of Nikoresminda village [Seehausen et al., 2016], below the tree line, that is 1442 m lower than Lake Bezdonnoe where we found its population at 2025 m. The tree line in the environs of Lake Bezdonnoe is approximately at 2000 m a.s.l. while solitary trees occur up to 2200 m a.s.l. It is noteworthy that in the much more northerly located Altai Mts (South Siberia), the tree line is situated at 2000–2500 m a.s.l. as well, while *C. aenea* (L.) occurs up to 2000 m a.s.l. [Belyshev, 1973], that is it does not penetrate to highlands proper. We do not know any other reports of occurrence and, moreover, breeding of *C. aenea* (L.) above the tree line. It is not excluded that our first finding in Dagestan is also the first known highland, and at the same time most elevated habitat of this species in the world.

«Reverse» vertical migrations of *A. juncea* (L.) of Lake Debrishara

Lake Debrishara is disposed in a half-cup-like depression (Fig. 5) of a Kokma Mt. Range spur at

2800 m a.s.l., while birch (*B. litwinovii* Doluch.) forests in this region are present on north-exposed slopes up to ca 2500 m a.s.l. According to our observations, just hatched individuals of *A. juncea* (L.) commenced their maiden flights off water rising at angles of 20–40º. At the same time we found a teneral individual on the ridge 114 m below the lake, but none on slopes above the lake, which were examined to about 3000 m a.s.l. At the same time, huge numbers of young individuals, some with still slightly glittering wings, were observed in the river valley just 1.5 km easterly and 400 m below Lake Debrishara. There was no other suitable breeding place of *A. juncea* (L.) in that region. These observations unequivocally suggest that the dragonflies emerged from the lake migrate to the river valley below for foraging. That is, in the case of the *A. juncea* (L.) population of Lake Debrishara, we face a vertical migration «opposite» to that common in dragonflies, when they breed in water bodies in lower valleys and ascend for foraging up the mountains.

It remains unknown if this migration is directional and regular. It looks quite natural that after emergence, the dragonflies migrate to valleys with patches of forest vegetation for foraging, since they are most favourable for this purpose, being rich in insects, warmer, protected from wind and provide trees and bushes convenient for resting. It is, however, unclear if the dragonflies of this population have an instinctive motivation then to ascend up the slopes for breeding and if they are capable to find Lake Debrishara by purpose, or we face just an undirected dispersal after emergence and concentration in places convenient for foraging, followed by chaotic wandering in search for places useful for breeding. In the latter case, only some part of those dragonflies returns to Lake Debrishara at random. To clarify this issue it would be useful to investigate the lake and its environs in early September, an estimated time when most of those dragonflies had to turn to breeding.

Unusual synthorax pattern and other characters of *A. juncea* (L.) of Lake Debrishara

A.N. Bartenev [Bartenef 1925, 1929a,b; see also Kosterin, 2023] described from Georgia the subspecies *A. juncea crenatoides* Bart., characterised by extended pale stripes of the synthorax and a shallow incision of the female vulvar lamina. Later he described from Khmelevskie Lakes in Krasnodarskiy Kray another subspecies, *A. juncea atshischgho* Bart. [Batrenef, 1929a, b, 1930; Kosterin, 2023], differing from the former one by presence in the female ovipositor of the so-called «lateral genital plates» (small folds at the sides of the S9 sternite in its anterior part), of variable expression. Kosterin [2023] reported the presence of these plates in two female specimens from the West (Lagonaki Plateau) and Central (Dombay environs) Caucasus and their absence in the females from Dagestan which were at his disposal that time, but left open the question if there exist two Caucasian subspecies of *A. juncea* (L.). Schneider et al. [2023] revealed that in the phylogenetic tree reconstructed from the primary structure of the nuclear *ITS*-region, all Caucasian specimens of *A. juncea* (L.) formed a branch opposed to the specimens originating from the rest of Eurasia. At the same time the *ITS*-region sequences of specimens from Central Caucasus, Dagestan and Georgia, as well as their sequences of the mitochondrial *COI* gene fragment, did not substantially differ from each other. On this basis, the subspecies name *A. juncea crenatoides* Bart. was assumed to be valid while *A. juncea atshischgho* Bart. was claimed to be its junior subjective synonym. Among 15 females from Dagestan highlands which we have in our disposal at present, 14 has no lateral genital plates (Fig. 41) but one of the three females from Lake Bezdonnoe has vestigial lateral genital plates in the anterior part of S9, at sides of its sternite just under the anterio-ventro-lateral corners of the tergite (Fig. 40). This fact once more proves variability of this character in the Caucasus and lack of any basis to recognise two subspecies of *A. juncea* (L.) in the Caucasus.

Our specimens correspond to *A. juncea crenatoides* Bart. by such characters as very broad main pale stripes of the synthorax (Figs 35–38), a shallow incision of the vulvar lamina in females (Figs 40–41), the cerci without an apical pointing in females and any apical bent down in males [Bartenef, 1929a, b, 1930].

The lower of the two small pale spots disposed on the metepisternum behind the spiracle deserves a special attention. It narrowly extends along the anterioventral metepimeron margin, as a «leg», as in a related species *Aeshna subarctica* Walker, 1908; this «leg», is considered to be one of the diagnostic characters of the latter distinguishing it from *A. juncea* (L.) [Bernard, Kosterin, 2010]. However in our specimens this spot does not occupy the spiracle as in *A. subarctica*, but is situated entirely behind it, as always in *A. juncea* (L.).

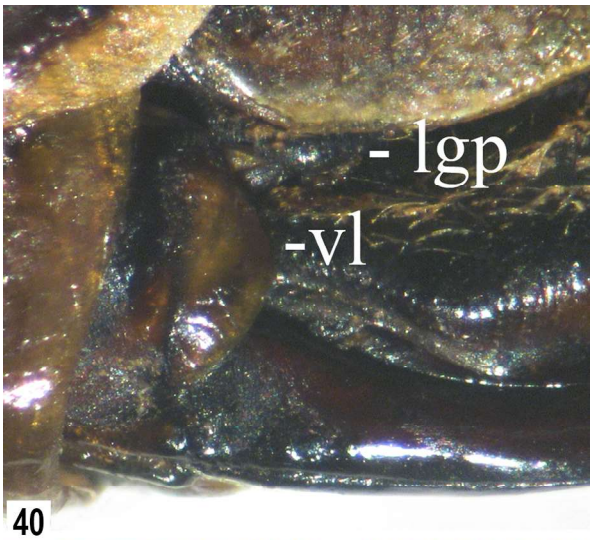
It is at the same time remarkable that 27.5 % of examined individuals from Lake Debrishara and its surroundings has an unusual character, the enlarged pale streak on the metepisternum and its merger at its upper end with the fore main pale stripe (on the mesepimeron), which was termed above as morph B with respect to the synthoracic pattern (Figs 37–38). It is curious that a paratype of the unrelated Irano-Azerbaijanian species *Aeshna vercanica* Schneider et al. 2015 which originated from Azerbaijan and was depicted in figure 10a in Schneider et al. [2015] was most probably a male of *A. juncea crenatoides* of the morph B.

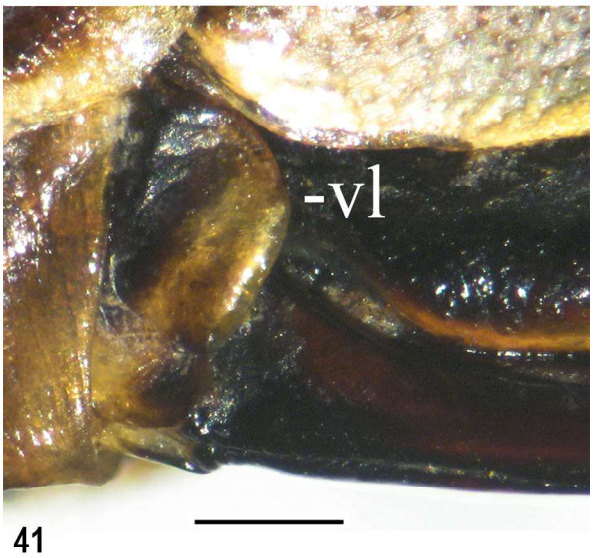
Earlier this synthoracic pattern was revealed in all specimens of *A. juncea* (L.) from highlands of Armenia [Ananian, Schroeter, 2020]. Also the same pattern is seen in all individuals photographed by Stanimira Deleva at a karstic lake on the Munzur Mountain in Tuniceli Il in SE Turkey (39.4569N, 39.2366E, 5.VII.2014) (Fig. 39) [iNaturalist, 2023; observation 49173785]. Before our studies in Lake Debrishara it could be possible to suppose that Armenia and SE Turkey were inhabited by a separate subspecies or even species characterised by the B-type of the synthorax pattern. However the presence

of both morphs A and B in the Debrishara population excludes any taxonomic value of this character. It should be specially stressed that in the analysis by Schneider et al. [2023], the Dagestan specimen was represented by a female of morph B, collected on 18.VII.2021, and the specimen from Armenia also by morph B. But they did not differ substantially in the *ITS* region sequence from specimen from Georgia and Karachay-Cherkes representing morph A. According to our analysis, there were just 5 variable sites, for which the two sequences from Transcaucasia (Georgia and Armenia) differed (four substitutions and one one-nucleotide deletion) from the two sequences from Russia (Dagestan and Karachay-Cherkes Republics), irrespectively to morphs A and B. The sequences of the *COI* fragment analysed of these four specimens had more, 21 variable sites but they showed no any inner clustering.

This unusual character of the synthorax pale pattern is in line with the general trend observed in Odonata, of expanding pale elements and reduction of dark elements of coloration in the southern direction. However, it by no means is an environmental modification, since in this case we face a clear-cut of alternative variation, namely dimorphism – existence of two contrasted morphs of the coloration pattern without any transition, which may only be of a genetic nature.

The ratio of morphs A and B was estimated in the Debrishara population as 3.15 : 1, which is intriguingly close to the Mendelian ration 3 : 1 (even too close for a random sample of ca half a hundred specimens only). We could very cautiously explain this with the following hypothesis: (i) morph A is determined by a dominant allele and morph B by a recessive allele of some gene; and (ii) the Debrishara population could once be founded by a single female, homozygous for one allele, which was fertilised by a male homozygous for the other allele, so that all their progeny was heterozygous. In such a population the initial frequency of alleles of 50 % could be retained, that would result in the phenotype ratio close to 3 A : 1 B. The weak point of this hypothesis is that in small populations, allele frequencies are apt to strong genetic drift, so that at early stages of this the increase of this population from few individuals to its recent huge size, the ratio of alleles could hardly be retained to be close to 50 %.





Figs 40–41. Oblique lateroventral view of the S9 base of two female specimens of *Aeshna juncea crenatoides* Bart. collected at Lake Bezdonnoe. 40 — vestigial 'lateral genital plate' present; 41 — vestigial 'lateral genital plate' lacking. Designations: lgp — 'lateral genital plate', vl — vulvar lamina. Scale bar 0.5 mm.

Figs 40–41. Основание 9-го сегмента брюшка двух экземпляров самок *Aeshna juncea crenatoides* Bart. с оз. Бедонное, вид снизу и сбоку. 40 — «боковая генитальная пластинка» присутствует; 41 — «боковая генитальная пластинка» отсутствует; Обозначения: lgp — «боковая генитальная пластинка», vl — генитальная пластинка. Масштабная линейка 0,5 мм.

Unusual sex ratio in the population of *A. juncea* (L.) of Lake Debrishara

The sex ratio in the population of *A. juncea* (L.) is strongly biased in favour of females as 2.6 : 1, which is also quite close to the Mendelian ratio 3:1. It should be stressed that strict Mendelian ratios can be found only in crosses of certain uniform types with respect to the genotypes involved, e.g. between two heterozygotes or between a heterozygote and homozygote. However, for such character as sex all natural crosses are uniform, namely between a female and male. Ca 95 % of dragonflies have chromosome sex determination via the XX (females) / X0 (males) mode [Kiauta, 1969; Mola et al., 2022], which provides the standard animal sex ratio 1:1. No report of a strong bias for sex ratio in *A. juncea* (L.) is known to us from literature, so most probably most its populations have the common equal sex ratio while that of Lake Debrishara is an exclusion.

No simple hypothesis can be put forward to explain this bias. We could speculate that in the Debrishara population prehistory, a spontaneous transition to the autosomal mode of sex determination took place, so that the female sex would be determined by the presence of at least one copy of the dominant allele of some functional feminising factor in some sex locus in one of the

autosomes, while its absence in a homozygote for the recessive null-allele would result in the male sex. In such a population, the frequency of males would be the square of the frequency of the recessive null-allele, which in the situation of the sex ratio close to 3:1 would again be close to 50 % (53 % if to calculate from our estimate of the male frequency). If the hypothetic founder female was also homozygous for the dominant, functional allele of the sex locus, all its offspring will again be heterozygous, so that the frequency of alleles of both alleles would be again 50 %. However, they all would be females. We should add to our hypothesis a single male which reached the nascent population next year and fertilised all those females, insignificantly shifting the null allele frequency to a greater value (as we again observed). However, the initial sex ratio would then change during the population growth not only due to gene drift but also due to to selection against sex imbalance (although this could be weak, since few males can be enough for fertilising all females). The hypothesised shift to the autosomal sex determination would make the former X-chromosome to become an autosome so that the male and female karyotypes would no longer differ, both having an even number of chromosomes. This could be checked by a simple cytological analysis.

Alternatively, a sex ratio biased in favour of females could result from *Wolbachia* Hertig. infection. However, molecular analysis of a male and female from the Debrishara population by Y. Ilinsky (pers. commn.) did not reveal presence of the *Wolbachia* Hertig. DNA.

Thus, the interpretation of strange facts observed in the population of *A. juncea* (L.) of Lake Debrishara suggests too many hypotheses. There is, however, no doubt that this population deserves further multi-facetted study, which would be complicated by the circumstance that the lake is accessible only through ascend for 500 m along quite a steep ridge by feet.

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