THE KARYOTYPE OF *CHIRONOMUS ULIGINOSUS* KEYL (DIPTERA, CHIRONOMIDAE)

I.I. Kiknadze[1], A.G. Istomina[1], W.F. Wülker[3], H.J. Vallenduuk[2]

[1] Institute of Cytology and Genetics, SB RAS, Novosibirsk, Russia,
[2] Institut fur Biologie I (Zoologie), Universitat Freiburg, D-79104, Germany;
[3] Buro Vallenduuk, 5464 Veghel PA, 0413-319117, The Netherlands

The paper describes the karyotype of *C. uliginosus* Keyl, insufficiently studied up to now. Four *C. uliginosus* populations from the Netherlands and one population from Germany were investigated. Banding sequences of all seven chromosome arms in the *C. uliginosus* karyotype were analyzed. Inversion polymorphism was observed in arms A, B, C, D, E, and F. A total of 18 banding sequences were recorded. The sets and number of banding sequences varied between populations, causing their cytogenetic differentiation. The comparison of banding sequence sets and frequencies between the Netherlands and Russian populations of *C. uliginosus* was carried out, and considerable cytogenetic differences between these distant populations were discovered.

Keywords: karyotype, morphology, *Chironomus*, banding sequences, chromosomal polymorphism, populations.

Introduction

Keyl (1962) described several new species by studying their karyotypes («cytospecies» by Keyl). The karyotypes of these «cytospecies» differed greatly from other known *Chironomus* karyotypes and Keyl believed that the «cytospecies» were new species. The validity of «cytospecies» was confirmed by morphological studies (Strenzke, unpublished data because of the unexpected death of author; Wülker *et al*., 1981; Webb, Scholl, 1985; Webb *et al*., 1985; Kiknadze *et al*., 1988; Wülker, 1999; Sæther, Spies, 2004; Moller-Pillot, 2009).

Chironomus uliginosus was one of the «cytospecies» identified by Keyl (1960, 1962). It is known now that *C. uliginosus* is widespread in Europe (Fauna Europaea). However, the karyotype of *C. uliginosus* has not been analyzed since Keyl's time. Keyl (1962) mapped only three chromosome arms (A, E, F) of seven chromosome arms in *C. uliginosus* karyotype. The banding sequences of arms C, D, B, G and chromosomal polymorphism in all chromosome arms were not studied. It was not until recently that Broshkov *et al*. (2008) presented the new data on *C. uliginosus* karyotype from several Russian populations. Some cytogenetic differences were found between the German populations described by Keyl (1962) and Russian populations. The main difference was related to a fixed inversion in arm G in Russia. Morphological data were not presented in the paper by Broshkov *et al*.

In this paper we present a detailed karyological description of *C. uliginosus* from European (the Netherlands and Germany) populations. The banding sequences in all seven chromosome arms (A. B, C, D, E, F, G) were studied, the chromosomal polymorphism in all arms except arm G was recorded, and the banding sequence pool was evaluated. The comparison of *C. uliginosus* karyotypes and chromosomal polymorphism between European and Russian populations demonstrated considerable cytogenetical differences between distant populations.

Materials and Methods

The karyotype and chromosomal polymorphism of *C. uliginosus* were investigated in four natural populations from the Netherlands and one population from Germany (Table 1). Besides, six squashes with *C. uliginosus* karyotypes from Germany and Sweden from W. Wülker's collection were analyzed. Four of this squashes were made from holotype *C. uliginosus* larvae. The data on

Table 1

Collection sites and numbers
of *Chironomus uliginosus* larvae analyzed

Locality	Collection date	Number of larvae
The Netherlands		
Bargerveen	17.04.2007	n = 6
	16.08.2007	n = 14
	05.09.2007	n = 12
	07.04.2008	n = 8
Mariapeel	18.07.2008	n = 6
	22.07.2008	n = 15
Peelvenen	05.11.2007	n = 5
	06.11.2007	n = 6
De Hamert	18.05.2007	n = 6
	01.09.2007	n = 2
Germany		
Leegmoor	02.05.2008	n = 3

chromosomal polymorphism of several Russian populations of *C. uliginosus* (Novosibirsk, Tchelyabinsk, Yaroslavl regions) were used for a comparison of West European and Asian populations.

Fourth instar larvae were fixed in 3 : 1 mixture of 100 % ethanol and glacial acetic acid for cytogenetic study. Isolated salivary glands were squashed for polytene chromosome preparation. Polytene chromosome squashes were made by the aceto-orcein method (Keyl H., Keyl I., 1959; Kiknadze *et al*., 1991). The polytene chromosomes were mapped in accordance with Keyl's system (1962) for arms A, E, F and Dévai *et al.*'s system (1989) for arms B, C, and D.

Detailed photomaps of all seven chromosome arms were made for the first time for European *C. uliginosus*. However, arms B and G were not mapped because of complex inversions differing banding sequences of these arms from standard *C. piger*.

The following equipment of the Center of Microscopy Analysis of Biological Objects of SB RAS in the Institute of Cytology and Genetics (Novosibirsk) has been used: microscope «Axioskop» 2 Plus, CCD camera AxioCam HRc, software package AxioVision 4 (Zeiss, Germany). The photographs of chromosomes were made at the magnification 100×.

Results

Karyotype structure

The *C. uliginosus* karyotype can be seen in Fig. 1. The four polytene chromosomes of *C. uliginosus* correspond to the haploid number of this species (n = 4) as usual in the genus *Chironomus*. Chromosome AE is submetacentric, chromosomes CD and BF are metacentric, and short chromosome G is telocentric. On the base of chromosome arm combination, *C. uliginosus* can be assigned to cytocomplex *pseudothummi*. The centromeric bands are not heterochromatinized. The nucleolus and three

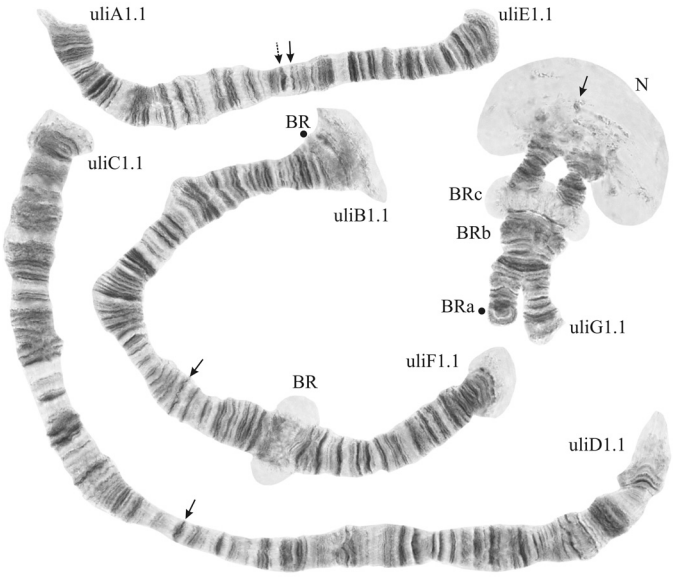

Fig. 1. Karyotype of *Chironomus uliginosus*. Symbols uliA1.1, uliB1.1, etc. designate genotypic combinations of banding sequences in chromosome arms; N – nucleolus; BR – Balbiani ring; arrows show centromeric bands.

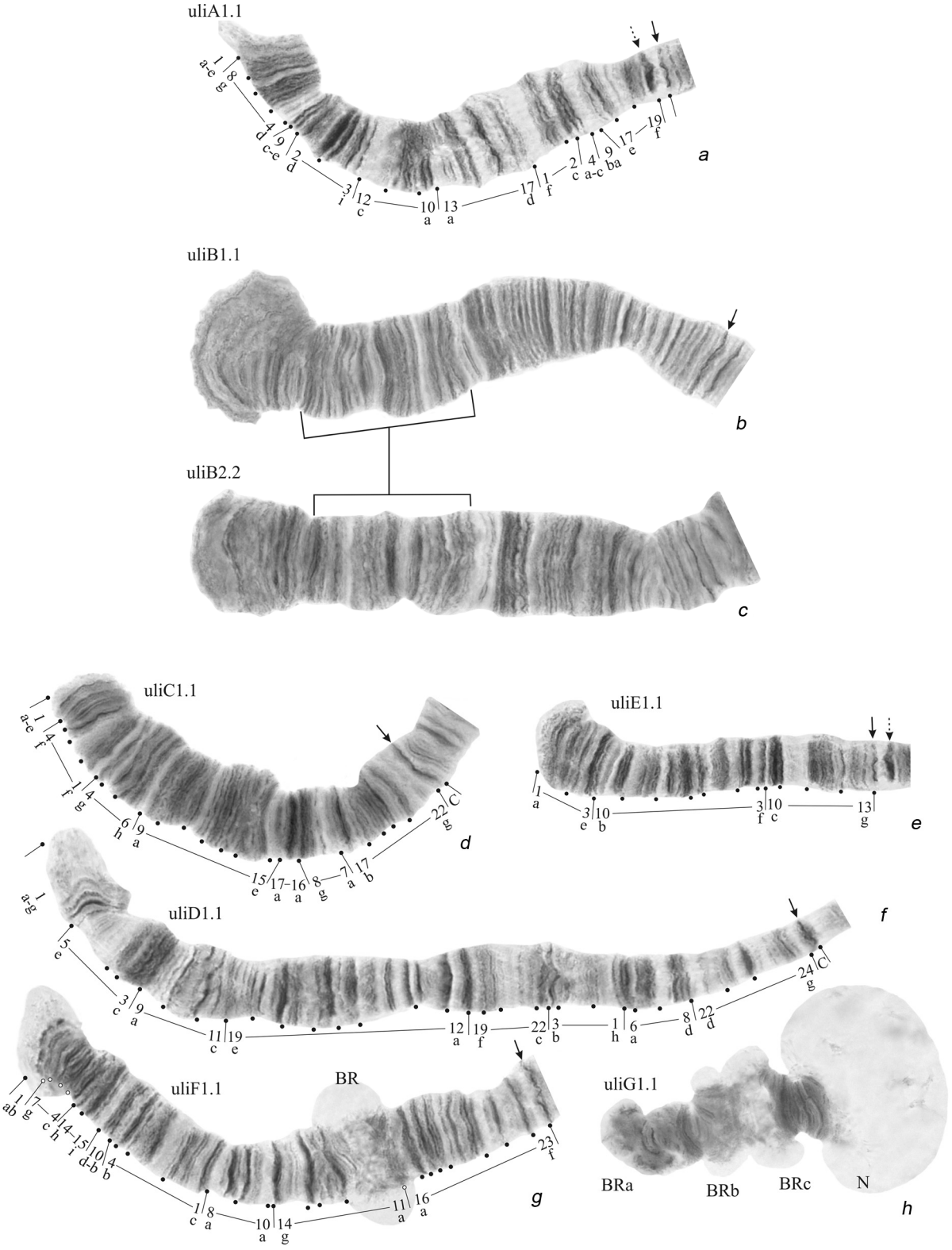

Fig. 2. Homozygous banding sequences in chromosome arms A (a), B (b, c), C (d), D (f), E (e), F (g) and G (h) of *Chironomus uliginosus*.

Table 2

Frequencies of banding sequences in populations of *Chironomus uliginosus*

Banding sequences	Populations				
	Bargerveen *n* = 40	Mariapeel *n* = 21	Peelvenen *n* = 11	De Hamert *n* = 8	Leegmoor *n* = 3
uliA1	1,000	0,976	1,000	1,000	1,000
uliA2	–	0,024	–	–	–
uliB1	0,637	0,666	0,591	0,875	1,000
uliB2	0,363	0,310	0,409	0,125	–
uliB3	–	0,024	–	–	–
uliC1	1,000	0,952	0,864	1,000	1,000
uliC2	–	0,024	0,045	–	–
uliC3	–	0,024	0,091	–	–
uliD1	0,900	0,881	0,864	1,000	1,000
uliD2	0,100	0,024	–	–	–
uliD3	–	0,071	0,045	–	–
uliD4	–	0,024	0,091	–	–
uliE1	1,000	0,976	1,000	1,000	1,000
uliE2	–	0,024	0	0	–
uliF1	0,987	0,000	0,955	1,000	1,000
uliF2	0,013	–	–	–	–
uliF3	–	–	0,045	–	–
uliG1	1,000	1,000	1,000	1,000	1,000

Balbiani rings are located on short arm G. Besides, Balbiani rings are present also on arms B and F.

We found that the karyotypes of *C. uliginosus* from all populations studied were identical with the karyotype described by Keyl (1960, 1962) and with the karyotypes of the holotype larvae.

Arm A occurred in one banding sequence uliA1 as a rule (Fig. 2, a, Table 2, Appendix). Another banding sequence, uliA2, was found only once in a larva with a long heterozygous pericentric inversion (Fig. 3, b, Tables 2, 3, Appendix). The banding sequence uliA1 was close to *C. dorsalis* and *C. luridus*, other members of *pseudothummi* cytocomplex.

Arm B was polymorphic with three banding sequences – uliB1, uliB2, and uliB3 (Figs 2, b, c, 3, a, c, Table 2, Appendix). The uliB1 sequence was predominant in the populations studied; uliB2 was also recorded at a high frequency, and it can be considered an alternative sequence to uliB1. The uliB2 sequence differed from uliB1 by a simple inversion. The uliB3 sequence was very rare (Table 2), it differed from uliB1 by an included inversion (Fig. 3, c). The uliB1 and uliB2 banding sequences were recorded in homo- and heterozygous states, and uliB3 was found only as a heterozygote (Table 3).

Arm C was polymorphic. It showed three banding sequences – uliC1, uliC2, and uliC3 (Figs 2, d, 3, d, e, Table 1, Appendix). The uliC1 sequence was predominant, whereas uliC2 and uliC3 were rare (Table 2); uliC2 differed from uliC1 by a simple inversion, and uliC3 differed from uliC1 by a long inversion, which occupied practically the entire central part of arm C (Appendix). The uliC1 sequence was recorded in homo- and heterozygous states, and uliC2 and uliC3 were always heterozygotes (Table 3).

Arm D was the most polymorphic. It occurred in four banding sequences – uliD1, uliD2, uliD3 and uliD4 (Figs 2, f, 3, f–h, Table 2, Appendix). The uliD1 and uliD2 sequences differed by a short simple inversion in the central part of the arm; uliD3

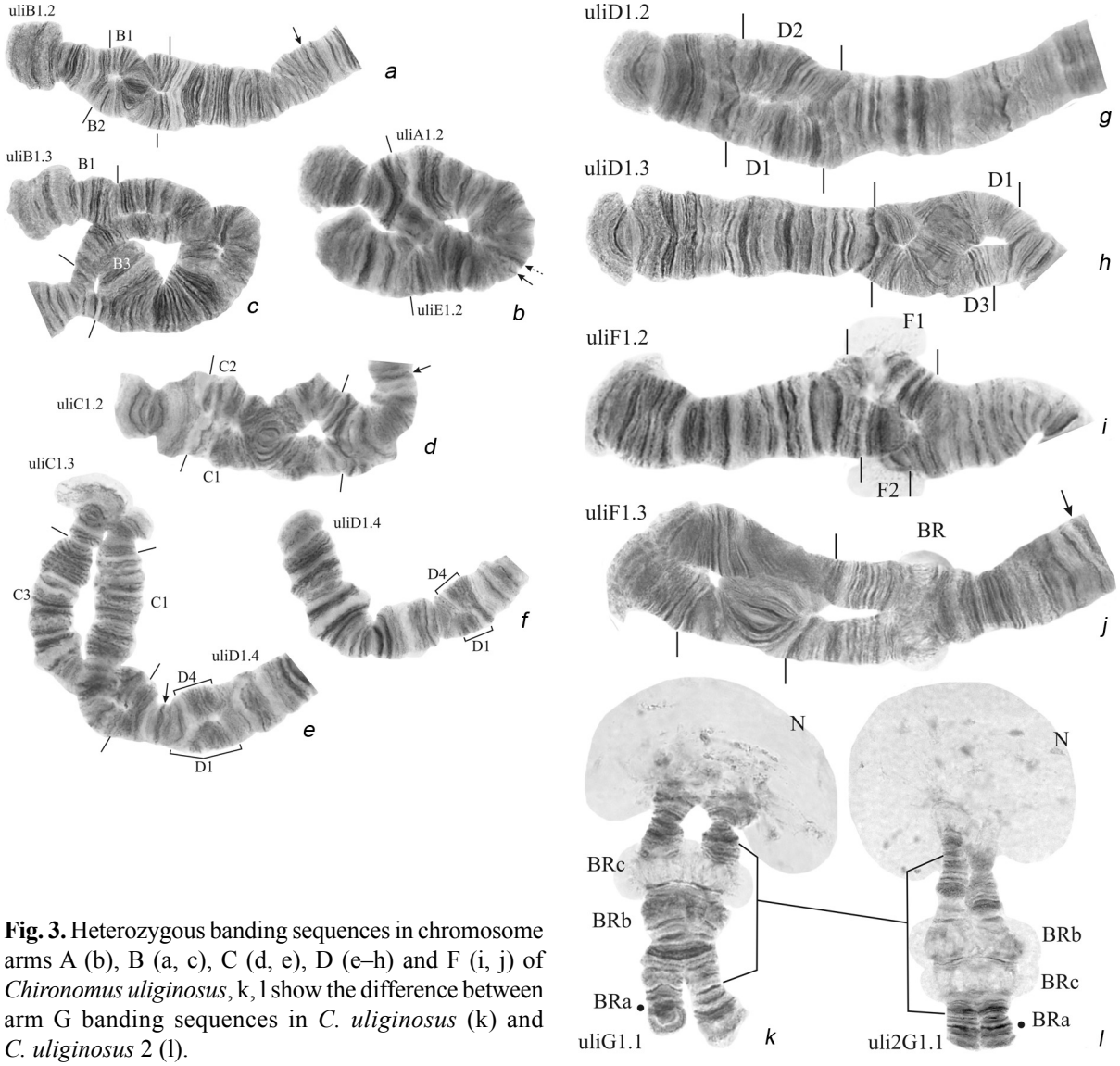

Fig. 3. Heterozygous banding sequences in chromosome arms A (b), B (a, c), C (d, e), D (e–h) and F (i, j) of *Chironomus uliginosus*, k, l show the difference between arm G banding sequences in *C. uliginosus* (k) and *C. uliginosus* 2 (l).

differed from uliD1 by a long simple inversion in the proximal part of the arm; uliD4 differed from uliD1 by a short simple inversion near the centromere region (Appendix). The uliD1 sequence was predominant; uliD2, uliD3, and uliD4 were rare (Table 2). The last two sequences were recorded only as heterozygotes (Table 3).

Arm E had practically one banding sequence uliE1. Another sequence, uliE2, was found only once in heterozygote uliE1.2 (Figs 2, e, 3, b, Table 2, Appendix). The uliE2 sequence was formed by a long pericentric inversion (Fig. 3, b). The uliE1 sequence belongs to the category of cosmopolitan sequences found in many *Chironomus* species on five continents (Eurasia, North and South America, Africa, Australia (Wülker, 1980; Kiknadze *et al*., 2008).

Arm F was polymorphic and occurred in three banding sequences: uliF1, uliF2, and uliF3 (Figs 2, g, 3, i, j, Table 2, Appendix). The uliF2 sequence differed from uliF1 by a short simple inversion in the proximal part of the arm, including BR (Fig. 3, i, Appendix); uliF3 differed from uliF1 by a short inversion in the distal part of arm (Fig. 3, j). The uliF1 sequence was predominant; uliF2 and uliF3 were rare and were found as heterozygotes (Tables 2, 3). The uliF1 sequence was close to *C. holomelas*, *C. dorsalis*, and *C. halophilus*.

Arm G occurred in one banding sequence uliG1 (Fig. 3, k, Table 2). As was mentioned above, arm G carries a nucleolus and Balbiani rings (BR). The most of salivary gland cells had two developed BRs (BRc and BRb (Fig. 3, k), the third BRa (Fig. 2, h)

Table 3

Frequencies of genotypic combinations of banding sequences in populations of *Chironomus uliginosus*

Genotypic combinations	Populations				
	Bargerveen *n* = 40	Mariapeel *n* = 21	Peelvenen *n* = 11	De Hamert *n* = 8	Leegmoor *n* = 3
uliA1.1	1,000	0,952	1,000	1,000	1,000
uliA1.2	0	0,048	0	0	0
uliB1.1	0,375	0,380	0,454	0,750	1,000
uliB2.2	0,100	0,048	0,273	0	0
uliB1.2	0,525	0,524	0,273	0,250	0
uliB1.3	0	0,048	0	0	0
uliC1.1	1,000	0,904	0,727	1,000	1,000
uliC1.2	0	0,048	0,091	0	0
uliC2.3	0	0,048	0,182	0	0
uliD1.1	0,800	0,761	0,727	1,000	1,000
uliD1.2	0,200	0,048	0	0	0
uliD1.3	0	0,143	0,091	0	0
uliD1.4	0	0,048	0,182	0	0
uliE1.1	1,000	0,952	1,000	1,000	1,000
uliE1.2	0	0,048	0	0	0
uliF1.1	0,975	1,000	0,909	1,000	1,000
uliF1.2	0,025	0	0	0	0
uliF1.3	0	0	0,091	0	0
uliG1.1	1,000	1,000	1,000	1,000	1,000

Table 4

Inversion polymorphisms in populations of *Chironomus uliginosus*

Characteristic of populations	Populations				
	Bargerveen *n* = 40	Mariapeel *n* = 21	Peelvenen *n* = 11	De Hamert *n* = 8	Leegmoor *n* = 3
Heterozygotes in population (%)	65,0	71,4	63,6	25,0	0
Average number of heterozygous inversions per individual	0,8	1,0	0,9	0,3	0
Number of banding sequences in population	10	16	14	8	7
Number of genotypic combinations of banding sequences in population	11	17	15	8	7

developed only in four cells of the special lobe of a salivary gland producing a tissue-specific protein.

Chromosomal polymorphism

As shown in Tables 2 and 3, six of seven chromosome arms in the Netherlands populations of *C. uliginosus* were polymorphic. Chromosomal polymorphism was not revealed in German population because of a few number of individuals. Two banding sequences were recorded in arms A and E, three banding sequences in arms B, C, F, and four banding sequences in arm D. Only arm G was monomorphic. A total of 18 banding sequences

were recorded in *C. uliginosus* studied (Table 2). They composed the banding sequence pool of this species. The numbers of sequences and genotypic combination of sequences varied in different populations (Table 4).

These data on chromosomal polymorphism showed that *C. uliginosus* could be considered a polymorphic species, although the general level of chromosomal polymorphism of this species is not as high as in many other *Chironomus* species: 40–60 banding sequences in their banding sequences pool (Kiknadze, Istomina, 2000). Keyl (1962) described *C. uliginosus* as a monomorphic species.

Discussion

We investigated morphologically similar larvae of 18 *Chironomus* populations in the Netherlands and distinguished 4 populations of *C. uliginosus* among them on the base of karyotype study. The karyotype proved to be the most useful taxonomic character for species identification at the larval stage. The main karyotype features of the larvae studied were identical with the *C. uliginosus* karyotype of the holotype larvae (Keyl, 1960, 1962; karyotype squash of holotype). We thoroughly analyzed the banding sequences in all seven chromosome arms, whereas Keyl had analyzed only three. Therefore, we can present new cytogenetic characteristics for European *C. uliginosus* populations. These populations had rather high levels of chromosomal polymorphism. Six of seven chromosome arms proved to be polymorphic, and as many as 18 banding sequences were recorded in populations studied. The sets and numbers of banding sequences and genotypic combinations of sequences varied in different populations to allow their cytogenetic differentiation.

Recently, Broshkov *et al*. (2008) have described karyotype and chromosomal polymorphism in several Russian *C. uliginosus* populations. They have found that main species specific banding sequences and chromosomal polymorphism in arms A, E, and F are identical in Russian and German populations (Keyl, 1962). As Keyl (1962) had not described banding sequences in arms C, D, and B, these sequences could not be compared in Russian and German populations. On the base of identity of arms A, E, and F, Broshkov *et al.* (2008) came to conclusion that the German and Russian populations belonged to *C. uliginosus*, but there are interpopulation differences related to the sets and frequencies of some sequences. The main difference was based on a fixed inversion in the central part of arm G in the Russian populations.

The quantitative characteristics of chromosomal polymorphism in arms C, D, and B in European populations were described in this paper for the

Table 5

Comparison of banding sequence sets between *Chironomus uliginosus* (European populations) and *C. uliginosus 2* (Russian populations)

Identical banding sequences	Banding sequences specific for *C. uligonosus*	Banding sequences specific for *C. uliginosus 2*
uliA1=uli2A1	uliA2	uli2B2 differs from uliB2 by simple short inversion
uliB1=uli2B1	uliB2	uli2C2 differs from uliC2 by simple long inversion
uliC2=uli2C1	uliB3	uli2C3 differs from uliC3 by included short inversion
uliD2=uli2D1	uliC1	uli2D2 differs from uliD2 by simple inversion
uliE1=uli2E1	uliC3	uli2D3 differs from uliD3 by complex inversion
uliF1=uli2F1	uliD1	uli2F2 differs from uliF2 by simple inversion
	uliD3	uli2G2 differs from uliG1 by simple inversion
	uliD4	
	uliE2	
	uliF2	
	uliF3	
	uliG1	

first time. They provided an opportunity to compare chromosomal polymorphism in all chromosomal arms in European and Russian populations.

This comparison showed a great difference in sets and frequencies between European and Russian populations, especially in arms C, D, and B. As mentioned above, 18 banding sequences were recorded in the Netherlands populations and 13 sequences in Russian populations. Among them six sequences were completely identical (Table 5); they belong to the category of main or alternative species-specific sequences (Kiknadze, 2008), found in homo- or heterozygous states, but their frequencies could be different in Europe and Russia. Twelve sequences were found only in the Netherlands and six, only in Russia (Table 5); the most of these sequences were rare and were found only as heterozygotes. The most important difference between the Netherlands and Russian populations was the fixed inversion in arm G (Figs 3, k, l). The banding sequence in arm G in the Netherlands corresponded to the sequence described by Keyl (1960). Therefore we conclude that the Netherlands populations corresponded to real *C. uliginosus*, and Russian populations can be considered as greatly differentiated geographic populations or even a subspecies, tentatively named *C. uliginosus* 2. The cytogenetic differentiation of geographic populations in *C. uliginosus* is very similar to differentiation in the *obtusidens*-group of subspecies and sibling-species (Wülker *et al*., 1983, Istomina *et al*., 1999, Kiknadze *et al*., 2007). It is necessary to investigate quantitative characteristics of chromosomal polymorphism in much more populations of *C. uliginosus* from different areas in Europe and Russia to clarify the taxonomic positions of distant populations of this species. Up to now there were only short descriptions of several *C. uliginosus* populations without quantitative analysis (Keyl, 1960, 1962; Krieger-Wolff, 1971; Wülker, 1999; Moller-Pillot, 2009).

Our data have shown that *C. uliginosus* is a polymorphic species, contrary to Keyl's (1962) view of this species as monomorphic. The percentage of inversion heterozygotes in population can reach 71 %, and the number of banding sequences per population, 16. However this level of chromosomal polymorphism is not as high as in many other *Chironomus* species (Kiknadze, Istomina, 2000; Kiknadze, 2008) and, correspondingly, *C. uliginosus* can be regarded as a species with moderate level of chromosomal polymorphism.

This work was supported by grants from the Presidium of the Russian Academy of Sciences: «Biodiversity and dynamics of gene pools» and «Origin and evolution of geobiosystems».

References

Broshkov A.D, Kiknadze I.I., Istomina A.G., Gunderina L.I. Karyotype structure of midge *Chironomus uliginosus* Keyl, 1960 (Diptera, Chironomidae) // Euroasian Entomol. J. 2008. V. 7. P. 57–67. (In Russ.).

Dévai Gy., Miskolczi M., Wülker W. Standardization of chromosome arms B, C and D in *Chironomus* (Diptera, Chironomidae) // Acta Biol. Debr. Oecol. Hung. 1989. V. 2(1). P. 79–92.

Istomina A.G., Kiknadze I.I., Siirin M.T. Karyological analysis of *Chironomus* species in *obtusidens*-group from Altai (Diptera, Chironomidae) // Tsitologia. 1999. V. 41. P. 1022–1031. (In Russ.).

Keyl H.-G. Die cytologische Diagnostik der Chironomiden. II Diagnosen der Geschwisterarten *Chironomus acidophilus* n. sp. and *C. uliginosus* n. sp. // Arch. Hydrobiol. 1960. V. 57. P. 187–195.

Keyl H.-G. Chromosomenevolution bei Chironomus. II Chromosomenbauten und phylogenetische Beziehungen der Arten // Chromosoma. 1962. V. 13. P. 464–514.

Keyl H.-G., Keyl I. Die cytologische Diagnostik der Chironomiden. I. Bestimmungstabelle fur die Gattung *Chironomus* auf Grund der Speicheldrusenchromosomen // Arch. Hydrobiol. 1959. V. 56. P. 43–57.

Kiknadze I.I. The role of chromosomal polymorphism in divergence of populations and species of the genus *Chironomus* // Entomol. Rev. 2008. V. 88. P. 509–524.

Kiknadze I.I., Grebenyuk L.P., Filippova M.A, Kerkis I.E. Karyological analysis of *Chironomus* species of pseudothummi cytocomplex from USSR water bodies // Biol. of Interland Waters Inform. Bull. 1988. V. 79. P. 56–59. (In Russ.).

Kiknadze I.I., Gunderina L.I., Butler V.G. *et al*. Chromosomes and continents // Biosphere Origin and Evolution / Eds N. Dobretsov, A. Pozanov, N. Kolchavov, G. Zavarzin. Springer-Verlag, 2008. P. 349–369.

Kiknadze I.I., Istomina A.G. Karyotypes and chromosomal polymorphism in Siberian chironomid species (Diptera, Chironomidae) // Siberian Ecol. J. 2000. V. 7. P. 445–460. (In Russ.).

Kiknadze I.I., Istomina A.G., Gunderina L.I. Cytogenetic differentiation of natural populations of *Chironomus obtusidens* // Entomol. Rev. 2007. V. 87. P. 658–669.

Kiknadze I.I., Shilova A.I., Kerkis I.E. *et al.* Karyotypes and larval morphology in tribe Chironominae. Atlas. Novosibirsk: Nauka, 1991. 113 p. (In Russian with English Summary).

Krieger-Wolff E., Wülker W. Chironomiden (Diptera) aus der Umgebung von Freiburg i. Br. (mit besonderer Berücksichtigung der Gattung Chironomus) // Beitr. naturk. Forsch. Südw. Dtl. 1971. V. 30. P. 133–145.

Moller-Pillot H.K.M. Chironomidae larvae of the Netherlands and adjacent lowlands. Zeist, The Netherlands, KNNV Publishing, 2009. 270 p.

Sæther O.A., Spies M. Fauna Europaea // Fauna Europaea: Diptera, Nematocera / Ed. H. De Jong. 2004. available at http://www.faunaeur.org/

Webb C.J., Scholl A. Identification of larvae of European species of *Chironomus* Meigen (Diptera, Chironomidae) by morphological characters // Syst. Entomol. 1985. V. 10. P. 353–372.

Webb C.J., Scholl A., Ryser H.M. Comparative morphology of the larval ventromental plates of European species of *Chironomus* Meigen (Diptera, Chironomidae) // Syst. Entomol. 1985. V. 10. P. 373–385.

Wülker W. Basic pattern in the chromosome evolution of the genus *Chironomus* (Diptera) // Z. Zool. Syst. Evol. 1980. V. 18. P. 112–123.

Wülker W. Fennoscandian *Chironomus* species (Diptera, Chironomidae) – identified by karyotypes and compared with the Russian and Central European fauna // Studia Dipterologica. 1999. V. 2. P. 425–436.

Wülker W., Ryser H.M., Scholl A. Revision der Gattung *Chironomus* Meigen VI. *C. holomelas* Keyl, *C. saxatilis* n. sp., *C. melanescens* Keyl // Rev. Suisse Zool. 1981. V. 88. P. 903–924.

Wülker W., Ryser H.M., Scholl A. Revision der Gattung *Chironomus* Meigen VIII. Arten mit Larvae des fluviatilis-Type (*C. acutiventris* n. sp. und *C. obtusidens* Goetgh. // Rev. Suisse Zool. 1983. V. 90. P. 725–745.

Appendix. Banding sequences in *Chironomus uliginosus*

uliA1	1a-e 8g-4d 9c-e 2d-3i 12c-10a 13a-17d 1f-2c 4a-c 9ba 17e-19f
uliA2	not mapped; formed by a large pericentric inversion
uliB1	not mapped
uliB2	not mapped, differs from uli2B2 by a simple short inversion
uliB3	not mapped
uliC1	1a-e 4f-1f 4g-6h 9a-15e 17a-16a 8g-7a 17b-22g differs from uli2C1 by a simple inversion
uliC2	1a-e 4f-1f 15e-9a 6h-4g 17a-16a 8g-7a 17b-22g
uliC3	1a-e 4f-1f 11d-15e 11c-9a 6h-4g 20c-17b 7a-8g 16a-17a 21a-22g
uliD1	1a-g 5e-3c 9a-11c 19e-12a 19f-22c 3b-1h 6a-8d 22d-24g differs from uli2D1 by a simple inversion
uliD2	1a-g 5e-3c 9a-11c 15e-19e 15d-12a 19f-22c 3b-1h 6a-8d 22d-24g
uliD3	1a-g 5e-3c 9a-11c 19e-12b 8d-6a 1h-3b 22c-19f 12a 22d-24g
uliD4	1a-g 5e-3c 9a-11c 19e-12a 19f-22c 3b-1i 8d-6a 1h 22d-24g
uliE1	1a-3e 10b-3f 10c-13g basic cosmopolitan
uliE2	not mapped, formed by a large pericentric inversion
uliF1	1ab 7g-4c 14h-15i 10d-b 4b-1c 8a-10a 14g-11a 16a-23f
uliF2	1ab 7g-4c 14h-15i 10d-b 4b-1c 8a-10a 14g-12a 19d-16a 11a-i 20a-23f
uliF3	not mapped
uliG1	not mapped, differs from uli2G1 by a fixed inversion