

Zoogeography of the stoneflies (Plecoptera) of the Kuril Archipelago

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Abstract

A revised checklist of the 41 species of stoneflies recorded from the Kuril Islands is provided along with data on their distribution. Distinct differences in species diversity between the southern and northern Kurils are shown on the basis of cluster and bootstrap analyses. The stonefly fauna of the northern Kurils, considered an impoverished remnant of Kamchatka, contains three zoogeographic elements: East Palaearctic, Beringian, and Kamchatka endemics. In contrast, the stonefly fauna of the southern Kurils is highly specific and more heterogeneous. In addition to wide spread East Palaearctic, Beringian, and Trans-Palaearctic elements, there are East Asian island and East Asian mainland-island species, with restricted Sakhalin-southern Kuril-Japanese distributions. East Asian insular autochthon species, which form the bulk of the southern Kuril stonefly fauna, are found to be endemics of the southern part of the Far East. The importance of the Kuril Islands as a dispersal route and center of origin for stonefly species is discussed.

Keywords: stoneflies, fauna, distribution, zoogeography, Kuril Islands.

Introduction

The islands of the Kuril Archipelago form the eastern boundary of the Sea of Okhotsk and a bridge between Hokkaido, the northernmost island of Japan, and the Russian Kamchatka Peninsula. A chain of more than 56 islands, the system covers an area of 15,600 square km, and provides 2,409 km of coastline. Stretching 1,200 km between Hokkaido and Kamchatka (from 43° to 51° N latitude), the Kurils divide the Sea of Okhotsk from the Pacific Ocean. All the Kurils are volcanic in origin, ranging in age from Upper Cretaceous to Late Pleistocene; each island has its unique geological and biological history. Substantial opportunities for *in situ* diversification are provided by great distances between island and mainland source biotas and significant barriers to plant and animal dispersal (e.g., deep channels between islands, associated with strong ocean currents) (Pietsch *et al.*, 2001).

The purpose of this study was to summarize our knowledge of the diversity of the stonefly fauna on islands of the Kuril Archipelago and to analyze origins and relationships of insular faunas and those of adjacent territories on the basis of the stonefly distributions, and to estimate the level of endemism. Plecoptera are very suitable for zoogeographical studies because of their evolutionary conservatism and a weak ability for dispersal. The consequence for most species is stenothermy and rheophily, and their distribution is restricted by cold, well-oxygenated running waters. Low vagility of adult stoneflies assumes the necessity of former land bridges or vicariant events to explain present-day disjunctive ranges (Stewart and Stark, 1988).

Material and Methods

Material was collected during six consecutive summers (1994-1999) on the 30 major islands of the Kuril Archipelago as a part a joint U. S., Russian, and Japanese biotic survey and inventory, which has come to be known as International Kuril Islands Project (IKIP). We have taken into consideration all other published records from the investigated area (Zhiltzova, 1981; Zhiltzova and Levanidova, 1984; Teslenko *et al.*, 1997; Teslenko and Minakawa, 2001). Stoneflies were collected with kick nets, sweep and beating sheets. The IKIP material alone contains more than 4,500 nymphs and adults, all deposited at the Institute of Biology and Soil Sciences, Russian Academy of Sciences, Far

Eastern Branch, Vladivostok, and at the School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington.

The faunal compositions of Kuril Island stoneflies were compared between islands, and with adjacent territories, based on the following data: Hokkaido (HK), 61 species (Shimizu, 1994, 1998, homepage; personal observations); Sakhalin (SK), 47 species (Zhiltzova, 1999; personal observation); Kamchatka (KM), 21 species (Zhiltzova and Levanidova, 1984); and Primorye (PR), 94 species (Zhiltzova and Levanidova, 1984, personal observations). Faunal similarity between any two islands (or adjacent territories) was evaluated by Jaccard's coefficient (Udvardy, 1969): $S = c/(a + b - c)$, where c is the number of species common to both islands and a or b is the number of species occurring on each island. The similarity matrix resulting from pair-wise calculations was then subjected to UPGMA cluster analysis (by NTSYS program, version 1.70). The significance of grouping of islands was statistically tested by the bootstrap technique of Felsenstein (1985).

Results and Discussion

Forty-one species of stoneflies, representing 22 genera and seven families, are listed in Table 1, along with their geographical distribution among the southern and northern Kuril Islands.

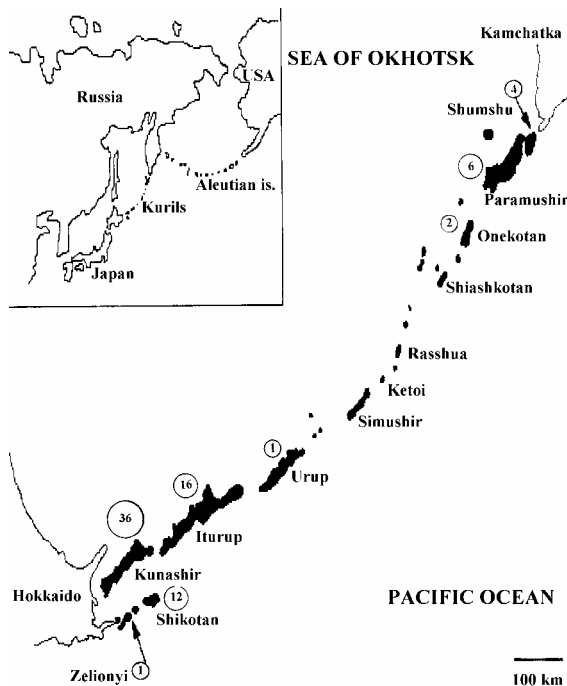


Fig. 1 - The stonefly species distribution on the islands of the Kuril Archipelago.

A pattern of uneven distributions throughout the Archipelago (Fig. 1) is a typical feature of the insular fauna: 37 stonefly species were recorded from the southern Kuril Islands (Zelionyi, Shikotan, Kunashir, Iturup, and Urup), and eight species from the northern islands (Onkotan, Paramushir, and Shumshu). Species diversity falls abruptly as one moves centrally from both the northern and southern ends of the Archipelago, the number of species dropping to zero on some of the central islands. It appears that differences in island size, and therefore available habitat for nymphs, are a primary determinants of diversity, coupled with the secondary effects of former connections between landmasses and distances from adjacent source biotas.

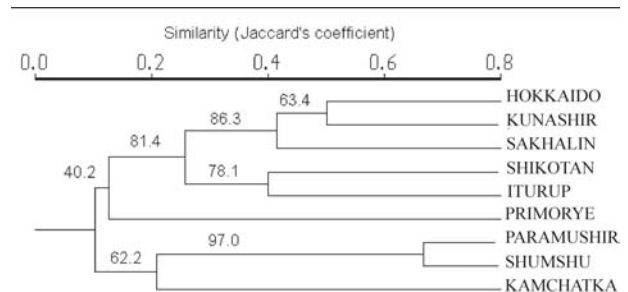


Fig. 2 - Dendrogram of faunal similarity of the stoneflies among the Kuril Islands and adjacent territories (UPGMA cluster analysis with bootstrap indexes (%), evaluated by Jaccard's coefficient).

The results of cluster and bootstrap analyses for estimates of faunal similarity among local insular localities and four adjacent territories are shown in Fig. 2. The stonefly fauna of the southern Kurils reveals a comparatively low level of similarity with that of the northern islands. Stretching 1,200 km between Hokkaido and Kamchatka, the islands of the Kuril Archipelago lie in the Amur-Manchurian and East Siberian zoogeographic Subregions, which differ from each other by climatic conditions. Zoogeographically, the Kuril stonefly fauna consists of two complexes of species of Oriental and Angarian origin. Oriental species are characterized as having been derived from the warm-requiring and temporarily warm-requiring Oriental Tertiary fauna, while Angarian (or boreal) taxa are thought to have originated in the ancient Angarian mountains, dispersing from them in response to climatic cooling. The stonefly fauna has a unique compound structure, with Oriental species prevalent in the southern part of the Archipelago, while the stonefly fauna of the northern part consists exclusively of boreal species.

Table 1 - The stonefly fauna list of the Kuril Islands. ZE - Zelionyi, SH - Shikotan, KU - Kunashir, IT - Iturup, UR - Urup, ON - Onkotan, PA - Paramushir, SU - Shumshu. AMB –Amphi-Beringian, AMP - Amphi-Pacific, TPA - Trans-Palaeartic, EPA - East Palaeartic, WB - West Beringian, PAC - Pacific, EAI – East Asian, island, EAL – East Asian, land-island; CEK- Conventional Endemic of Kamchatka.

SPECIES/ISLAND	SOUTHERN KURIL ISLANDS					NORTHERN KURIL ISLANDS			DISTRIBUTIONAL RANGE
	ZE	SH	KU	IT	UR	ON	PA	SU	
<i>Arcynopteryx polaris</i> KLAPALEK, 1912							•	•	EPA
<i>Megarctys ochracea</i> KLAPALEK, 1912		•	•	•					EPA
<i>Skwala pusilla</i> KLAPALEK, 1912		•	•	•		•			EPA
<i>Stavsolus ainu</i> TESLENKO, 1999		•	•						EAI
<i>Isoperla altaica</i> SAMAL, 1939			•	•					EPA
<i>Kamimuria tibialis</i> PICTET, 1841			•						EAI
<i>Gibosia okamotoi</i> ZHILTZOVA, 1979			•						EAI
<i>Alloperla mediata</i> (NAVAS, 1925)	•	•	•	•			•	•	EPA
<i>A. kurilensis</i> ZHILTZOVA, 1978			•						EAI
<i>Sweltsa sapporoensis</i> (OKAMOTO, 1912)		•	•						EAI
<i>Suwallia kerzhneri</i> ZHILTZOVA et ZWICK, 1971		•	•						EPA
<i>S. teleckojensis</i> (SAMAL, 1939)		•	•	•	•		•	•	EPA
<i>Taenionema japonicum</i> (OKAMOTO, 1922)			•				•	•	EPA
<i>Amphinemura standfussi</i> RIS, 1902			•						TPA
<i>A. dentifera</i> ZHILTZOVA, 1979			•	•					EAI
<i>A. decemseta</i> OKAMOTO 1922		•	•						EAI
<i>A. flavostigma</i> OKAMOTO, 1922		•	•	•					EAI
<i>Protonemura curvata</i> ZHILTZOVA, 1981			•						EAI
<i>P. ermolenkoi</i> ZHILTZOVA, 1981				•					EAL
<i>Nemoura geei</i> WU, 1929			•	•					EAL
<i>N. papilla</i> OKAMOTO, 1922			•						EAL
<i>N. fulva</i> (SAMAL, 1921)		•	•	•					EAL
<i>N. jezoensis</i> (OKAMOTO, 1922)			•						EAL
<i>N. longicercia</i> (OKAMOTO, 1922)		•	•	•					EAI
<i>N. parafulva</i> ZHILTZOVA, 1981			•	•					EAI
<i>N. sachalinensis</i> MATSUMURA, 1911		•	•	•					EAI
<i>N. transversospinosa</i> ZHILTZOVA, 1979			•						EAI
<i>N. uenoi</i> KAWAI, 1956			•						EAI
<i>N. kuwayamai</i> KAWAI, 1966			•						EAI
<i>Podmosta weberi</i> RICKER, 1952							•		AMB
<i>Capnia nigra</i> (PICTET, 1833)			•	•					TPA
<i>C. iturupiensis</i> ZHILTZOVA, 1980			•	•					EAI
<i>C. levanidovae</i> KAWAI, 1969						•			CEK
<i>Eucapnopsis brevicauda</i> OKAMOTO, 1922			•						AMP
<i>Takagripopteryx nigra</i> OKAMOTO, 1922			•						EAI
<i>T. zhuikovae</i> ZHILTZOVA 1980				•					EAI
<i>Mesocapnia gorodkovi</i> ZHILTZOVA et BAUMANN 1986							•		WB
<i>Paraleuctra cercia</i> (OKAMOTO, 1922)			•						PAC
<i>P. gracilis</i> KAWAI, 1967			•						EAI
<i>Perlomyia secunda</i> (ZAPEKINA-DULKEIT, 1955)			•						EPA
<i>Rhopalopsole insularis</i> ZHILTZOVA, 1975			•						EAI
Total : 41	1	12	35	16	1	2	6	4	

The results of cluster and bootstrap analyses suggest that stoneflies have colonized the islands from the mainland; however, it is unlikely that the island chain served as a bridge for biotic exchange between Hokkaido and Kamchatka. My data indicates that the northern Kuril stonefly fauna is poor, of relatively homogenous and low specificity, consisting of three zoogeographic elements (Fig. 3). The first element includes five

East Palaeartic species (*Arcynopteryx polaris*, *Skwala pusilla*, *Alloperla mediata*, *Suwallia teleckojensis*, *Taenionema japonicum*) that are widely spread throughout the Asian Far East. The origin and ranges of these boreal species are within the limits of former Angarian landmasses that are situated in present-day northeastern Asia and western North America, and along the Bering Strait during the Tertiary.

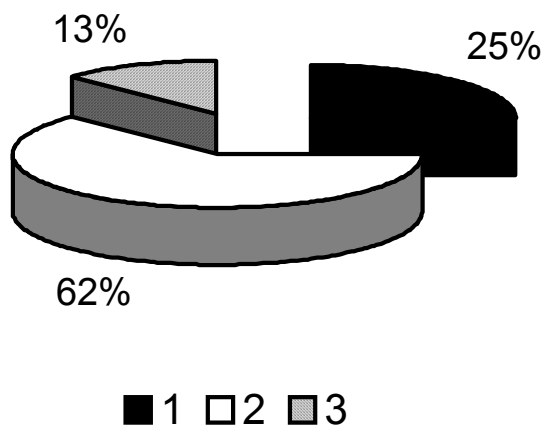


Fig. 3 - Correlation of the zoogeographical elements in the stonefly fauna of the northern Kuril Islands: 1 - Beringian, 2 - East Palaearctic, 3 - the Kamchatka endemics.

The Beringian element yielded two species, with Beringian disjunction, *Podmosta weberi* and *Mesocapnia gorodkovi*. Besides on the Kamchatka Peninsula, they are distributed primarily on the landmasses of the outlying Pacific Seas. These species represent Beringian faunal fragments left behind after final disintegration of the Bering land bridge. *P. weberi*, with its amphi-Pacific, amphi-Beringian distribution (Stewart and Ricker, 1997), is believed to have originated in the mid- to late Pliocene in Beringia (Levanidova, 1982). The majority of the species of *Podmosta* are more diverse in the Nearctic region (e.g., four North American and one Asian species), which suggests that stonefly dispersal was primarily from east to west across the Bering land bridge, when it was available for terrestrial exchange, three to six times during the Pleistocene (Stewart and Stark, 1988; Stewart and Ricker, 1997). According to Ricker (1964), these historical events permitted the probable arrival of some Holarctic species into Asia, *P. weberi* most probably being among them. Ancestors of the west-Beringian species *M. gorodkovi* appeared in the Angarian mountains in the Tertiary (Levanidova and Zhiltzova, 1976). During glacial Pleistocene periods, the pre-existing Pliocene fauna was displaced to the plains and low mountain streams, including Beringia. Pleistocene glacial events that occurred on both sides of the Pacific basin divided an ancestral form of *Mesocapnia* into eastern and western populations: the west-Beringian *M. gorodkovi* is most closely related to the Nearctic species *Mesocapnia bergi* (RICKER, 1965) in western North America. They both may be considered products of Beringian disjunction and subsequent speciation.

Capnia levanidovae belongs to the third element of autochthonous origin as a Kamchatka endemic. The stonefly fauna of the northern Kuril Islands should be considered as an impoverished remnant of the fauna of Kamchatka, characterized as having been mainly derived from the ancient Angarian and Beringian faunas (Levanidova, 1982). For the northern Kuril Islands, the main source of colonization is the Kamchatka Peninsula, which was an island itself until the end of the Middle Pleistocene (Meleceszev, 1974). However, the modern Kamchatka stonefly fauna retains insular features. A predominance of weak endemism and allochthonous species should be noted. Stonefly fauna impoverishment may be explained by arctic climatic conditions and the low-lying landscape of the Kamchatka isthmus, which acted as a barrier to continental rheophytic faunal colonization (Levanidova, 1982). On the other hand, ocean level fluctuations, volcanic activity, and great glacial screens reduced the potential faunal dispersal in Kamchatka during the Pleistocene. Opportunities for dispersal have appeared within the last glacial termination and glacial degradation during the Holocene climatic optimum (Chereshnev, 1998). In the Holocene, after the final continental separation and Beringian discontinuance, the expansion of some Angarian and Beringian species to northeastern Asia and Kamchatka occurred. In central Kamchatka during the glacial period, a river refugium that existed in depression, free from ice (Chereshnev, 1998) was of great importance to the genesis of the Kamchatka and northern Kuril Island faunas. Paramushir and Shumshu were joined with Kamchatka about 18,000-20,000 years ago (Melekeszev, 1974). This land mass stretched up to what is presently the Forth Kuril Strait, suggesting a Pleistocene dispersal of stoneflies from Kamchatka to the Northern Kuril Islands. The last glacial period came to an end about 10,000 years ago when the temperature increased. The melting of the ice sheets and the ocean transgressions in the Holocene separated Shumshu Island from the southern extremity of Kamchatka. The isolation of Paramushir occurred later, about 9,000 years ago (Velizhanin, 1976).

Contrary to the stonefly fauna of the northern Kurils, that of the southern Kurils is very specific and more heterogeneous, reflecting the existence of four distinct zoogeographic elements (Fig. 4):

1. Trans-Palaearctic species, of unknown origin, represented by *Capnia nigra* and *Amphinemura standfussi* having enormous geographic ranges in Europe, the Caucasus,

Siberia, Mongolia, Russian Far East, and Japan, with broad ecological scope, and resulting in highly diverse habitat utilization.

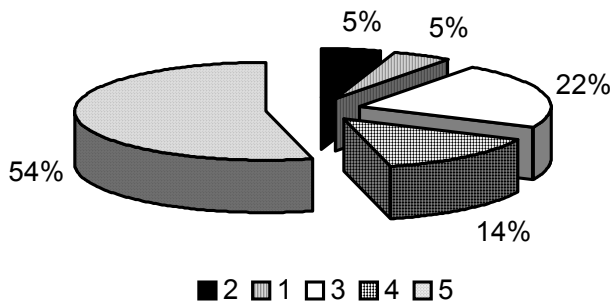


Fig. 4 - Correlation of the zoogeographical elements in the stonefly fauna of the southern Kuril Islands: 2- Beringian, 1- Trans Palaeartic, 3 – East Palaeartic, 4- East Asian mainland-island, 5- East Asian, island.

2. The Beringian element, represented by *Eucapnopsis brevicauda* and *Paraleuctra cerci*, with distribution patterns that support the existence of ancient transcontinental Beringian connections. The amphi-Pacific distribution of the Holarctic *E. brevicauda* (Stewart and Ricker, 1997) moves aside from the Bering Strait to the continental coast of the Sea of Okhotsk. According to Levanidova (1982), the latter species had a Beringian origin in the Tertiary. The distribution range of *Paraleuctra cercia* stretches along the western Pacific coast from Kamchatka to Honshu. *Paraleuctra sara* (CLAASSEN, 1937), from the eastern Pacific, forms with *P. cercia* a pair of vicariant species. Extensive mid to late Pliocene, trans-Bering exchange involved *Paraleuctra* among other genera. The dispersal of *Paraleuctra* was primarily from east to west across the Bering Bridge (Stewart and Stark, 1988).

3. East-Palaeartic species having an Angarian origin (*Megarcys ochracea*, *S. pusilla*, *Isoptera altaica*, *A. mediata*, *Suwallia kerzhneri*, *S. teleckojensis*, *T. japonicum*, *Perlomya secunda*) have extended geographic ranges in the Far East. Aside from those of the continental Far East, most of the species inhabit Sakhalin and Japan. Thus, there are grounds to assume that their dispersal on the islands of the southern part of Kuril Archipelago took place from the north through Sakhalin toward the end of the Pleistocene or beginning of the Holocene, when the connection had been restored between the southern part of the Kurils and the continental part of the Far East, along the terrestrial Sakhalin bridge, when Sakhalin, Kunashir, Habomai, and Hokkaido were a peninsula of the Amur region (Velizanin, 1970).

The Quaternary decline in temperature was accompanied by the warm-requiring and temporarily warm-requiring faunal displacement and penetration of boreal species from the north to the south. Separation of Sakhalin from the continental coast took place about 6,000 or 7,000 years ago (Velizanin, 1976), and from Hokkaido, about 10,000 years ago (Karrey, 1968).

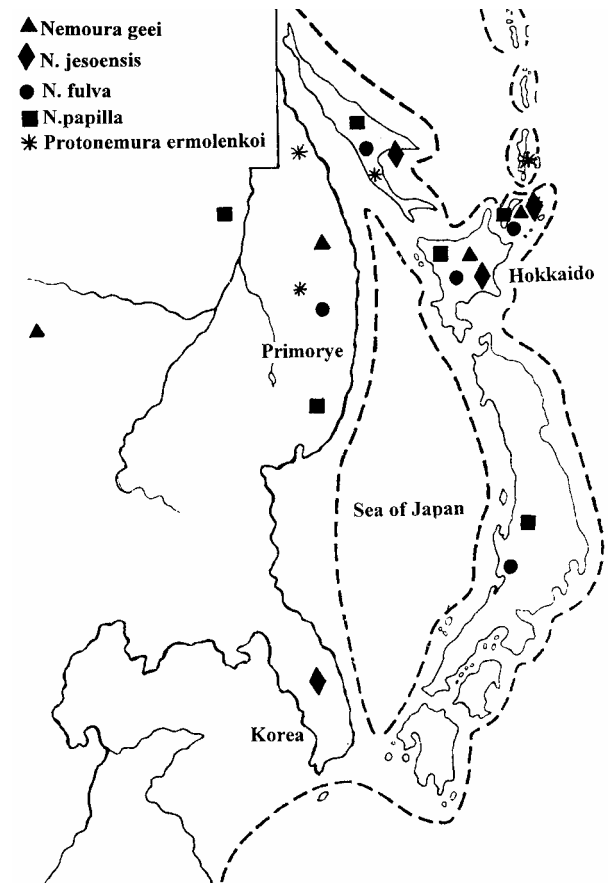


Fig. 5 - The East Asian mainland-island species distribution in the southern Kurils. Dotted line means outlines of the mainland in the Middle Pleistocene (on Kryvolutskaja, 1973).

4. An East Asian element is the basis for the southern Kuril stonefly fauna. Among of East Asian species, two species-groups are evident, a mainland group and a mainland-island group. The mainland-island species (*Nemoura fulva*, *N. geei*, *N. papilla*, *N. jesoensis*, and *Protonemura ermolenkoi*), besides the southern Kurils, occur in the Northeast of China, Korea, south of Primorye, Sakhalin, and Japan (Fig. 5). Archaic distributional ranges of these five species reflect a primary genetic consolidation of the continental and insular faunas. It is known that the area mentioned above was a borderland region of the Asian continent during the Pliocene. At the same time, the Sea of Japan was a freshwater reservoir

into which the Amur River, Pale Huang Ho River, the Korea Peninsula Rivers, and Rivers of the southern and western coasts of the Japanese Islands flowed (Lindberg, 1972). During the Pleistocene, the shape of the Sea of Japan was altered significantly: the freshwater reservoir turned into a semi-isolated and partly freshwater basin and eventually a sea basin, when the Tsushima, Tsugaru, and La Perouse straits appeared. These events suggest that the Pliocene stonefly migrations from the continent to former Japanese Islands, Kuril Islands, and Sakhalin were probable before the Tsushima, Tsugaru, and La Perouse straits opened, not later than the end of the Pleistocene (Oshima, 1991).

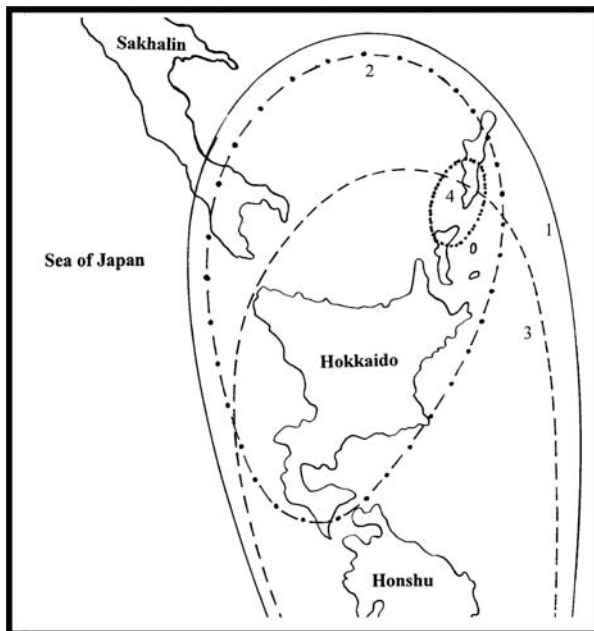


Fig. 6 - Ranges of East Asian-island species in the southern Kurils: 1 – Sakhalin-Kuril-Japanese; 2 – Sakhalin-Kuril-Hokkaido; 3 – Kuril-Japanese; 4 – southern Kuril endemics.

Distribution of the remaining 20 East Asian island species that occur in the southern Kuril Islands (Kunashir, Iturup, and Shikotan) is restricted to southern Sakhalin, Hokkaido, or Honshu. They have an autochthonous insular origin and are predominate in the faunal structure. They are major element and are responsible for giving the southern part of the Kuril chain its strikingly unique stonefly fauna. Their distributions differ from each other on interior insular range size, which reflect the definite stage of geological history of the islands (Kryvolutskaja, 1973). Four subgroups can be recognized (Fig. 6): (1) species with Sakhalin-Kuril-Japanese distribution (*Takagriopteryx nigra*, *Amphinemura dentifera*, *Nemoura longicercia*,

Nemoura parafulva, *Nemoura transversospinosa*, *Nemoura uenoï*), that appeared in the Sakhalin-Kuril Japanese area before disintegration of the separate islands; (2) Sakhalin-Kuril-Hokkaido species (*Stavsolus ainu*, *Gibosia okamotoi*, *Sweltsa sapporonensis*, *Rhopalopssole insularis*, *Paraleuctra gracilis*, *Nemoura kuwayamai*, and *Nemoura sachalinensis*); (3) Kuril-Japanese species (*Kamimuria tibialis*, *Alloperla kurilensis*, *Amphinemura decemseta*, *Amphinemura flavostigma*, and *Protonemura curvata*) that do not occur on Sakhalin and whose northern distributional boundaries are limited to Kunashir, Shikotan, or Iturup, the speciation of which took place in the Holocene after the separation of Sakhalin from Hokkaido, about 10,000 years ago (Karrey, 1968; Fujii *et al.*, 1971); and (4) southern Kuril endemics, the youngest of all these species (*Takagriopteryx zhuikovae* and *Capnia iturupiensis*) found only on Kunashir and Iturup. The final separation of these islands from Hokkaido was in the Holocene, about 7,500 years ago (Velizhanin, 1976), which suggests a more recent speciation.

The mainland-island and island species are considered to be endemic to the Russian Far East. Thus, the southern Kuril Islands are one of the centers of endemism that exists within the Amur-Manchurian Subregion. The genera *Takagriopteryx* and *Gibosi*, while appearing to have an Oriental origin, both have restricted distributions on Sakhalin, Kunashir, Iturup, and Japan. The particular geographic position of the Southern Kuril Islands, being directly open to invasion by oriental species, subject to repeatedly land bridges formation between adjacent islands and the continental coast, their unique insular isolation, their high level of volcanic activity, and a history relatively free from glaciation, are all factors in this high level of speciation. As a result of comparatively weak glaciation, a diverse mountainous landscape, and the great variety of microclimatic conditions, part of the Tertiary fauna survived here. These factors explain the abundance of the endemic species in the Sakhalin-Kuril-Japanese chain.

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