

Stoneflies (Plecoptera) of the Russian Far East: diversity and zoogeography

Valentina A. Teslenko*

Institute of Biology and Soil Sciences, Russian Academy of Sciences, Far Eastern Branch, Vladivostok, Russia

(Received 28 October 2008; final version received 9 February 2009)

Based on an extensive field survey of stoneflies in mountain streams and rivers across the different climatic zones of the Russian Far East (from polar deserts in the north to the subtropics in the south), we describe the diversity of the stonefly fauna and analyse its zoogeography. The stonefly fauna of the Russian Far East is rich and unique; it includes 139 species from 45 genera and eight families, with endemism at the generic level. By stonefly distribution patterns, the 24 zoogeographical districts to which Russian Far Eastern streams are assigned can be consolidated into Beringian, East Siberian and East Asian Subregions. Similarities between the local stonefly faunas of the 24 zoogeographic districts were evaluated using Sorensen's coefficient of similarity, and the resulting similarity matrix then subjected to UPGMA cluster analysis. The non-relict stonefly fauna originated from three primary sources: a southern source on the Asian mainland by way of the Amur River Basin; a northeastern Asiamerican source from across the Beringian Bridge, and a western source in Siberia, including a few European taxa.

Keywords: Plecoptera; distribution; diversity; zoogeographical regions; Russian Far East

Introduction

Easternmost Russia, well known in Russia as the Russian Far East (RFE) and known elsewhere as eastern Siberia, represents the northeastern edge of the Asian continent, at the northwestern edge of the Pacific Ocean (Figure 1). The whole area covers more than three million square kilometers, ranging from 42°15'N to 71°30'N latitude and from 122°E to 169°W longitude. This includes the area east of the Kolyma River, the upper Indigirka River, the east side of the Yudoma River (the Lena River Basin), and the Amur River Basin from the confluence of the Shilka and Argun' Rivers. The land is bordered in the north by the Eastern-Siberian and Chukchi Seas (Arctic Ocean Basin) and in the east by the Bering Sea, the Sea of Okhotsk and the Sea of Japan (Pacific Ocean Basin).

Five broad vegetation zones succeed each other from north to south, ranging from polar deserts on Wrangel and Gerald Islands with plants scattered or absent, to

*Email: teslenko@ibss.dvo.ru

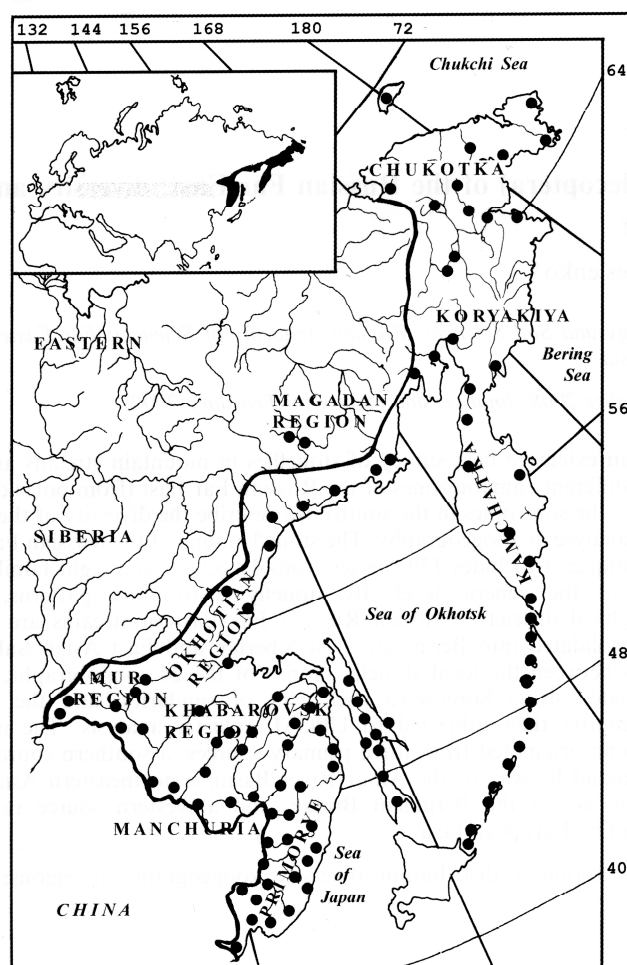


Figure 1. Northeast Asia with the area of the Russian Far East delimited by a pronounced line. Dots indicate sampling sites.

diverse mixed forests of broad-leaved trees and Korean pine in the south. Between these extremes are the tundra zone, the zone of Beringian woodlands with low dwarf-pine forest, and the boreal zone with dominant larch forests (Krestov 2003).

Systematic investigations of the Plecoptera fauna of the RFE were carried out under the leadership of Professor V. Ya. Levanidov in 1948. The results of this taxonomic and faunistic study formed the basis for keys (Zhiltzova 1979; Zhiltzova and Zapekina-Dulkeit 1986; Zhiltzova and Teslenko 1997; Teslenko and Zhiltzova, in press), annotated lists (Levanidova and Zhiltzova 1979; Zhiltzova and Levanidova 1984), and papers by the famous plecopterologist L.A. Zhiltzova, who described many Far Eastern stonefly species for the first time (see references in Zhiltzova 2003). The latest list included 128 species (Zhiltzova and Levanidova 1984).

Field research carried out in poorly known and insular regions of the RFE by L.A. Zhiltzova during two decades yielded a number of new taxa, as well as new data on distribution of both new and previously known species (Zhiltzova and Teslenko 1989; Teslenko and Zhiltzova 1992, 1997; Zhiltzova et al. 1993; Teslenko and Minakawa 1999; Teslenko 2006a). Important additions were made to the knowledge

of stoneflies inhabiting difficult-to-access coastal streams along the Sea of Okhotsk, Tukuringra, Sotkhan, Lesser Khingan, and Sikhote-Alin Ranges, Bureya, the middle and lower Amur River Basins, the Kuril Archipelago and Sakhalin Island (Teslenko 1992, 2002, 2003, 2004, 2005, 2006b, 2007b, 2008; Arefina et al. 2003). Up-to-date data on stonefly distribution patterns were used to propose a schema assigning RFE watercourses to different zoogeographic divisions (Teslenko 2007a). The object of the present study is to describe the species diversity and distribution of Plecoptera fauna in different parts of the RFE, and to analyse how the fauna formed.

Materials and methods

Stonefly distributions were analysed in the 174 River Basins of the RFE (Figure 1). Twenty-four zoogeographical districts with local faunas were established (Figure 2), taking into consideration the presence of endemic species, particular properties of faunal structure, various combinations of taxa, abrupt impoverishment of stonefly fauna at generic and specific levels, and paleogeographic events creating similarities in faunal composition and origin (Berg 1962; Kryzhanovsky 2002).

The distribution patterns of stoneflies (Zhiltzova and Levanidova 1984) were assigned to the following zoogeographical categories (Table 1):

- (1) HOL – Holarctic, circumpolar, five species.
- (2) AMP – Amphi-Pacific, two species distributed on both sides of the Pacific, from the Bering Land to the continental coast of the Pacific.
- (3) AMB – Amphi-Beringian, three species with Beringian disjunction, occurring in West and East Beringia and representing Beringian faunal fragments left behind after the final disintegration of the Bering Land Bridge.
- (4) TPA – Trans-Palaeartic, eight species with large geographical ranges across the Palaeartic Region (Europe, Caucasus, Siberia, RFE and Japan).
- (5) EPA – East Palaeartic, 45 species widely spread throughout the Asian Far East, including south-eastern Siberia, Mongolia, northern China, Korea and Japan. The western boundary of the East Palaeartic Region lies along the Yenisei River Basin, Altai, the Sayan Mountains, and Mongolia.
- (6) PAC – Pacific (a subgroup of the East Palaeartic category), five species widely distributed in the RFE, along the western coast of the Pacific Ocean.
- (7) WB – West Beringian, seven species inhabiting the north-east of the RFE and adjacent areas of eastern Siberia. In this category, four species belong to endemic or glacial relicts of the north-east of the RFE (ENERFE).
- (8) EA – East Asian (or Palaeartic), 69 species, some of which are endemic to the south of the RFE (ESRFE). This category includes three subgroups:
 EAM – East Asian Mainland species distributed in the Amur R. Basin, the Amurskaya Oblast', Khabarovskiy and Primorskiy krai, Korea, and China;
 EAM-I – East Asian Mainland-Island species distributed in the Amur River Basin, Primorskiy krai, Korea, China as well as Sakhalin Island, the Southern Kuril Islands and Japan;
 EAI – East Asian Island species inhabiting only Sakhalin Island, the Southern Kuril Islands and Japan.

Similarities between the local stonefly faunas in the 24 zoogeographical districts were evaluated using Sorensen's coefficient of similarity: $S = 2a/(b + c)$, where a is the number of species common to both districts, and b and c are the number of

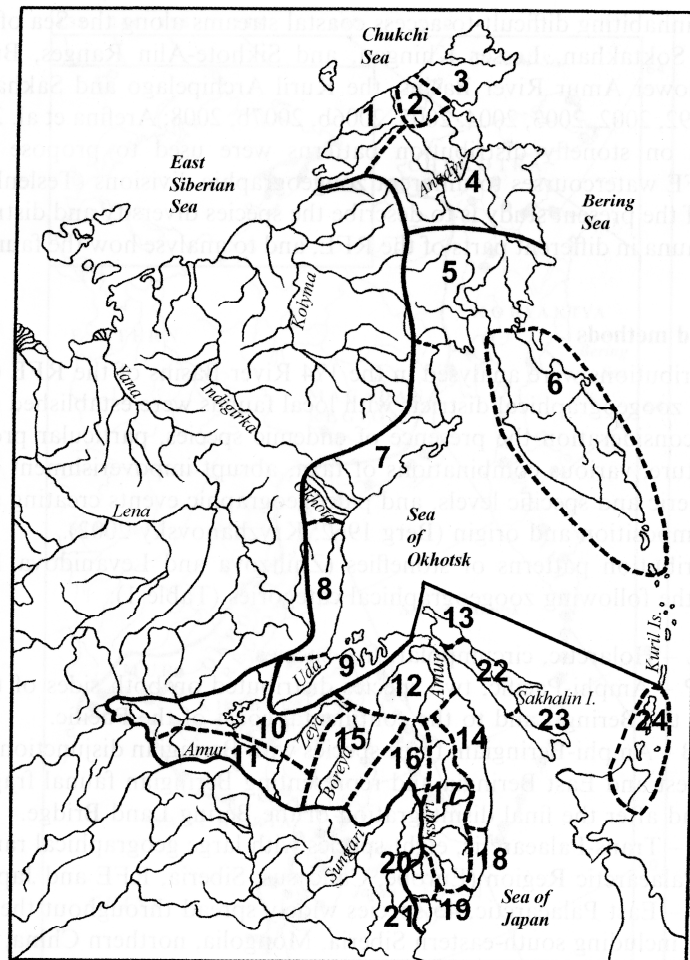


Figure 2. Zoogeographical division of the Russian Far East according to distribution patterns of stoneflies. Solid line indicates Subregion boundaries, dotted line indicates district boundaries. Beringian Transitional Subregion: 1 – Chaun; 2 – Amguema; 3 – Chukchi; 4 – Anadyr. East Siberian Subregion: 5 – Koryakiya; 6 – Kamchatka; 7 – Okhotsk; 8 – South Okhotsk; 9 – Shantar. East Asian Subregion: 10 – Upper Zeya; 11 – Amur-Zeya; 12 – Low Amur; 13 – North-Sakhalin; 14 – North-Primorye; 15 – Bureya; 16 – Middle Amur; 17 – Ussuri; 18 – Centre-Primorye; 19 – South-Primorye; 20 – Khanka; 21 – East-Manchurian; 22 – Tym'-Poronay; 23 – South-Sakhalin; 24 – South-Kuril.

species occurring in the local fauna of each district (Legendre and Legendre 1998). The similarity matrix resulting from pair-wise calculations was then subjected to UPGMA cluster analysis. The accuracy of each cluster was estimated by bootstrap analysis using the program Free Tree (Pavlicek et al. 1999). Bootstrap values were deduced from 1000 replications.

Results and discussion

The stonefly fauna of the Russian Far East (RFE) currently includes 139 species from 46 genera and eight families (Table 1). There are one endemic genus (*Capniella*)

Table 1. List of stoneflies (Plecoptera) of the Russian Far East and their distribution patterns: HOL – Holarctic, AMP – Amphi-Pacific, AMB – Amphi-Beringian, TPA – Trans-Palaeartic, EPA – East Palaeartic, PAC – East-Palaeartic Pacific, WB – West Beringian, EAM – East-Asian mainland; EAM-I – East-Asian, mainland-island; EAI – East-Asian, island; ESRFE – endemic of the South of the Russian Far East; ENERFE – endemic of the North-East of the Russian Far East.

Euholognatha

Fam. Taeniopterygidae

- | | |
|--|------------|
| 1. <i>Mesyatsia makartchenkoi</i> Tesl. et Zhiltz., 1992 | EAM, ESRFE |
| 2. <i>Taeniopteryx nebulosa</i> (L., 1758) | TPA |
| 3. <i>Taenionema japonicum</i> (Okamoto, 1922) | EPA |
| 4. <i>Strophopteryx rickeri</i> Zhiltz., 1976 | EAM, ESRFE |

Fam. Nemouridae

- | | |
|---|------------|
| 5. <i>Amphinemura borealis</i> (Morton, 1894) | TPA |
| 6. <i>A. coreana</i> Zwick, 1973 | EAM |
| 7. <i>A. decemseta</i> Okamoto, 1922 | EAI |
| 8. <i>A. dentifera</i> Zhiltzova, 1979 | EAI |
| 9. <i>A. flavostigma</i> Okamoto, 1922 | EAI |
| 10. <i>A. standfussi</i> Ris, 1902 | TPA |
| 11. <i>A. steinmanni</i> Zwick, 1973 | EAM |
| 12. <i>A. verrucosa</i> Zwick, 1973 | EAM |
| 13. <i>Protonemura curvata</i> Zhiltzova, 1981 | EAI |
| 14. <i>P. ermolenkoi</i> Zhiltzova, 1982 | EAM-I |
| 15. <i>Nemoura arctica</i> Esben-Petersen, 1910 | HOL |
| 16. <i>N. despinosa</i> Zhiltzova, 1977 | EAM |
| 17. <i>N. geei</i> Wu, 1929 | EAM-I |
| 18. <i>N. fulva</i> (Šamal, 1921) | EAM-I |
| 19. <i>N. jezoensis</i> (Okamoto, 1922) | EAM-I |
| 20. <i>N. kuwayamai</i> Kawai, 1966 | EAI |
| 21. <i>N. longicercia</i> (Okamoto, 1922) | EAI |
| 22. <i>N. manchuriana</i> Ueno, 1941 | EAM |
| 23. <i>N. matsumura</i> Claassen, 1911 | EAI |
| 24. <i>N. nigrodentata</i> Zhiltz., 1980 | EAM |
| 25. <i>N. parafulva</i> Zhiltzova, 1981 | EAI |
| 26. <i>N. papilla</i> Okamoto, 1922 | EAM-I |
| 27. <i>N. sachalinensis</i> Matsumura, 1911 | EAI |
| 28. <i>N. transversospinosa</i> Zhiltzova, 1979 | EAI |
| 29. <i>N. uenoi</i> Kawai, 1954 | EAI |
| 30. <i>N. ussuriensis</i> Zhiltzova, 1979 | EAM, ESRFE |
| 31. <i>Podmosta weberi</i> Ricker, 1952 | AMB |
| 32. <i>Zapada quadribanchiata</i> (Zhiltzova, Ricker) | PAC |

Fam. Capniidae

- | | |
|--|------------|
| 33. <i>Capnia ahngerii</i> Koponen, 1949 | EPA |
| 34. <i>C. aligera</i> Zap.-Dulk., 1975 | EPA |
| 35. <i>C. bargusina</i> Zapekina-Dulkeit, 1975 | EPA |
| 36. <i>C. iturupiensis</i> Zhiltzova, 1980 | EAI, ESRFE |
| 37. <i>C. kolymensis</i> Zhiltzova, 1979 | WB, ENERFE |
| 38. <i>C. kurnakovi</i> Zhiltzova, 1978 | WB, ENERFE |
| 39. <i>C. levanidovae</i> Kawai, 1969 | WB, ENERFE |
| 40. <i>C. lepnevae</i> Zapekina-Dulkeit, 1960 | EPA |
| 41. <i>C. nearctica</i> Banks, 1918 | AMB |
| 42. <i>C. nigra</i> (Pictet, 1833) | TPA |
| 43. <i>C. potikhae</i> Zhiltzova, 1996 | EAM, ESRFE |
| 44. <i>C. pygmaea</i> Zetterstedt, 1840 | TPA |
| 45. <i>C. rara</i> Zapekina-Dulkeit, 1970 | EPA |

(continued)

Table 1. (Continued).

46. <i>C. atra</i> Morton, 1896	TPA
47. <i>C. sidimiensis</i> Zhiltzova, 1979	EAM, ESRFE
48. <i>S. tshukotica</i> Zhiltzova et Levanidova, 1978	WB, ENERFE
49. <i>Capniella nodosa</i> Klapálek, 1920	EPA
50. <i>C. ghilarovi</i> Zhiltzova, 1988	EAM, ESRFE
51. <i>Eucapnopsis brevicauda</i> (Claassen, 1924)	AMP
52. <i>Isocapnia arcuata</i> Zhiltzova, 1975	EPA
53. <i>I. guentheri</i> (Joost, 1970)	EPA
54. <i>I. kudia</i> Ricker, 1959	EPA
55. <i>I. orientalis</i> Zhiltzova, 1975	PAC
56. <i>Mesocapnia variabilis</i> Klap., 1920	HOL
57. <i>M. gorodkovi</i> Zhiltzova et Baumann, 1976	WB,
58. <i>Paracapnia khorensis</i> Zhiltzova, 1972	EAM
59. <i>P. sikhotesis</i> Zhiltzova, 1978	EAM, ESRFE
60. <i>P. recta</i> Zhiltzova, 1984	EAM
61. <i>P. leisteri</i> Zhiltzova et Potikha, 2005	EAM, ESRFE
62. <i>Takagripopteryx nigra</i> Okamoto, 1922	EAI
63. <i>T. imamurai</i> Kohno, 1954	EAI
64. <i>T. zhuikovae</i> Zhiltzova, 1980	EAI, ESRFE
Fam. Leuctridae	
65. <i>Leuctra fusca</i> (L., 1758)	TPA
66. <i>Paraleuctra cercia</i> (Okamoto, 1922)	EPA
67. <i>P. gracilis</i> Kawai, 1967	EAI
68. <i>P. zapekinae</i> Zhiltzova, 1974	EPA
69. <i>Perlomyia kiritshenkoi</i> Zhiltzova, 1974	EAM, ESRFE
70. <i>P. levanidovae</i> (Zhiltzova, 1975)	EAM, ESRFE
71. <i>P. mahunkai</i> Zwick, 1973	EAM
72. <i>P. martynovi</i> Zhiltzova, 1975	EAM, ESRFE
73. <i>P. secunda</i> (Zapekina-Dulkeit, 1955)	EPA
74. <i>P. smithae</i> (Nelson et Hanson, 1973)	EAM
75. <i>P. insularis</i> Zhiltzova, 1975	EAM, ESRFE
Systellognatha	
Fam. Pteronarcyidae	
76. <i>Pteronarcys reticulata</i> Burmeister, 1839	EPA
77. <i>P. sachalina</i> Klapálek, 1908	EAM-I
Fam. Perlodidae	
78. <i>Arcynopteryx amurensis</i> Zhiltzova et Levanidova, 1978	EPA
79. <i>A. compacta</i> McLachlan, 1892	HOL
80. <i>A. polaris</i> Klapálek, 1912	EPA
81. <i>Diura bicaudata</i> (Linnaeus, 1758)	HOL
82. <i>D. knowltoni</i> (Frison, 1937)	AMP
83. <i>D. majuscula</i> (Klapálek, 1912)	EPA
84. <i>D. nanseni</i> (Kempny, 1900)	HOL
85. <i>Levanidovia mirabilis</i> Teslenko et Zhiltzova, 1989	EAM, ESRFE
86. <i>Megarcys magnilobus</i> Zhiltzova, 1988	EPA
87. <i>M. ochracea</i> Klapálek, 1912	EPA
88. <i>M. pseudochracea</i> Zhiltzova, 1977	EAM
89. <i>Pictetiella asiatica</i> Zwick et Levanidova, 1971	EPA
90. <i>P. zwicki</i> Zhiltzova, 1976	WB
91. <i>Skwala pusilla</i> (Klapálek, 1912)	EPA
92. <i>Stavsolus manchuricus</i> Teslenko, 1999	EAM
93. <i>S. ainu</i> Teslenko, 1999	EAI
94. <i>Isoperla altaica</i> Šámal, 1939	EPA
95. <i>I. asiatica</i> Raušer, 1968	EPA

(continued)

Table 1. (Continued).

96. <i>I. eximia</i> Zapekina-Dulkeit, 1975	EPA
97. <i>I. flavescens</i> Zhiltzova et Potikha, 1986	EAM
98. <i>I. kozlovi</i> Zhiltzova, 1972	EPA
99. <i>I. lunigera</i> (Klapálek, 1923)	EPA
100. <i>I. maculata</i> Zhiltzova, 1977	EAM
101. <i>I. obscura</i> (Zetterstedt, 1840)	TPA
102. <i>I. ornata</i> Zhiltz., 1988	EAM
103. <i>I. pseudornata</i> Zhiltzova, 1988	EAM
104. <i>Kaszabia nigricauda</i> (Navás, 1968)	EPA
105. <i>Kogotus tiunovi</i> Teslenko, Zhiltzova et Zwick, 1993	EAM, ESRFE
Fam. Perlidae	
106. <i>Acroneuria unimaculata</i> Zhiltzova, 1979	EAM, ESRFE
107. <i>Agnentina brevipennis</i> (Navás, 1912)	EPA
108. <i>A. extrema</i> (Navás, 1912)	EPA
109. <i>Claassenia brachyptera</i> Brinck, 1949	EPA
110. <i>Gibosia okamotoi</i> Zhiltzova, 1979	EAI, ESRFE
111. <i>Kamimuria exilis</i> (McLachlan, 1872)	EPA
112. <i>K. tibialis</i> Pictet, 1841	EAI
113. <i>K. lyubaretzi</i> Teslenko, 2006	EAM, ESRFE
114. <i>Neoperla ussurica</i> Sivec et Zhiltzova, 1996	EAM
115. <i>Oyamia nigribasis</i> Banks, 1920	EAM
116. <i>Paragnetina flavotincta</i> (McLachlan, 1872)	EPA
Fam. Chloroperlidae	
117. <i>Utaperla orientalis</i> Nelson et Hanson, 1969	PAC
118. <i>Paraperla lepnevae</i> (Zhiltzova, 1978)	PAC
119. <i>Alaskaperla longidentata</i> (Raušer, 1968)	EPA
120. <i>Alloperla deminuta</i> Zapekina-Dulkeit, 1970	EPA
121. <i>A. mediata</i> (Navás, 1925)	EPA
122. <i>A. joosti</i> Zwick, 1972	EPA
123. <i>A. kurentzovi</i> Zhiltzova et Zapekina-Dulkeit, 1977	EAM, ESRFE
124. <i>A. kurilensis</i> Zhiltzova, 1978	EAM-I
125. <i>A. rostellata</i> (Klapálek, 1923)	EPA
126. <i>Haploperla lepnevae</i> Zhiltzova et Zwick, 1971	EPA
127. <i>H. maritima</i> Zhiltzova et Levanidova, 1978	EAM
128. <i>H. ussurica</i> Navás, 1934	EAM
129. <i>Plumiperla diversa</i> (Frison, 1935)	AMP
130. <i>Suwallia asiatica</i> Zhiltzova et Levanidova, 1978	EAM
131. <i>S. decolorata</i> Zhiltzova et Levanidova, 1978	PAC
132. <i>S. kerzhneri</i> Zhiltzova et Zwick, 1971	EPA
133. <i>S. sachalina</i> Zhiltzova, 1978	EAI, ESRFE
134. <i>S. talalajensis</i> Zhiltzova, 1976	WB,
135. <i>S. teleckojensis</i> (Šámal, 1939)	EPA
136. <i>Sweltsa colorata</i> (Zhiltzova, 1978)	EAM
137. <i>S. illiesi</i> Zhiltzova, 1977	EAM
138. <i>S. insularis</i> Zhiltzova, 1978	EAI, ESRFE
139. <i>S. lepnevae</i> Zhiltzova, 1977	EAM, ESRFE

and 27 endemic species (*Strophopteryx rickeri*, *Mesyatsia makartchenkoi*, *Nemoura ussuriensis*, *Capnia kolymensis*, *C. kurnakovi*, *C. levanidovae*, *C. potikhae*, *C. sidimiensis*, *C. tshucotica*, *C. iturupiensis*, *Capniella ghilarovi*, *Paracapnia sikhotensis*, *P. leisteri*, *Takagriopteryx zhuikovae*, *Perlomyia kiritshenkoi*, *P. levanidovae*, *P. martynovi*, *P. insularis*, *Levanidovia mirabilis*, *Kogotus tiunovi*, *Acroneuria unimaculata*, *Kamimuria lyubaretzi*, *Gibosia okamotoi*, *Alloperla kurentzovi*, *Suwallia*

sachalina, *S. insularis*, *Sweltsa lepnevae*). Possibly, some of them may in future be found in contiguous areas of Korea, China and Japan like several other species in the Southern part of RFE (*Amphinemura coreana*, *A. decemseta*, *A. dentifera*, *A. flavostigma*, *A. steinmanni*, *Protonemura curvata*, *Nemoura despinosa*, *N. kuwayamai*, *N. longicercia*, *N. manchuriana*, *N. matsumura*, *N. parafulva*, *N. sachalinensis*, *N. transversospinosa*, *N. uenoi*, *Paracapnia recta*, *Takagriopteryx nigra*, *T. imamurai*, *Paraleuctra gracilis*, *Stavsolus ainu*, *Kamimuria tibialis*, *Sweltsa colorata*, and *Suwallia asiatica*).

The stonefly fauna of the RFE comprises more than 41% of the total number of species known in Russia (Teslenko and Zhiltzova, in press), despite the fact that the area of the RFE is only 18% of the country's total. RFE stonefly diversity is two times greater than that of Korea (Kim et al. 1998; Ham and Bae 2000; Jin and Bae 2005) and Mongolia (Teslenko and Bazova, in press), and is similar to the levels found for Alaska and Western Canada (Stewart and Oswood 2006). At the same time, the diversity of the Plecoptera fauna in the RFE is three times less than that of Japan (Shimizu 2000), and considerably less than in China, although Chinese stoneflies have yet been poorly and patchily studied (Sivec and Yang 2001; Fochetti and Tierno de Figueroa 2008).

A UPGMA cluster analysis of the species similarities among 24 local faunas shows four major assemblages (Figure 3).

The first assemblage of clusters includes the stonefly fauna in the streams and rivers of the polar deserts on Wrangel Island as well as those in the tundra zone of Chukchi Peninsula and the Anadyr River Basin (Chaun, Amguema, Chukchi, and Anadyr zoogeographical districts), belonging to the Beringian Transitional Palaearctic Subregion (Figures 2 and 3). The stonefly fauna of this Subregion is relatively impoverished, but is similar to faunas in the same type of Bering and Arctic

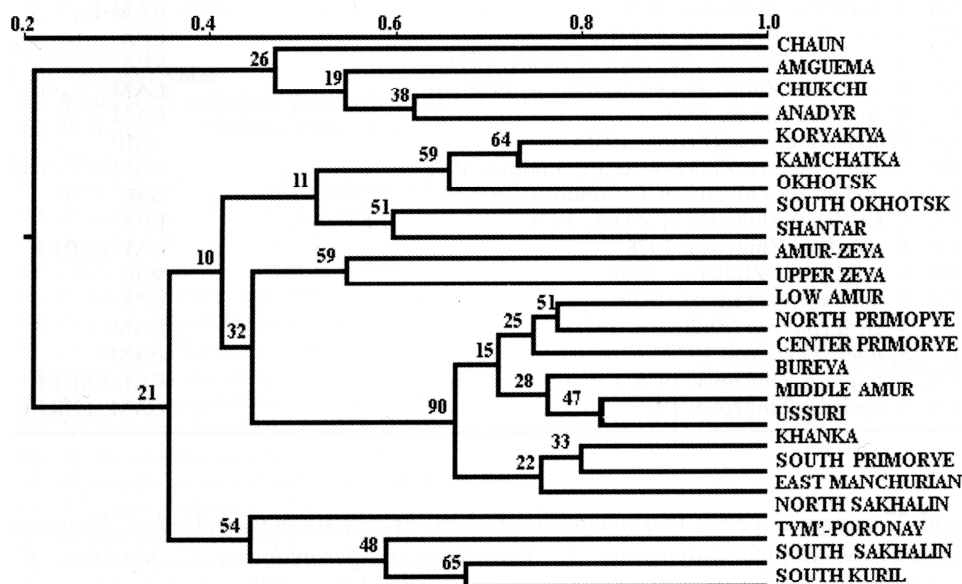


Figure 3. Similarity of 139 species of stoneflies among 24 zoogeographical districts of the Russian Far East. Bootstrap probabilities (expressed in percentage) are indicated at node of each cluster.

tundra streams in the north-western Nearctic Zoogeographic Region. In the Beringian Transitional Palaearctic Subregion, 16 stonefly species from nine genera and four families were registered. All of them are cool-adapted species with high ecological plasticity, and many are able to inhabit both lotic and lentic ecosystems under Arctic conditions. They have Circumpolar, Amphi-Beringian, West Beringian, East Palaearctic, and Trans-Palaearctic patterns of distribution (Figure 4). Five species (*Arcynopteryx compacta*, *Capnia nearctica*, *Mesocapnia variabilis*, *Nemoura arctica*, *Podmosta weberi*) are also present in the stonefly fauna of Alaska and the Arctic coast of north-western North America, including the Colville, Noatak and Kuskokwim Rivers, and the rivers of Steward Peninsula.

The second assemblage of clusters combines the stonefly fauna of the East Siberian Palaearctic Subregion with the Koryakiya, Kamchatka, Okhotsk, South Okhotsk, and Shantar zoogeographical districts (Figures 2 and 3). Fifty-six species from 28 genera and eight families were noted here. This relatively high level of species diversity is accompanied by an increase in the variety of distribution patterns: in addition to Circumpolar, Amphi-Beringian, West Beringian, East Palaearctic, and Trans-Palaearctic species, stoneflies with Amphi-Pacific (*E. brevicauda*, *P. diversa*) and East Asian distribution patterns (*I. maculata*, *M. rseudochracea*, *P. martynovi*, *P. ermolenkoi*) were also registered (Figure 4). Species with East Palaearctic distribution predominated.

The third assemblage of clusters reflects the similarity in stonefly fauna between the East Asian or Palaearcheartic (Semenov-Tyan-Shansky 1935) Subregion with the zoogeographical districts covering the Amur River Basin (Amur-Zeya, Upper Zeya, Low Amur, Bureya, Middle Amur, and Ussuri zoogeographical districts), Manchurian Mountains (Khanka and East-Manchurian zoogeographical districts) and the Sikhote-Alin Mountains (North, Centre and South Primorye) (Figures 2 and 3). The stonefly fauna in the East Asian Subregion within the limits of the RFE are very diverse and includes 131 species from 45 genera and eight families. The

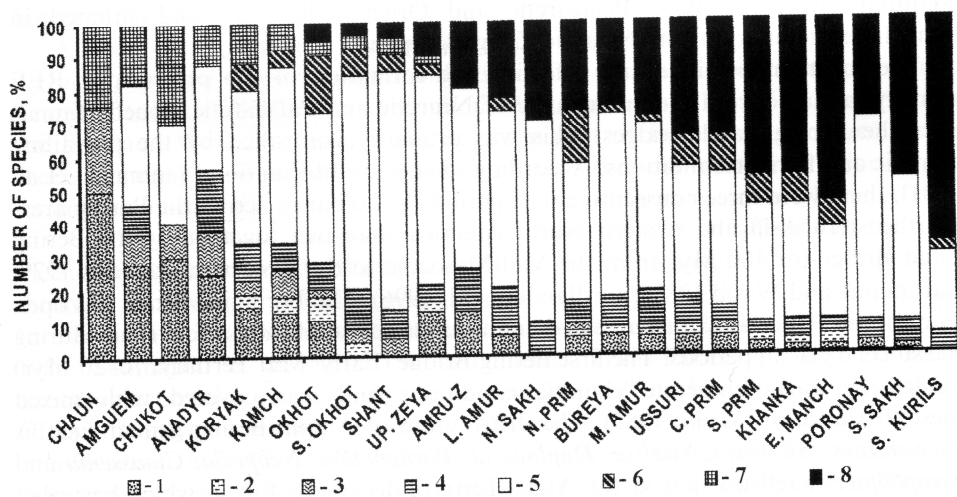


Figure 4. Correlations of the distribution patterns in the local stonefly faunas among 24 zoogeographical districts. Pattern of distribution: 1 – Holarctic; 2 – Amphi-Pacific; 3 – Amphi-Beringian; 4 – Trans-Palaearctic; 5 – East Palaearctic; 6 – Pacific; 7 – West Beringian; 8 – East Asian.

transitional disposition of fauna is more pronounced in the Amur-Zeya district (in the upstream area of the Zeya River Basin) bordering the East Siberian Subregion. Here the stonefly species with East Palaearctic distribution predominate, and species with East Asian distribution patterns are limited to the downstream area of the Zeya River Basin and the portion of the Amur River adjacent to the Zeya's mouth. On the contrary, in the local faunas of the Khanka, East-Manchurian and South-Primorye zoogeographical districts, East Asian (or Palaearctic) species predominate over the East Palaearctic (Figure 4).

The fourth assemblage of clusters includes the stonefly fauna of Sakhalin Island and the Southern Kuril Islands (North-Sakhalin, Tym'-Poronay, South-Sakhalin, and South-Kuril zoogeographical districts) due to the large number of common East Asian insular autochthonous (Manchurian-Japanese) species, 40% of which are shared with the Japanese fauna, especially in the South-Sakhalin and South-Kuril zoogeographical districts (Figures 2–4). Distinct differences between local insular stonefly faunas of the Southern and Northern Kurils were shown in previous research (Teslenko 2003). The stoneflies of the Southern Kurils extend only as far north as Urup Island, and De Vries Strait effectively limits the northward dispersal of stoneflies. In the Northern Kurils, the stonefly fauna is considered to be an impoverished remnant of Kamchatkan fauna, and consists exclusively of boreal East Palaearctic, Amphi-Beringian and West Beringian species which were restricted in southward distribution at Onkotan Island. In the central ocean Kuril Islands, no stoneflies were found. This gap between the southern and northern parts of the Kuril Archipelago is considered as a transition zone between the East Asian (Palaearctic) and East Siberian subregions. The presence of this important boundary between two large biogeographical regions in the central Kurils was clearly demonstrated by UPGMA cluster analyses of the entire Kuril biota (Pietsch et al. 2003).

The distribution patterns displayed by RFE stoneflies correlate well with the geological history of the northeastern edge of the Asian continent, which is in continuity with the West Palaearctic and Oriental Regions, and situated in immediate proximity of the Nearctic Zoogeographical Region.

The most important events affecting the formation of the present-day RFE stonefly fauna concern the interchange of Nearctic and Palaearctic stonefly faunas over the Bering Land Bridges. This was primarily controlled by the prevailing climatic and floristic conditions. According to current information (Sanmartin et al. 2001), there were three consecutive time periods of exchange across the Bering area. Northeastern Asia and western North America were tied together by the Bering Land Bridge for 100 Myr from the Mid-Mesozoic to the Pliocene (Mathews 1979; Lafontaine and Wood 1988; Nordlander et al. 1996). The Beringian Strait was open in the Late Pliocene, with terrestrial connections re-established a few times during Pleistocene glacial periods. The first Bering Bridge (Early–Mid Tertiary, 70–20 Myr) existed in warm-temperate climatic conditions and was covered with mixed mesophytic forest (Wolfe 1985). The distribution of Amphi-Bering genera such as *Pteronarcys*, *Alloperla*, *Sweltsa*, *Haploperla*, *Paragnetina*, *Neoperla*, *Claassenia* and *Strophopteryx* reflects that of the Arcto-Tertiary deciduous forest, which has relict elements persisting in Asia and North America that suggest a Miocene dispersal for these genera (Stewart and Stark 2002). The second bridge (Late Tertiary, 20–3 Myr) was covered by taiga forest (Lafontaine and Wood 1988). Trans-Beringian exchange II was more extensive (Mid- to Late Pliocene), following a global decline in climatic

conditions to cooler and drier conditions. This exchange involved 16 genera, including cool-adapted, boreal, and partly warm-temperate stoneflies. Among them were *Utaerla*, *Paraleuctra*, *Isocapnia* (Stewart and Stark 2002), and probably *Zapada*. The third bridge (Quaternary, 3–0 Myr) formed during the Pleistocene, with alternation of glacial and interglacial epochs. Throughout this period, trans-Beringian biotic exchange was probably dominated by arctic, tundra-adapted Plecoptera, permitting the dispersal of the Holarctic and Beringian species *Diura bicaudata*, *Arcynopteryx compacta*, *Nemoura arctica*, *Podmosta weberi*, *Plumiperla diversa*, *Mesocapnia variabilis*, *Capnia nearctica*, *Eucapnopsis brevicauda*, which still inhabit both sides of the Bering Strait.

Distinct faunistic differences between north-eastern and southern parts of the RFE may be explained by clear-cut differences in glacier formation during the Pleistocene. Glacier formation was governed by the configuration of land and seas – relationships that differ between Europe, Asia, America and the northeastern and southern parts of the RFE. Over much of the northeast, glaciers were confined to higher mountains (Lafontaine and Wood 1988), leaving part of southern RFE unglaciated throughout the Pleistocene. This ice-sheet-free area included the Middle Amur River Basin, southern Primorye, the South Kuril Islands and the south of Sakhalin Island, and explains the widely distributed thermophilic and ward-adapted oriental Tertiary fauna that survived in these regions. In the small salmon rivers of southern Primorye, the South Kurils, and the south of Sakhalin Island, stoneflies with East Asian distribution patterns provide a basis for the species diversity.

The principal directions of oriental fauna dispersal were determined by the river systems of China and Korea in the Amur River Basin during the Tertiary. In the remainder of the Southern RFE, the Pleistocene cooling influence is apparent in the presence of insular permafrost; stoneflies with East Palaearctic distribution predominate here (including *Capniella*, considered an endemic genus of the East Palaearctic Subregion), the East Asian, Beringian, Holarctic, and Trans-Palaearctic, but taxa are not numerous.

A small group of seven species (*Taeniopteryx nebulosa*, *Leuctra fusca*, *Capnia nigra*, *C. pygmaea*, *Amphinemura standfussi*, *A. borealis*, and *Isoperla obscura*) exhibit Trans-Palaearctic distribution throughout Asia (including the RFE), Europe, and the East and West Palaearctic. The northern part of Europe was covered by ice sheets during glacial periods of Pleistocene, and the east–west orientation of the mountains effectively prevented organisms from migrating to southern refugia. The Tertiary fauna of the Western Palaearctic was seriously affected in the Late Pleistocene by massive glacial extinction. Faunistic interchanges were only possible through Asia Minor and the mountain systems, as the Central European plains formed a barrier, and only a few taxa could move across the Polar Circle (Zwick 1980; Sanmartin et al. 2001). Some common Trans-Palaearctic and Holarctic circumpolar species survived due to dispersal along the border of the Northern Glacier (*Capnia pygmaea*, *C. nigra*, *Mesocapnia variabilis*, *Nemoura arctica*, *Amphinemura borealis*, *Diura bicaudata*, *D. nanseni*, *Arcynopteryx compacta*), or along the border of Southern (Alpine) Glacier (*Isoperla obscura*) in the Western Palaearctic (Illies 1953).

Protonemura is a Palaearctic genus and has its greatest diversity in the Western Palaearctic. This indicates that west-to-east dispersal may have occurred after the final closure of the Turgai Strait, Bering Strait II, most probably in the Quaternary.

The most significant time period for the formation of the present RFE stonefly fauna was probably the Early–Late Tertiary, when the northern part of the Oriental Region was included in the Laurasian landmass and covered by the same boreotropical flora as Japan and China: during at least that period, connections existed between the Eastern Palaearctic and Oriental Regions (Wolfe 1977; Tiffney 1985). Stonefly dispersal or vicariance in the RFE includes Oriental genera such as *Acroneuria*, *Neoperla*, *Agnetina*, *Paragnetina*, *Claassenia*, which have at present Holarctic or Amphi-Beringian distributions (the first Bering Bridge, Early–Mid Tertiary, 70–20 Myr), and such genera as *Stavsolus*, *Levanidovia*, *Oyamia*, *Kamimuria*, *Gibosia*, *Mesyatsia*, and *Takagriopteryx*, which have an East-Asian distribution pattern, limited mainly towards the south part of the RFE including the south of Sakhalin Island and the South Kuril Islands.

Isoperla, *Capnia*, *Amphinemura*, and *Nemoura* are widespread Holarctic genera with high species diversity in the Nearctic, Palaearctic and Oriental Regions. This suggests that the Palaearctic members of each genus may be of Asiamerican origin. From the mid-Jurassic to the Late Tertiary, the Palaearctic was divided into a western (Euramerican) and eastern (Asiamerican) half by an epicontinental seaway, the Turgai Strait, located east of the Ural Mountains. The Turgai Strait dried during the Oligocene, permitting extensive biotic exchange between both sides of the Palaearctic during the Late Tertiary and the Quaternary.

Thus, the stonefly fauna of the RFE originated from three primary sources: a southern source from the Asian mainland, by the way of Amur River Basin; a north-eastern, Asiamerican source by way of the Beringian Bridge; and a western source in Siberia, which included a few European taxa.

Acknowledgements

The author thanks the DFG (Deutsche Forschungsgemeinschaft) for the opportunity to participate in the XVI International Symposium on Plecoptera. The work described here was supported by the Far Eastern Branch Russian Academy of Sciences, Grant Nos. 06-III-A-140 (V. Bogatov, principal investigator) and No 06-I-BBS-101 (T. Tiunova, principal investigator).

References

- Arefina, T.I., Ivanov, P.Yu., Kocharina, S.L., Lafer, G.Sh., Makarchenko, M.A., Teslenko, V.A., Tiunova, T.M., and Khamenkova, E.V. (2003), 'Aquatic insect's fauna from Taui River Basin (Magadan Territory)', *Vladimir Ya. Levanidov's Biennial Memorial Meetings*, 2, 45–60 (Vladivostok: Dalnauka; in Russian).
- Berg, L.S. (1962), 'Zoogeographical division of Palaearctic and Amur Region according to freshwater fish distribution', *Isbrannye Trudy*, 5, 320–360 (Moscow: AS USSR; in Russian).
- Fochetti, R., and Tierno de Figueroa, J. (2008), 'Global diversity of stoneflies (Plecoptera; Insecta) in freshwater', *Hydrobiologia*, 595, 365–377.
- Ham, S.A., and Bae, Y.J. (2000), 'The stonefly genus *Megaleuctra* (Plecoptera: Leuctridae) new to East Palaearctic Region, with description of *Megaleuctra saebat* new species', *Entomological News*, 113, 336–361.
- Illies, J. (1953), 'Beitrag zur Verbreitungsgeschichte der europäischen Plekopteren', *Archiv für Hydrobiologie*, 48, 35–74.
- Jin, Y.H., and Bae, Y.J. (2005), 'The wingless stonefly family Scopuridae (Plecoptera) in Korea', *Aquatic Insects*, 27, 21–34.
- Kim, J.S., Bae, Y.J., and Zhiltzova, L.A. (1998), 'Bibliographic review, systematic status, and biogeographic notes on Korean and Far East Russian stoneflies (Insecta: Plecoptera) with their new Korean records', *Korean Journal of Biological Sciences*, 2, 419–425.

- Krestov, P.V. (2003), 'Forest vegetation of Easternmost Russia (Russian Far East)', in *Forest vegetation of Northeast Asia*, Dordrecht: Kluwer, pp. 93–180.
- Kryzhanovsky, O.L. (2002), *Composition and distribution of entomofaunas of the globe*, Moscow: Association of the Scientific Publication KMK (in Russian).
- Lafontaine, J.D., and Wood, D.M. (1988), 'A zoogeographic analysis of the Noctuidae (Lepidoptera) of Beringia, and some inferences about past Beringian habitat', *Memoirs of the Entomological Society of Canada*, 144, 109–123.
- Legendre, L., and Legendre, P. (1998), *Numerical Ecology. Developments in Environmental modeling* (2nd ed.), Amsterdam: Elsevier.
- Levanidova, I.M., and Zhiltzova, L.A. (1979), 'An annotated list of the Stoneflies (Plecoptera) of the Soviet Far East', *Internationale Revue der gesamten Hydrobiologie*, 64, 551–576.
- Mathews, J.V. (1979), 'Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. Canada and its insect fauna', *Memoirs of the Entomological Society of Canada*, 108, 31–86.
- Nordlander, G., Liu, Z., and Ronquist, F. (1996), 'Phylogeny and historical biogeography of the cynipoid wasp family Ibalidae (Hymenoptera)', *Systematic Entomology*, 21, 151–166.
- Pavlicek, A., Hrda, S., and Flegr, J. (1999), 'Free Tree – ware program for construction of phylogenetic trees on the basis of distance data and bootstrap/jackknife analysis of the tree robustness. Application in the RAPD analysis of the genus *Frenkelia*', *Folia Biologica (Praha)*, 45, 97–99.
- Pietsch, W., Bogatov, V., Amaoka, K., Zhuravlev, Yu., Barkalov, V., Gage, S., Takachashi, H., Lelej, A., Storozhenko, S., Minakawa, N., Bennett, D., Anderson, T., Ohara, M., Prozorova, L., Kuwahara, Y., Kholin, S., Yabe, M., Stevenson, D., and MacDonald, E. (2003), 'Biodiversity and Biogeography of the islands of the Kuril Archipelago', *Journal of Biogeography*, 30, 1297–1310.
- Sanmartin, I., Engloff, H., and Ronquist, F. (2001), 'Patterns of animal dispersal, vicariance and diversification in the Holarctic', *Biological Journal of the Linnean Society*, 73, 345–390.
- Semenov-Tyan-Shansky, A. (1935), 'Limits and zoogeographical subdivision of Palaearctic Region for terrestrial animals on the ground of the coleopterous insects distribution', *Trudy Zoologicheskogo Instituta*, 2, 397–410.
- Sivec, I., and Yang, P. (2001), 'Stoneflies of Taiwan within the oriental stonefly fauna diversity', in *Trends in Research in Ephemeroptera and Plecoptera*, ed. E. Dominguez, New York: Kluwer Academic/Plenum Publishers, pp. 401–404.
- Shimizu, T. (2000), 'Biodiversity of Asian streams with particular reference to stonefly studies in Japan', in *The 21st Century and Aquatic Entomology in East Asia. Proceedings of the 1st Symposium of Aquatic Entomologists in East Asia*, ed. J. Bae, Seoul: Korean Society of Aquatic Entomology, pp. 11–19.
- Stewart, K.W., and Oswood, M.W. (2006), *The stoneflies (Plecoptera) of Alaska and western Canada*, Columbus, OH: Caddis Press.
- Stewart, K.W., and Stark, B.P. (2002), *Nymphs of North American Stonefly Genera (Plecoptera)* (2nd ed.), Columbus, OH: Caddis Press.
- Teslenko, V.A. (1992), 'Order Plecoptera', in *Insects of the Khingan Reserve*, Vladivostok: Dalnauka, 1, pp. 52–55 (in Russian).
- Teslenko, V.A. (2002), 'Aquatic Insects', in *Flora and Fauna of Kuril Islands (Materials of International Kuril Islands Project)*, Vladivostok: Dalnauka, pp. 109–117 (in Russian).
- Teslenko, V.A. (2003), 'Zoogeography of the stoneflies (Plecoptera) of the Kuril Archipelago', in *Research Update on Ephemeroptera and Plecoptera*, ed. E. Giano, Perugia: University of Perugia, pp. 421–428.
- Teslenko, V.A. (2004), 'New records of stoneflies from Sakhalin and Moneron Islands', in *Flora and Fauna of Sakhalin Island (Materials of International Sakhalin Island Project)*, Vladivostok: Dalnauka, 1, pp. 149–153 (in Russian).
- Teslenko, V.A. (2005), '*Levanidovia mirabilis*, *Kogotus tiunovi*, *Mesyatsia makartchenko*', in *Red Data Book Primorsky Krai Animals. Rare and endangered species of animals*, Vladivostok: AVK "Apel'sin", pp. 118–121 (in Russian).
- Teslenko, V.A. (2006a), 'A new species of *Kamimuria* (Plecoptera, Perlidae) from the Russian Far East', *Zootaxa*, 1307, 55–62.

- Teslenko, V.A. (2006b), 'Review of stonefly fauna (Plecoptera) of the East-Manchurian Mountains', in *Flora and Fauna of "Kedrovaya Pad" Reserve*, Vladivostok: Dalnauka, pp. 63–90 (in Russian).
- Teslenko, V.A. (2007a), 'A survey of stonefly fauna (Plecoptera) in respect of stream zonation in the Far East of Russia', *Euroasian Entomological Journal*, 6, 157–180 (in Russian).
- Teslenko, V.A. (2007b), 'The Stoneflies (Plecoptera)', in *Hydro-ecological monitoring in Bureyskaya Hydro-Electric Power Station zone influences*, Khabarovsk: Institute of Water and Ecological Problems FEB RAS, pp. 145–160 (in Russian).
- Teslenko, V.A. (2008), 'Fauna and distribution of stoneflies (Insecta, Plecoptera) in Zeya River Basin', in *Freshwater ecosystems of Amur River Basin*, Vladivostok: Dalnauka, pp. 151–171 (in Russian).
- Teslenko, V.A., and Zhiltzova, L.A. (1992), 'A new species of the genus *Mesyatsia* Ricker from the South Primorye (the Soviet Far East)', *Aquatic Insects*, 14(1), 57–63.
- Teslenko, V.A., and Bazova, N.V. (in press), 'To the stonefly fauna (Plecoptera) of the transboundary Selenga River Basin', *Entomological Review*.
- Teslenko, V.A., and Minakawa, N. (1999), 'Two New species of the Genus *Stavsolus* Ricker from the Asian Far East (Plecoptera: Perlodidae)', *Aquatic Insects*, 21, 19–32.
- Teslenko, V.A., and Zhiltzova, L.A. (1997), 'New and little known species of stoneflies (Plecoptera: Nemouridae and Perlodidae) from Russian Far East', *Aquatic Insects*, 19, 23–35.
- Teslenko, V.A., and Zhiltzova, L.A. (in press), *Key to the stoneflies (Insecta, Plecoptera) of Russia and Adjacent Countries. Imago and Nymphs*. Vladivostok: Dalnauka (in Russian).
- Tiffney, B.H. (1985), 'Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America', *Journal of the Arnold Arboretum*, 66, 73–94.
- Wolfe, J.A. (1977), 'Paleogene floras from Gulf of Alaska region', *US Geological Survey Professional Papers*, 997, 1–108.
- Wolfe, J.A. (1985), 'Distribution and major vegetational types during the Tertiary', in *The Carbon Cycle and atmospheric CO₂: Natural variations archean to present*, eds. E.T. Sundquist and W.S. Broecker, Washington, DC: American Geophysical Union, pp. 357–375.
- Zhiltzova, L.A. (1979), 'New stonefly species from family Nemouridae (Plecoptera) from the Asian part of the USSR. New species of the insects in Asian part of the USSR', *Trudy Zoologicheskogo Instituta AS USSR*, 88, 10–14 (in Russian).
- Zhiltzova, L.A. (2003), *The Stoneflies (Plecoptera). Group Euholognatha*, Sankt-Petersburg: Nauka (in Russian).
- Zhiltzova, L.A., and Levanidova, I.M. (1984), 'An annotated list of the stoneflies (Plecoptera) of the Soviet Far East', in *Biology of fresh waters of the Far East*, Vladivostok: FESC AS USSR, pp. 18–45 (in Russian).
- Zhiltzova, L.A., and Teslenko, V.A. (1989), 'Description of *Levanodovia mirabilis* gen. et sp. nov., and key for nymphs of genera Perlodinae (Plecoptera, Perlodidae) from the Russian Far East', in *Systematics and ecology of river organisms*, Vladivostok: FEB AS USSR, pp. 5–14 (in Russian).
- Zhiltzova, L.A., and Teslenko, V.A. (1997), 'Order (Plecoptera)', in *Key to fresh-water invertebrates of Russia and adjacent lands*, 3, Sankt-Petersburg: Zoological Institute RAS, pp. 247–264, 364–399 (in Russian).
- Zhiltzova, L.A., Teslenko, V.A., and Zwick, P. (1993), 'A new species of genus *Kogotus* Ricker from Southern Primorye (the Russian Far East) (Plecoptera: Perlodidae)', *Aquatic Insects*, 15, 177–184.
- Zhiltzova, L.A., and Zapekina-Dulkeit, Yu. I. (1986), 'Order Plecoptera – stoneflies', in *Key for insects of Far East of the USSR*, Leningrad: Nauka, pp. 172–234 (in Russian).
- Zwick, P. (1980), 'Plecoptera (Steinfliegen)', in *Handbuch der Zoologie*, Berlin: Walter de Gruyter.