

Karyotypes and sex chromosome diversity in three stonefly species (Plecoptera: Perlodidae, Perlidae) from Siberia

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Academic editor: R. Yakovlev | Received 7 August 2026 | Accepted 4 September 2026 | Published 14 October 2026

<http://zoobank.org/23E4814F-CBF9-42FF-B25A-D9292E32B811>

Citation: Buleu OG, Bugrov AG (2026) Karyotypes and sex chromosome diversity in three stonefly species (Plecoptera: Perlodidae, Perlidae) from Siberia. Acta Biologica Sibirica 12: 1309–1319. <https://doi.org/10.5281/zenodo.23318893>

Abstract

The current paper focuses on studying morphology of the autosomes and sex chromosomes in karyotypes of three stonefly species from Siberia. We provide new cytogenetic data for species from Perlodidae (*Arcynopteryx dichroa* (McLachlan, 1872), *Megarcys ochracea* (Klapálek, 1912)) and Perlidae (*Kamimuria exilis* (McLachlan, 1872)) families. The karyotype of male and female of *A. dichroa* consists of 13 pairs of chromosomes ($2n_{\text{♂}}^{\text{♀}}=26$). The sex determination mechanism in *A. dichroa* is XY/XX. The male *M. ochracea* consists of 8 pairs of chromosomes ($2n_{\text{♂}}=16$). The karyotype of females *M. ochracea* consists of 9 pairs of chromosomes ($2n_{\text{♀}}=18$). The sex determination mechanism in *M. ochracea* is $\text{♂}X_1X_2/\text{♀}X_1X_2X_2$. The male *K. exilis* karyotype consists of 10 pairs of autosomes and one unpaired X-chromosome ($2n_{\text{♂}}=21$, the determination of sex is X0). The karyotype of female *K. exilis* consists of 11 pairs of chromosomes ($2n_{\text{♀}}=22$, the determination of sex is XX). All chromosomes of the studied stonefly species are metacentric or submetacentric. Pericentromeric C-bands were revealed for all chromosomes of *K. exilis*. Additionally, their mid-size submetacentric chromosomes possesses small telomeric C-bands in the long arms. The submetacentric X-chromosomes of the male and female *K. exilis* also have small intercalary C-bands proximally in the long arm (XR). New data on Plecoptera chromosomes confirm the unusual diversity of karyotypes of these insects in the Polyneoptera cohort.

Keywords

Plecoptera, karyotype, autosomes, sex chromosomes, C-banding

Introduction

Stoneflies (Plecoptera) are amphibiotic insects whose nymphs live in fast-flowing rivers. They are distributed primarily in the temperate zones of the Northern and Southern Hemispheres. Plecoptera is a relatively small insect order, with 4,281 species representing 17 families (DeWalt et al. 2026). Among those, approximately 340 stonefly species from 9 families have been described for Russia and adjacent countries (Zhiltzova 2010). A significant part, 122 stonefly species from 8 families, have been recorded in Siberia (Zapekina-Dulkeit and Dulkeit 1980).

Cytogenetically, stoneflies are one of the least studied groups among the Polyneoptera cohort. Before the current study, the karyotypes of 16 stonefly species from Europe, North America, and Japan (Nakahara 1919; Junker 1923; Itoh 1933; Matthey 1946; Matthey and Aubert 1947) and one species from the vicinity of Novosibirsk (Russia) (Bugrov et al. 2024) had been described. These studies are all available results concerning research of karyotypes and mechanisms of sex determination in Plecoptera. In review papers focused on the evolution of insect sex chromosomes, stoneflies are often cited as a group with highly diverse karyotypes and chromosomal sex determination (White 1973; Blackman 1995). Our research group has been studying the evolution of sex chromosomes in grasshoppers for many years (Bugrov and Grozeva 1998; Bugrov et al. 2001, 2016; Jetybayev et al. 2017; Buleu et al. 2020), and therefore we focused on information about the intriguing diversity of cytological mechanisms of sex determination in stoneflies.

The main focus of this study is to investigate the karyotypes of stoneflies, including the method of C-differential chromosome staining, which we first applied in the cytogenetics of stoneflies (Bugrov et al. 2024). The current study provides a comparative cytogenetic analysis of the stoneflies *Arcynopteryx dichroa* (McLachlan, 1872), *Megarcys ochracea* (Klapálek, 1912) and *Kamimuria exilis* (McLachlan, 1872) from some rivers of the Altai Republic and the Novosibirsk region.

Materials and methods

Nymphs of different ages were collected during spring and fall 2020–2025, in the Altai Republic and the Novosibirsk region (Table 1).

During fieldwork, the nymphs of the stoneflies were collected and kept in a container with river water and transported in a cooler bag. In the laboratory, the nymphs were kept in containers with river water at 2–4 °C. Chromosome preparations were made from testes and ovaries of about 50–100 male and female nymphs from each species. No more than 7–10 % of the nymphs were available for cytogenetic analysis. Chromosome preparations and C-banding were performed as described earlier by Bugrov et al. (2024). Microscopic analysis was performed at the Centre for Microscopy of Biological Objects of the Siberian Branch of the Russian Academy of Sciences (Novosibirsk, Russia). Chromosomes were studied with an

Axioskop 2 Plus microscope (Zeiss, Germany) equipped with a CCD camera. The AxioVision software package (Zeiss, Germany) was used for image capture and analysis.

For the taxonomic determination of stonefly nymphs we used the key to the stoneflies of Russia and adjacent countries (Teslenko and Zhiltzova 2009).

Table 1. Location of the Plecoptera species studied in this work

Taxa	Species	Location
Perlodidae	<i>Arcynopteryx dichroa</i>	Altai Republic, Biya River near Artybash village (51°47'12"N 87°14'37"E)
	<i>Megarcys ochracea</i>	Altai Republic, Kislaya River, 3 km north of Shebalino village (51°19'47"N 85°40'11"E)
Perlidae	<i>Kamimuria exilis</i>	Novosibirsk region, Ik river in the vicinity of Novososedovo village (54°38'28"N 83°58'51"E)

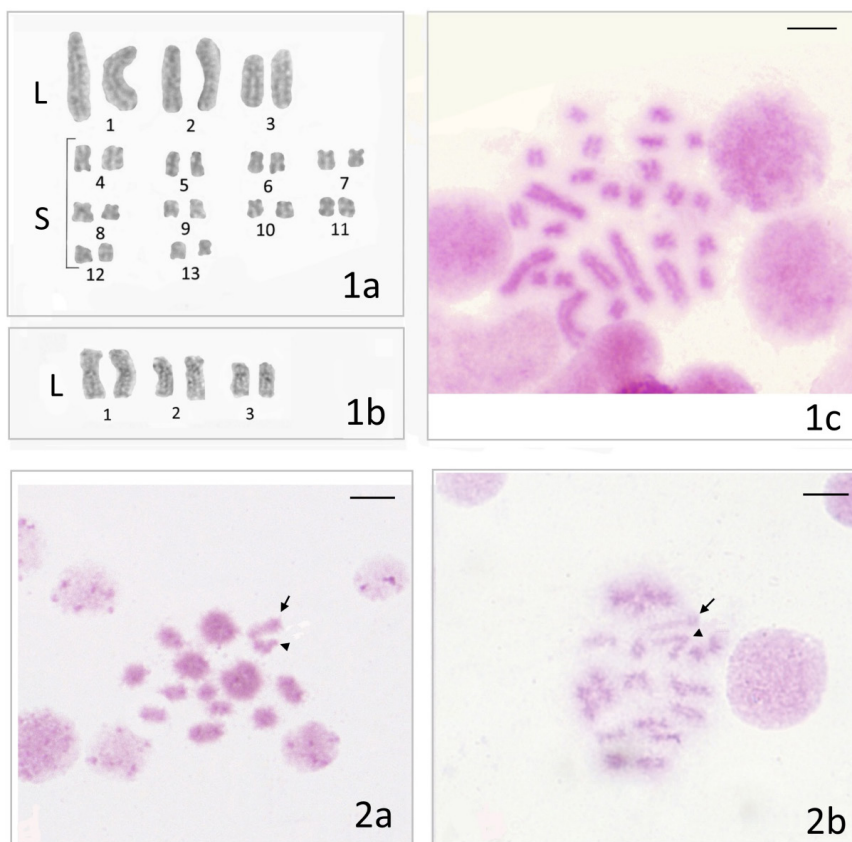
Results

Arcynopteryx dichroa

The male and female karyotypes of *A. dichroa* consist of 13 pairs of chromosome ($2n_{\text{♂}}=26$). In the female karyotype, we distinguished two classes of chromosomes: large (L) and small (S) (Fig. 1a). In the early stages of spermatogonial and oogonial metaphases, the localization of the centromere in chromosomes was difficult to achieve (Figs 1a, c). Analysis of metaphase chromosomes allowed for a more precise determination of the centromere position and morphology of chromosomes. Thus, the first pair of chromosomes (L1) is metacentric, while the second and third pairs (L2, L3) are submetacentric (Fig. 1b). The remaining chromosomes of the set are subcentric and metacentric (S4–S13) (Figs 1a, c).

In meiosis, male chromosomes form 13 bivalents (Figs 2a, b). The 12 bivalents are symmetric, of which the large ones (L1–L3) form two (Fig. 2a) or one distal chiasmata (Fig. 2b). The remaining bivalents form only one chiasma (Figs 2a, b). One bivalent is asymmetric (Figs 2a, b) and formed by a single metacentric chromosome, which is likely homologous to the chromosome of the fourth pair of the female karyotype (Fig. 1a). The second chromosome of this bivalent is large and submetacentric (Figs 2a, b). There is no homology of this submetacentric chromosome with other female chromosomes (Figs 1a, c). In the meiosis prophase, the chromosomes of this bivalent conjugate with their terminal regions (Fig. 2a) or are always adjacent to each other (Fig. 2b).

A comparative analysis based on the morphology and behavior of the asymmetric bivalent in meiosis suggests that these are sex chromosomes. Therefore, we assume that the mechanism for determining chromosomal sex in *A. dichroa* is XY male, XX female.



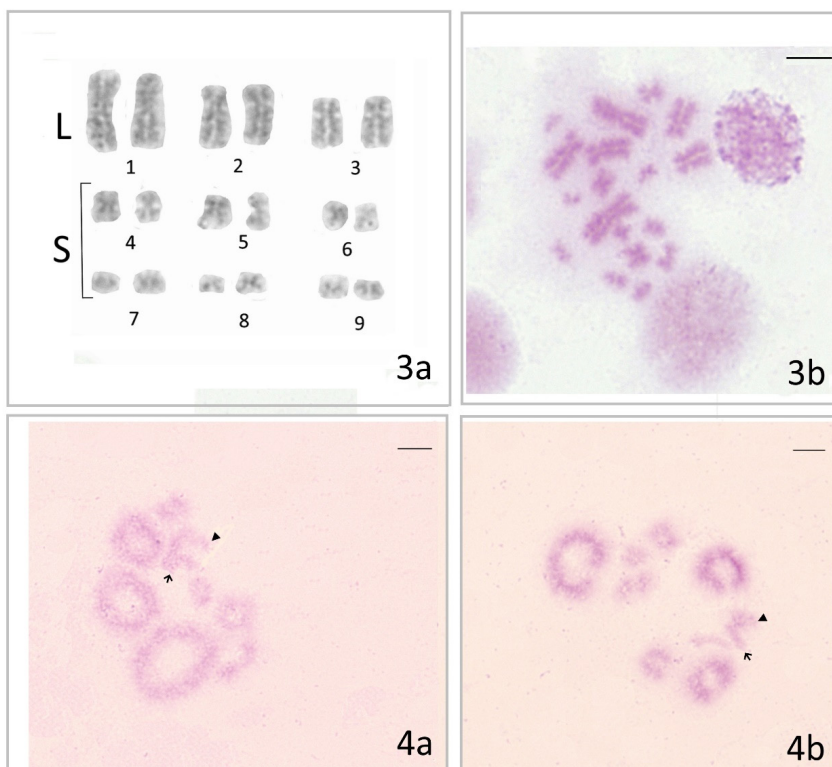
Figures 1–2. Mitosis (1) and meiosis (2) of *Arcynopteryx dichroa*. **1a** – karyogram of oögonial prometaphase; **1b** – oögonial metaphase of L1–L3 chromosome pairs; **1c** – oögonial prometaphase; L – large, S – small chromosomes. **2a** – metaphase I; **2b** – diakinesis. Arrows indicate metacentric the X-chromosome. Arrowhead – indicates submetacentricity of the Y-chromosome. Giemsa staining. Scale bar: 5 µm.

Megarcys ochracea

The set of female *M. ochracea* consists of 9 pairs of chromosomes pairs ($2n_{\text{♀}}=18$, Figs 3a, b). In the female karyotype we distinguished large (L) and small (S) chromosomes (Fig. 3a). The first pair of chromosomes (L1) is large and metacentric. The second and third pairs of chromosomes (L2, L3) are submetacentric. The remaining chromosomes of the set (S4–S9) are also biarmed, they are small and sub- and metacentric (Fig. 3a).

The set of male *M. ochracea* chromosomes has been reconstructed on the basis of meiotic chromosomes (Figs 4a, b). Chromosomes form 8 bivalents in the prophase of male meiosis. Seven bivalents are symmetrical. Three bivalents, made by pairing large chromosomes (L1–L3), form two distal chiasmata (Figs 4a, b). The re-

maining bivalents (S4–S9) form one or two chiasms (Fig. 4). One bivalent is asymmetric, formed by unpaired chromosomes of different lengths (Figs 4a, b). One of the chromosomes is biarmed. This chromosome is probably homologous to the metacentric chromosome of the fourth pair (S4) of the female karyotype (Fig. 3a). The second chromosome of this bivalent has an unclear morphology and is likely homologous to one of the small chromosome pairs. Chromosomes of this bivalent conjugate in the terminal regions during meiotic prophase (Fig. 4a). On the basis of chromosome analysis during meiotic prophase, it can be concluded that the male chromosome set consists of seven pairs of autosomes and two heterosomes. Therefore, we propose to design them as X1 and X2 sex chromosomes ($2n\sigma=16$). Thus, the determination of chromosomal sex in *M. ochracea* is X_1X_2 for male and $X_1X_1X_2X_2$ for female.

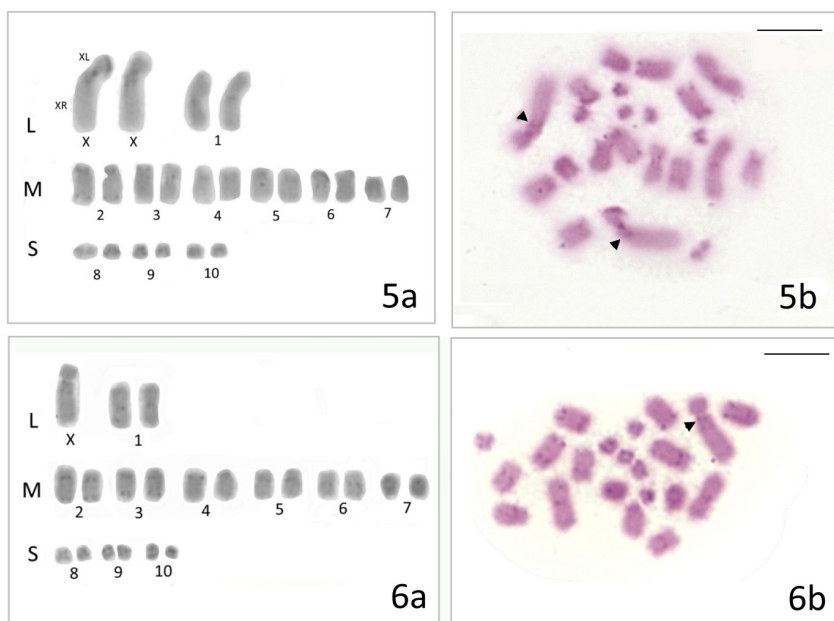


Figures 3–4. Mitosis (1) and meiosis (2) of *Megarcys ochracea*. **3a** – karyogram of the oogonial metaphase; **3b** – oogonial metaphase. L – large, S – small chromosomes. **4a, b** – metaphase I. Arrow – indicates metacentric chromosome. Arrowhead indicates a small chromosome of unclear morphology. Giemsa staining. Scale bar: 5 μ m.

Kamimuria exilis

The set of female *K. exilis* consists of 11 pairs of chromosomes ($2n = 22$, Figs 5a, b). The set of male *K. exilis* consists of 10 pairs and one unpaired chromosome ($2n\sigma=21$, Figs 6a, b). In the karyotype of males and females we distinguish three classes of chromosomes: large (L), medium (M), and small (S) (Figs 5a, 6a). The first pair of chromosomes (L1) is metacentric. The remaining chromosomes of the set are also biarmed, subcentric, and metacentric (M2–M7, S8–S10, Figs 5a, b, 6a, b). The male has one large submetacentric chromosome (L), which does not have a pair. In kind, the female has two similar large-size submetacentric (L) chromosomes. Thus, assumed that these are the male sex chromosome X0 (Figs 6a, b) and female sex chromosomes XX (Figs 5a, b).

The C band of the *K. exilis* chromosomes showed small C positive bands in the pericentromeric regions in all chromosomes of the set (Figs 5a, b, 6a, b). The middle submetacentric (M2, M3) chromosomes in the long arm have small telomeric C bands (Figs 5a, b, 6a, b). The submetacentric X-chromosomes of male and female *K. exilis* have small intercalary C-bands proximally in the long arm (XR, Figs 5b, 6b are indicated by arrows). One of the female X-chromosomes has telomeric C-bands in the short arm (Figs 5a, b).



Figures 5–6. Spermatogonial metaphase of male and oogonial metaphase of female *Kamimuria exilis*. **5a** – karyogram of the oogonial metaphase; **5b** – oogonial metaphase. **6a** – karyogram of the spermatogonial metaphase; **6b** – spermatogonial metaphase. L – large, M – medium, S – small chromosomes. Arrowhead – indicates intercalary C-block. C-banding. Scale bar: 5 μm .

Discussion

The karyotypes of Polyneoptera insects have long been the cytogeneticists' focus, thanks to relatively simple methods of studying both mitotic and meiotic chromosomes. Over the century-long history of such studies, the karyotypic features of more than 1,500 species from the Orthoptera, Blattoptera, Mantoptera and other orders have been determined. The results of these studies were reported in reviews of the comparative karyology of these groups. In addition to the morphology of karyotypes, new trends were described in the evolution of chromosome sets, caused mainly by centric translocations and pericentric chromosome inversions. These works also emphasize the evolutionary stability of karyotypes and the sex determination systems (mainly ♂X0/♀XX) in each order of the Polyneoptera group (White 1973; Hewitt 1979; John 1983; Husemann et al. 2022). Compared to orders mentioned above, Plecoptera remain the least studied group of insects in the Polyneoptera cohort in cytogenetic terms. At the time of writing, the karyotypes of only 17 species belonging to the Perlidae and Perlodidae families had been described. One likely reason for this is the difficulty in obtaining cells for cytogenetic analysis.

Analysis of available data shows that the number of chromosomes in the diploid sets of these insects is highly variable, ranging from $2n♂=10$ to $2n♂=33$. The determination of chromosomal sex is also exceptionally variable. Three of the stonefly species studied have a determination of sex ♂X0/♀XX, 10 species have a determination of sex ♂X₁X₂0/♀X₁X₁X₂X₂, two species have a determination of sex ♂X₁X₂X₃, and one species has a determination of sex ♂XY/♀XX. As for the chromosome morphology, the presence of both two-armed and one-armed (acrocentric) chromosomes in karyotypes, as well as small chromosomes of unclear morphology, was shown (Nakahara 1919; Junker 1923; Itoh 1933; Matthey 1946; Matthey and Aubert 1947, Bugrov et al. 2024).

The stoneflies that we studied had a predominance of biarmed chromosomes. This also applies to whose small chromosomes, the morphology we were able to determine using high-resolution microscopy. *A. dichroa* belongs to a group of species with a 26-chromosome karyotype. Morphologically, the autosomes of *A. dichroa* are metacentric and submetacentric. The sex chromosomes of females are metacentric, while in males one chromosome is metacentric and the other is submetacentric (Figs 1, 2). The different morphology of the male sex chromosomes could be interpreted as X₁X₂0. In this case, the female karyotype should consist of 28 chromosomes for the determination as X₁X₁X₂X₂. However, female karyotype analysis revealed 26 chromosomes, as in males. This feature once again confirms that the determination of chromosomal sex in this species is XY male XX female. The same variant of chromosome set and sex determination was previously identified in the taxonomically close species *Skwala compacta* (Bugrov et al. 2024). In this regard, it should be emphasized that to reliably determine the mechanism of sex determination in stoneflies, it is necessary to examine the karyotype of both males and females.

The male *M. ochracea* consists of 16 chromosomes ($2n\♂=16$), while the female – 18 chromosomes ($2n\text{♀}=18$). The morphology of autosomes in *M. ochracea* is meta- and submetacentric. The female sex chromosomes are metacentric, while the male ones are meta- and acrocentric (Figs 3, 4). The difference in the number of chromosomes in male and female *M. ochracea* indicates the determination of sex $\♂X_1X_2/\text{♀}X_1X_1X_2X_2$ in this species. The same variant of chromosomal sex determination has been described in most stoneflies of this family (Junker 1923; Matthey 1946; Matthey and Aubert 1947).

The karyotype of male *K. exilis* consists of 21 chromosomes ($2n\♂=21$), female – 22 ($2n\text{♀}=22$). The autosome morphology is meta- and submetacentric. The sex chromosomes of males and females are submetacentric (Figs 5, 6). The determination of chromosomal sex is X0 in males and XX in females. This type of sex determination was previously identified only in three species of stoneflies from the Perlidae family (Itoh 1933; Matthey and Aubert 1947).

Differential staining of chromosomes is widely used to identify additional cytogenetic markers in insect karyotypes. The location of heterochromatin C-bands in stonefly chromosomes is currently known only for *S. compacta* (Bugrov et al. 2024) and *K. exilis* (Figs 5, 6). In the pericentromeric region, C-blocks were detected on all chromosomes of *K. exilis* and *S. compacta*. Telomeric C-bands of heterochromatin were detected only in the *K. exilis* karyotype in two middle submetacentric autosomes. The sex chromosomes of male and female *K. exilis* have pericentromeric C-bands and an intercalary C-bands in the long arm (XR-arm). The short arms of the X and Y chromosomes in *S. compacta* are entirely heterochromatic. Fully heterochromatic arms and intercalary blocks on sex chromosomes have previously been reported in stick insects (Liehr et al. 2017) and acridids (Jetybayev et al. 2017).

In contrast to the well-studied mechanisms of autosome and sex chromosome evolution in grasshoppers (Hewitt 1979; Bugrov et al. 2001; Castillo et al. 2010; Palacios-Gimenez et al. 2013; Bugrov et al. 2016; Jetybayev et al. 2017; Bugrov et al. 2020), katydids (Warchałowska-Śliwa, 1998) and cockroaches (Cohen and Roth 1970; Nalepa et al. 2002), the evolution of autosome and sex chromosome morphology in stoneflies remains the most intriguing problem. The discovery of intercalary C heterochromatic blocks in the biarmed chromosomes of *K. exilis* suggests that tandem translocations may have occurred in the evolution of the karyotype of this species. Without additional data on the localization of C heterochromatin in karyotypes of other Perlidae species, we cannot yet discuss the evolution of the morphology of chromosome sets in this group of stoneflies.

Conclusion

New data on the karyotypes of three stonefly species highlight the unique position of this insect group within the Polyneoptera cohort, both in diversity of their chromosome sets and in sex determination mechanisms. We hope that resuming the

study of stonefly karyotypes at a new technical level, nearly 80 years after the last publication on this topic (Matthey and Aubert 1947), will help us to get closer to understanding the mechanisms of autosome and sex chromosome evolution in this group of insects.

Acknowledgments

The study was funded by the Federal Fundamental Scientific Research Program for 2026-2030 – Grant No. FWGS-2026-0007. Microscopy was performed at the Core Facility for Microscopy of Biological Objects, the Institute of Cytology and Genetics SB RAS (reg. No. 3054), Russia.

We thank Dr. Valentina A. Teslenko (Russian Academy of Sciences, RAS Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch) for the confirmation of our determination of *A. dichroa*. We also thank Dr. Igor Sukhikh, (University College Dublin, Ireland) for English correction of the manuscript.

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