



# Geographical distribution and hosts of the cestode *Paranoplocephala omphalodes* (Hermann, 1783) Lühe, 1910 in Russia and adjacent territories

Pavel Vlasenko<sup>1</sup> · Sergey Abramov<sup>1</sup> · Sergey Bugmyrin<sup>2</sup> · Tamara Dupal<sup>1</sup> · Nataliya Fomenko<sup>3</sup> · Anton Gromov<sup>4</sup> · Eugeny Zakharov<sup>5</sup> · Vadim Ilyashenko<sup>6</sup> · Zharkyn Kabdolov<sup>7</sup> · Artem Tikunov<sup>8</sup> · Egor Vlasov<sup>9</sup> · Anton Krivopalov<sup>1</sup>

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## Abstract

*Paranoplocephala omphalodes* is a widespread parasite of voles. Low morphological variability within the genus *Paranoplocephala* has led to erroneous identification of *P. omphalodes* a wide range of definitive hosts. The use of molecular methods in the earlier investigations has confirmed that *P. omphalodes* parasitizes four vole species in Europe. We studied the distribution of *P. omphalodes* in Russia and Kazakhstan using molecular tools. The study of 3248 individuals of 20 arvicoline species confirmed a wide distribution of *P. omphalodes*. Cestodes of this species were found in *Microtus arvalis*, *M. levis*, *M. agrestis*, *Arvicola amphibius*, and also in *Chionomys gud*. Analysis of the mitochondrial gene *cox1* variability revealed a low haplotype diversity in *P. omphalodes* in Eurasia.

**Keywords** *Paranoplocephala omphalodes* · Cestodes · Voles · Haplotype · *cox1* · Eurasia

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✉ Anton Krivopalov  
krivopalov@gmail.com

- <sup>1</sup> Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia
- <sup>2</sup> Institute of Biology, Karelian Research Centre of the Russian Academy of Sciences, Petrozavodsk, Russia
- <sup>3</sup> AO Vector-Best, Novosibirsk, Russia
- <sup>4</sup> A.N. Severtsov Institute of Ecology and Evolution, The Russian Academy of Sciences, Moscow, Russia
- <sup>5</sup> Institute of Biological Problems of Cryolithozone, Siberian Branch of the Russian Academy of Sciences, Yakutsk, Russia
- <sup>6</sup> Kemerovo State University, Kemerovo, Russia
- <sup>7</sup> Pavlodar State Pedagogical University, Pavlodar, Kazakhstan
- <sup>8</sup> Institute of Chemical Biology and Fundamental Medicine, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia
- <sup>9</sup> V.V. Alekhin Central-Chernozem State Nature Biosphere Reserve, Zapovednyi, Kursk Oblast, Russia

## Introduction

Cestodes of the genus *Paranoplocephala* Lühe, 1910 (family Anoplocephalidae) parasitizing the small intestine of arvicoline rodents are widespread in the Holarctic. Low morphological variability within the genus has led to erroneous identifications of *Paranoplocephala omphalodes* (Hermann, 1783) Lühe, 1910 in the wide range of definitive hosts (24 species of rodents from the 10 genera) (Ryzhikov et al. 1978), and hence to mistakes in the depiction of the geographical distribution of this cestode. Using molecular methods, Haukisalmi et al. (2004) have shown that several species of cestodes were identified previously as *P. omphalodes* by morphological criteria. It became apparent that the range of definitive hosts of *P. omphalodes* is restricted mainly to the rodents of the genus *Microtus* (subgenus *Microtus*): field vole *M. agrestis* (L., 1761), common vole *M. arvalis* (Pall., 1778), and east European vole *M. levis* (Miller, 1908) (Haukisalmi et al. 2004). In accordance with available molecular studies of rodent tapeworms, *P. omphalodes* is only found in the European part of the continent (Italy, Hungary, and Finland) (Haukisalmi et al. 2014). The information on the distribution of *P. omphalodes* in its definitive hosts in Russia was based entirely on morphological studies (Spasskii 1951;

Chechulin et al. 2010). According to those studies, the combined geographic range of the *Microtus* spp. reported as definitive hosts of *P. omphalodes* extends beyond the European part of the continent, up to the Lena River in the north-east, and to the Western Sayan Mountains and the west shore of the Lake Baikal in the south-east (Wilson and Reeder 2005). Therefore, the purpose of our work was to study the occurrence of *P. omphalodes* in different species of definitive hosts and its geographical distribution in Russia and adjacent areas, using sequences of the mitochondrial *cox1* gene.

## Materials and methods

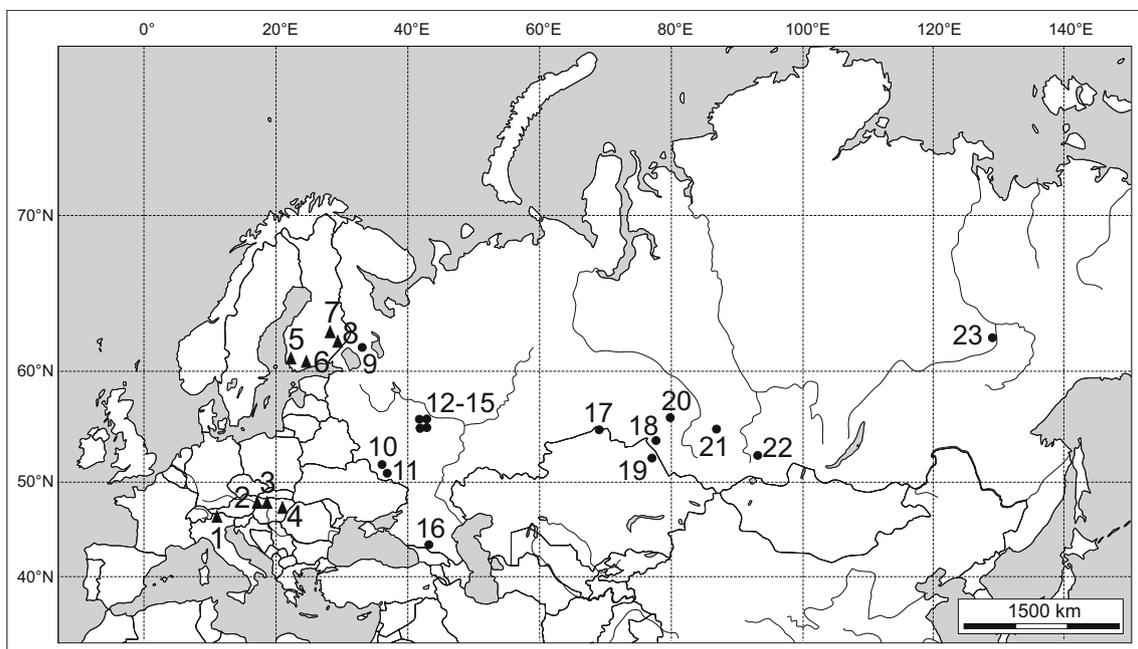
### Data collection

During fieldwork, all rodents were dissected and examined for helminths immediately after trapping with live or snap traps. The systematic position and Latin names of the definitive hosts are given according to Wilson and Reeder (2005). A total of 3248 individuals of 20 arvicoline species from 7 genera were examined (Online Resource 1). The collected material from the Institute of Systematics and Ecology of Animals Siberian Branch of the Russian Academy of Sciences was also used. The cestodes were relaxed in tap water, then fixed in 70% ethanol. For the morphological identification, the cestodes were stained in Ehrlich's acid haematoxylin, differentiated in a 3% aqueous solution of ferric ammonium sulphate,

dehydrated in a graded ethanol series, cleared in eugenol, and mounted in Damar gum; their morphology was studied under the Zeiss AxioScop 40 compound microscope. Species identification of cestodes was done based on Tenora et al. (1986), Chechulin and Gulyaev (1998), and Haukisalmi et al. (2006, 2007a, b). Twenty cestode specimens morphologically identified as *P. omphalodes* were sequenced. Information on the geographic origin and definitive hosts of the studied cestodes is provided in Fig. 1 and Table 1, respectively. All *P. omphalodes* vouchers were deposited in the parasitological collection of the Zoological Museum of the Institute of Systematics and Ecology SB RAS (ISEA SB 2184/1 (ex. 68), ISEA EV 467 (ex. 294), ISEA EV 863 (ex. 295), ISEA AK 14/Bel.202 (ex. 328), ISEA AK 14/Bel.208 (ex. 334), ISEA AK 14/Bel.216 (ex. 342), ISEA AG 540-143 (ex. 269), ISEA AG 626-147 (ex. 273), ISEA AG 514-145 (ex. 271), ISEA AG 431-144 (ex. 270), ISEA AG 646-128 (ex. 274), ISEA PV 17/Bez.46 (ex. 299), ISEA PG 15/Pet.1 (ex. 91), ISEA TD Kar.93 2-14 (ex. 84), ISEA ZK 95-58 (ex. 184), ISEA AK 15/8A (ex. 104), ISEA AK 1224-142 (ex. 268), ISEA PV 15/4 (ex. 102), ISEA PV 15/12 (ex.105), ISEA AK 13/D23 (ex.174)).

### Molecular identification

Total DNA was extracted from tissue by using a “PREP-NA” kit (DNA-Technology Company, Moscow, Russia). A 507 nucleotide long fragment of the mitochondrial gene



**Fig. 1** Geographical distribution of sampling localities of *P. omphalodes*. Circles indicate samples collected by the authors; triangles indicate samples according to Haukisalmi et al. (2004). Locality numbers refer to Table 1

cytochrome c oxidase subunit I (*cox1*) was amplified using primers and the PCR conditions of Haukisalmei et al. (2004). PCR products were purified using a GeneJET Gel Extraction Kit (Thermo Fisher Scientific, USA). Sequencing was performed in both directions in OOO “SYNTOL” (Moscow, Russia). The sequences were aligned using ClustalW in Geneious 11 (Biomatters Inc.; <https://www.geneious.com>). Original sequences were submitted to the GenBank (Table 1). In addition, 13 sequences of *P. omphalodes* from the GenBank database were used (Table 1). The number of haplotypes was calculated using the program DNASP 6

(Rozas et al. 2017). Network 5.0.0.3 software (<https://www.fluxus-engineering.com>) was used to visualize the median-joining network of phylogenetic relationships among haplotypes (Bandelt et al. 1999). Analysis of genetic distances was conducted in MEGA 6 (Tamura et al. 2013).

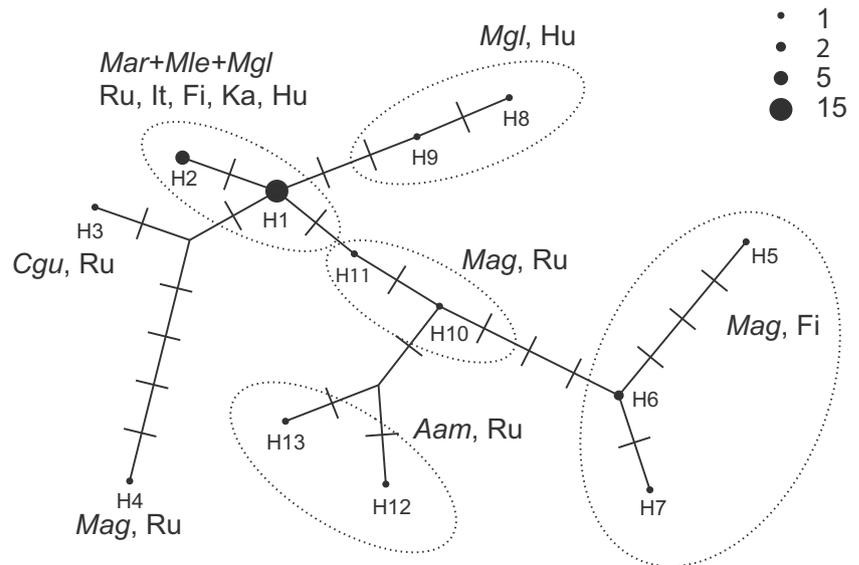
## Results and discussion

Based on the morphological analysis, *P. omphalodes* was only found in only 5 of the 20 rodent species examined in our study,

**Table 1** List of examined specimens with ISEA museum specimen numbers and GenBank accession numbers according to geographical origin. Specimens with accession numbers MK440571–MK440590 were collected and sequenced by authors

Locality (number)	Coordinates	GenBank acc. no.	Museum specimen acc. no.	Final host
Trento, Italy (1)	46° 04' 00.0" N 11° 08' 00.0" E	AY181527	–	<i>Microtus arvalis</i>
Hanság, Hungary (2)	47° 39' 19.5" N 16° 45' 35.0" E	AY181537	–	<i>Myodes glareolus</i>
" , " "	47° 39' 19.5" N 16° 45' 35.0" E	AY189954	–	<i>Myodes glareolus</i>
Osl, Hungary (3)	47° 38' 22.2" N 17° 04' 26.4" E	AY181539	–	<i>Myodes glareolus</i>
Déaványa, Hungary (4)	47° 02' 02.9" N 20° 56' 46.0" E	AY181535	–	<i>Microtus arvalis</i>
" , " "	47° 02' 02.9" N 20° 56' 46.0" E	AY181536	–	<i>Microtus arvalis</i>
" , " "	47° 02' 02.9" N 20° 56' 46.0" E	AY181538	–	<i>Microtus arvalis</i>
Turku, Finland (5)	60° 30' 00.0" N 22° 19' 00.0" E	AY181526	–	<i>Microtus agrestis</i>
Espoo, Finland (6)	60° 12' 00.0" N 24° 40' 00.0" E	AY181522	–	<i>Microtus agrestis</i>
" , " "	60° 12' 00.0" N 24° 40' 00.0" E	AY181525	–	<i>Microtus agrestis</i>
Heinävesi, Finland (7)	62° 25' 22.0" N 28° 37' 54.3" E	AY181524	–	<i>Microtus agrestis</i>
Punkaharju, Finland (8)	61° 45' 20.1" N 29° 23' 35.7" E	AY181521	–	<i>Microtus levis</i>
Kaskesnavolok, Karelia Republic, Russia (9)	61° 35' 38.8" N 33° 19' 23.0" E	MK440589	ISEA SB 2184/1 (ex. 68)	<i>Arvicola amphibius</i>
Zapovednyi, Kursk Oblast, Russia (10)	51° 35' 02.6" N 36° 06' 27.6" E	MK440581	ISEA EV 467 (ex. 294)	<i>Microtus arvalis</i>
" , " " , " "	51° 35' 02.6" N 36° 06' 27.6" E	MK440582	ISEA EV 863 (ex. 295)	<i>Microtus arvalis</i>
Belgorod, Russia (11)	50° 39' 32" N 36° 38' 58" E	MK440571	ISEA AK 14/Bel.202 (ex. 328)	<i>Microtus arvalis</i>
" , " "	50° 39' 32" N 36° 38' 58" E	MK440572	ISEA AK 14/Bel.208 (ex. 334)	<i>Microtus arvalis</i>
" , " "	50° 39' 32" N 36° 38' 58" E	MK440573	ISEA AK 14/Bel.216 (ex. 342)	<i>Microtus arvalis</i>
Afanasovo, Vladimir Oblast, Russia (12)	55° 39' 03.6" N 41° 50' 04.1" E	MK440575	ISEA AG 540–143 (ex. 269)	<i>Microtus arvalis</i>
Popolutovo, Vladimir Oblast, Russia (13)	55° 40' 12.5" N 41° 54' 14.1" E	MK440577	ISEA AG 626–147 (ex. 273)	<i>Microtus arvalis</i>
" , " " , " "	55° 40' 12.5" N 41° 54' 14.1" E	MK440580	ISEA AG 514–145 (ex. 271)	<i>Microtus arvalis</i>
Zimenki, Vladimir Oblast, Russia (14)	55° 40' 26.1" N 41° 47' 23.7" E	MK440574	ISEA AG 431–144 (ex. 270)	<i>Microtus arvalis</i>
Bulatnikovo, Vladimir Oblast, Russia (15)	55° 41' 00.0" N 41° 44' 00.0" E	MK440578	ISEA AG 646–128 (ex. 274)	<i>Microtus levis</i>
Bezengi, Kabardino-Balkar Republic, Russia (16)	43° 09' 32.6" N 43° 12' 10.5" E	MK440584	ISEA PV 17/Bez.46 (ex. 299)	<i>Chionomys gud</i>
Petropavlovsk, Kazakhstan (17)	54° 47' 36.0" N 69° 08' 50.0" E	MK440579	ISEA PG 15/Pet.1 (ex. 91)	<i>Microtus arvalis</i>
Karasuk, Novosibirsk Oblast, Russia (18)	53° 43' 40.1" N 77° 51' 38.8" E	MK440585	ISEA TD Kar.93 2–14 (ex. 84)	<i>Microtus levis</i>
Pavlodar, Kazakhstan (19)	52° 09' 15.2" N 77° 08' 55.4" E	MK440576	ISEA ZK 95–58 (ex. 184)	<i>Microtus arvalis</i>
Kreshchenskoe, Novosibirsk Oblast, Russia (20)	55° 47' 25.5" N 79° 57' 10.9" E	MK440587	ISEA AK 15/8A (ex. 104)	<i>Arvicola amphibius</i>
Azhendarovo, Kemerovo Oblast, Russia (21)	54° 45' 26.6" N 87° 01' 31.4" E	MK440583	ISEA AK 1224–142 (ex. 268)	<i>Microtus arvalis</i>
Ergaki, Krasnoyarsk Krai, Russia (22)	52° 21' 06.8" N 93° 10' 22.7" E	MK440586	ISEA PV 15/4 (ex. 102)	<i>Microtus agrestis</i>
" , " " , " "	52° 21' 06.8" N 93° 10' 22.7" E	MK440588	ISEA PV 15/12 (ex.105)	<i>Microtus agrestis</i>
Yakutsk, Sakha Republic, Russia (23)	62° 01' 28.7" N 129° 36' 42.3" E	MK440590	ISEA AK 13/D23 (ex.174)	<i>Microtus agrestis</i>

**Fig. 2** Median-joining network for *P. omphalodes* constructed using the haplotypes of *cox1* fragment sequences. Node labels indicate posterior probabilities. The size of the circles is proportional to the number of haplotypes. Dashes between haplotypes represent mutational steps between them. *Aam*, *A. amphibius*; *Mar*, *M. arvalis*; *Mag*, *M. agrestis*; *Mle*, *M. levis*; *Mgla*, *M. glareolus*; *Cgu*, *C. gud.* It, Italy; Hu, Hungary; Fi, Finland; Ru, Russia; Ka, Kazakhstan



namely Eurasian water vole *Arvicola amphibius* (L., 1758), gudaaur snow vole *Chionomys gud* (Satunin, 1909), *Microtus agrestis*, *M. arvalis*, and *M. levis*. The analysis of variability in the *cox1* gene of the cestodes from these voles confirmed our morphological identification. A total of 32 sequences of the partial *cox1* gene (507 base pairs) were compared studied and 13 haplotypes were identified. The comparison revealed a relatively low intraspecific variability in the *cox1* gene of *P. omphalodes* compared with that reported for other species of *Paranoplocephala* such as *P. jarrelli* and *P. kalelai* (Haukisalme et al. 2004; Haukisalme et al. 2006). Maximum distance between sequences of *P. omphalodes* in the dataset (*p*-distance) is 0.028 and the average distance (*d*) is 0.006. In *P. jarrelli*, these distances were 0.730 and 0.514, while in *P. kalelai*, they were 0.717 and 0.449, respectively. The examination of the haplotype networks constructed by means of median-joining (MJ) and reduced median showed similar results (Fig. 2). Despite the wide geographic distribution of sampling localities, most of the studied specimens of *P. omphalodes* were similar to each other in *cox1*.

Cestodes parasitizing *M. arvalis*, *M. levis*, and *Myodes glareolus* from Italy (Trento), Hungary (Dévaványa, Hanság, and Osl), Finland (Punkaharju), the south of central Russia (Belgorod and Vladimir Oblast), northeastern Kazakhstan (Petrovavlovsk and Pavlodar), and south of West Siberia (Karasuk and Azhendarovo) are represented by only two extremely close haplotypes — H1 and H2 (15 and 5 specimens, respectively). The wide distribution of haplotypes across such a large area may indicate a rapid geographic expansion of the involved species of definitive hosts across this territory. The closest to H1 and H2 are haplotypes of the cestodes found in *Myodes glareolus* (H8 and H9) from Hungary (Hanság), *Chionomys gud* (H3) from Bezengi (North Caucasus), and

*M. agrestis* (H10 and H11) from Ergaki (Krasnoyarsk region). Haplotypes H12 and H13 of *P. omphalodes*, found in Siberian (Kreshchenskoe) and Karelian (Kaskesnavolok) *Arvicola amphibius* respectively, are close to each other and are directly related to the H10 haplotype from the Siberian *M. agrestis*. The cestodes parasitizing *M. agrestis* from Finland (Turku, Espoo, Heinävesi) form a separate group (H5–H7). Haplotype H4 from *M. agrestis* collected at the eastern periphery of this vole range (left bank of the Lena River, Yakutia) is most distant from the “Finnish” group of haplotypes of *M. agrestis*.

The H1 haplotype, typical for the cestodes from *M. arvalis* and *M. levis*, was also found in the cestode from *M. glareolus* (Hanság, Hungary), provides the evidence of different vole species sharing the same parasite and even the same haplotype. Obviously, the exchange of parasites between host species occurs when they use the same habitat. The H1 haplotype is one of the two most abundant haplotypes of *P. omphalodes* parasitizing *M. arvalis* and *M. levis*. Cestodes parasitizing *M. arvalis* and *M. levis* represent closely related and widespread haplotypes H1 and H2. These sibling vole species occur in the same habitats, which are open landscapes with meadow or steppe vegetation or agrocenosis. These species are reproductively isolated (Malygin 1983), but in overlapping areas, they form mixed populations (Mezhzherin et al. 2017) which promotes mutual exchange of parasites. The bank vole *Myodes glareolus* is more abundant and frequent in woodland habitats, and rare or absent in shrublands and grasslands (Markova et al. 2018); in mosaic biotopes, this species may have contact with *M. arvalis* and *M. levis*. At the same time, we did not find *P. omphalodes* in bank voles in the Asian part of the continent. *Paranoplocephala*

*omphalodes* parasitizing *M. agrestis* is characterized by six haplotypes, which is substantially more diverse than in *M. arvalis* and *M. levis*. *M. agrestis* is taxonomically close to *M. arvalis* and *M. levis* and may occur in the same localities. However, unlike *M. arvalis* and *M. levis*, this species prefers more humid biotopes with rich vegetation cover and also inhabits biotopes with forest vegetation (Markova et al. 2018). Apparently, this has ensured its wider distribution across the Eurasia (Shenbrot and Krasnov 2005) which historically had a significant forest coverage. Perhaps, the difference in the haplotype diversity of cestodes, parasitizing different vole species, can be explained by the different expansion history of the definitive hosts after the last glaciation event (Sibiryakov et al. 2018; Stojak et al. 2019).

The cestodes found in the gudaur snow vole inhabiting the mountains of the North and Central Caucasus (Bannikova et al. 2013) have a haplotype close to the haplotypes of the cestodes from *M. arvalis* and *M. levis*. We suppose that the presence of *P. omphalodes* in *C. gud* is a result of host-switching through contact with common voles in areas of cohabitation, as in the case with the bank vole.

The similarity of the haplotypes of *P. omphalodes* found in *A. amphibius* and *M. agrestis* also suggests the possible exchange of this parasite. Water voles prefer to live in wetlands, riverbanks, near ponds, and streams. But at the end of the summer period, the water voles often move into biotopes with mesophytic vegetation, where field voles also occur (Chechulin et al. 2010).

Thus, our study showed a broad distribution of *P. omphalodes* in Eurasia and its parasitism in 6 vole species. *Arvicola amphibius* and *C. gud* were for the first time confirmed as hosts of *P. omphalodes* using molecular methods. In northern Asia, *P. omphalodes* parasitizes the same vole species as in Europe, namely *M. arvalis*, *M. levis*, *M. agrestis*, and *A. amphibius*. Analysis of the mitochondrial gene *cox1* variability revealed a low haplotype divergence levels in *P. omphalodes* from Asia.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** Voles were trapped using snap traps and live traps. All traps were checked twice daily. Live animals were euthanized with chloroform inhalation immediately after the capturing. The present research has met the requirements guided by the order of the High and Middle Education Ministry (Rules of work with the use of experimental animals, no. 742 from 13.11.1984) and additionally by the Federal Law of the Russian Federation no. 498-FZ from 19.12.2018 (On responsible treatment of animals).

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