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Biogeography of the Dytiscidae (Coleoptera) of Kamchatka: Preliminary Note

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Abstract Thirty-eight species of predaceous diving beetles (Dytiscidae) are known from the Kamchatka peninsula. Cluster analysis showed that the Kamchatkan fauna is more similar to that of the northeasternmost part of Asia and the North Kurils. The faunas of these three regions are characterized by the predominance of Holarctic elements. No species endemic to Kamchatka is known. Future studies to clarify the biogeography of dytiscids in North East Asia are considered necessary.

Key words: Dytiscidae, biogeography, Kamchatka Peninsula.

The fauna of the Kamchatka Peninsula is generally characterized by a very low species diversity (Kurentzov, 1963; 1966; Levanidova, 1982). However, relatively poor knowledge of the fauna of many taxa in combination with some taxonomic problems have made it difficult to make more firmly based estimates of species richness and faunal composition. Since 1993, we have carried out taxonomic studies of Far Eastern dytiscids. At present, the diving beetle fauna of Primorye, Sakhalin, the Kuriles and Kamchatka (Nilsson, unpublished data; Nilsson and Kholin, 1994; Nilsson et al., 1997; Nilsson et al., 1999) are well known. The present report gives a brief review of the biogeography of the Dytiscidae of the Kamchatka Peninsula and its relationships to adjacent regions.

Materials and Methods

The faunal composition of Kamchatka (KAM: Nilsson et al., 1999) was compared with those of six neighboring regions, based on the following literature: northeasternmost part of Asia (NEA: Zasypkina et al., 1996); the North and South Kurils (NKR and SKR: Nilsson et al., 1997; Nilsson et al., 1999); Sakhalin Island (SAK: Nilsson and Kholin, 1994), Primorye (PRM: Nilsson, unpubl. data), and Hokkaido, Japan (HOK: Mori and Kitayama, 1993). Table 1 shows the distribution records of species in these regions.

Comparison of the fauna of the northeasternmost part of Asia (about 60 species) with other regions may be speculative because of taxonomic problems, and also the need for its species composition to be revised. Existing knowledge of the Hokkaido dytiscid fauna is more firmly based (about 50 species).

Statistical analyses. Faunal similarity between the geographical regions was estimated by Sorensen's coefficient of similarity (Legendre and Legendre, 1983). The similarity matrix resulting from pairwise calculations was subjected to UPGMA cluster analysis (by NTSYS program, version 1.70). The significance of grouping of the regions was tested statistically by the bootstrap technique (Felsenstein, 1985) as follows: 1) The same number of species as the total were resampled randomly from the original data matrix without changing the distribution of each species among the regions. Consequently, each bootstrap sample gave a new data matrix with the same set of regions but with some of the original species duplicated and others dropped by the process of resampling. 2) A new dendrogram was deduced from each bootstrap sample. 3) This process was repeated 1000 times. 4) For each regional cluster deduced from the original data matrix, the relative frequency of its occur-

Table 1. List of species of Dytiscidae found in northeasternmost part of Asia (NEA), Kamchatka (KAM), North Kurils (NKR), South Kurils (SKR), Sakhalin (SAK), Primorye (PRM) and Hokkaido (HOK).

Species	Region							Distribution
	NEA	KAM	NKR	SKR	SAK	PRM	HOK	
COLYMBETINAE								
Agabus aequalis Sharp, 1882					+	+		East Palearctic
Agabus affinis Paykull, 1798	+	+				+		Palearctic
Agabus alinae Lafer, 1988						+		East Palearctic
Agabus arcticus Paykull, 1798	+	+	+					Holarctic
Agabus balkei Fery et Nilsson, 1993	+	+						East Palearctic
Agabus biguttulus Thomson, 1867		+						Palearctic
Agabus brandti Harold, 1880						+		East Palearctic
Agabus clavicornis Sharp, 1882	+							Holarctic
Agabus clypealis Thomson, 1867	+	+	+					Holarctic
Agabus confinis Gyllenhal, 1808	+		+					Holarctic
Agabus congener Thuberg, 1794	+			+	+	+	+	Palearctic
Agabus conspicuus Sharp, 1873				+	+		+	Japano-Kurilian
Agabus costulatus Motschulsky, 1859	+	+	+			+		East Palearctic
Agabus coxalis Sharp, 1882	+	+			+			Holarctic
Agabus daisetsuzanus Kamiya, 1938[1]							+	?
Agabus discolor Harris, 1828		+	+					Holarctic
Agabus erichsoni Gemminger et Harold, 1868					+	+	+	Holarctic
Agabus infuscatus Aubé, 1838	+							Holarctic
Agabus japonicus Sharp, 1873			+	+	+	+	+	East Palearctic
Agabus kholini Nilsson, 1994					+	+		East Palearctic
Agabus labiatus Brahm, 1790					+			Palearctic
Agabus laferi Nilsson, 1994						+		East Palearctic
Agabus lapponicus Thomson, 1867	+							Palearctic
Agabus lineatus Gebler, 1848	+							Palearctic
Agabus luteaster Zaitzev, 1906	+							East Palearctic
Agabus mandsuricus Guignot, 1956						+		East Palearctic
Agabus matsumotoi Satô et Nilsson, 1990					+		+	Japano-Kurilian
Agabus moestus Curtis, 1835	+							Holarctic
Agabus neglectus Erichson, 1837	+							Palearctic
Agabus nigroaenus Erichson, 1837[2]	+							Holarctic
Agabus opacus Aubé, 1837	+	+			+	+		Holarctic
Agabus serricornis Paykull, 1799	+							Palearctic
Agabus sikhotealinensis Lafer, 1988						+		East Palearctic
Agabus thomsoni J. Sahlberg, 1871	+		+					Holarctic
Agabus tristis Aubé, 1838	+	+	+					Holarctic
Agabus udege Nilsson, 1994						+		East Palearctic
Agabus vittiger Gyllenhal, 1827	+							Palearctic
Agabus zetterstedti Thomson, 1856	+							Palearctic
Colymbetes dahuricus Aubé, 1836	+	+	+		+	+		Holarctic
Colymbetes dolabratus Paykull, 1798	+	+	+					Holarctic
Colymbetes tolli Zaitzev, 1906					+		+	East Palearctic
Ilybiosoma striolatus Gyllenhal, 1808	+							Palearctic
Ilybius angustior Gyllenhal, 1808	+	+	+		+			Holarctic
Ilybius anjae Nilsson, 1999					+	+	+	East Palearctic
Ilybius apicalis Sharp, 1873				+	+	+	+	East Palearctic
Ilybius chishimanus Kôno, 1944		+	+			+		East Palearctic
Ilybius cinctus Sharp, 1882						+		East Palearctic
Ilybius crassus Thomson, 1856	+							Palearctic
Ilybius discedens Sharp, 1882		+	+					Holarctic
Ilybius guttiger Gyllenhal, 1808	+							Palearctic

Table 1. Continued

Species	Region							Distribution
	NEA	KAM	NKR	SKR	SAK	PRM	HOK	
Ilybius lateralis Gebler, 1832						+		East Palearctic
Ilybius nakanei Nilsson, 1994				+	+		+	Japano-Kurilian
Ilybius poppiusi Zaitzev, 1907	+							East Palearctic
Ilybius subaeneus Erichson, 1837	+							Holarctic
Ilybius weymarni J. Balfour-Browne, 1947[3]							+	Japanese
Platambus fimbriatus Sharp, 1884						+	+	East Palearctic
Platambus koreanus, 1997						+		East Palearctic
Platambus optatus Sharp, 1884							+	Japanese
Platambus pictipennis Sharp, 1873				+	+		+	Japano-Kurilian
Platambus sawadai Kamiya, 1932							+	Japanese
Platambus ussuriensis Nilsson, 1997						+		East Palearctic
Rhantus erraticus Sharp, 1884							+	Japanese
Rhantus notaticollis Aubé, 1837	+	+	+	+	+	+	+	Palearctic
Rhantus suturalis MacLeay, 1825				+	+	+	+	Palearctic
Rhantus suturellus Harris, 1828	+	+	+					Holarctic
Rhantus yessoensis Sharp, 1891							+	East Palearctic
COPELATINAE								
Copelatus weymarni J. Balfour-Browne, 1946						+	+	East Palearctic
DYTISCINAE								
Acilius canaliculatus Nicolai, 1822	+	+			+	+		Palearctic
Acilius japonicus Brinck, 1939							+	Japanese
Acilius sulcatus Linnaeus, 1758					+	+		Palearctic
Cybister japonicus Sharp, 1873						+	+	East Palearctic
Dytiscus circumcinctus Ahrens, 1811	+	+						Holarctic
Dytiscus dauricus Gebler, 1832	+	+	+	+	+	+	+	Holarctic
Dytiscus delictus Zaitzev, 1906			+			+		East Palearctic
Dytiscus latro Sharp, 1882						+		East Palearctic
Dytiscus marginalis czerskii Zaitzev, 1953						+	+	East Palearctic
Eretes sticticus Linnaeus, 1767						+	+	Palearctic
Graphoderus adamsii Clark, 1864						+	+	East Palearctic
Graphoderus austriacus Sturm, 1834						+		Palearctic
Graphoderus bieneri Zimmermann, 1921						+		East Palearctic
Graphoderus perplexus Sharp, 1882		+						Holarctic
Graphoderus zonatus Hoppe, 1795	+			+	+	+	+	Palearctic
Hydaticus aruspex Clark, 1864					+	+	+	Holarctic
Hydaticus bowringii Clark, 1864							+	East Palearctic
Hydaticus grammicus Germar, 1827						+	+	Palearctic
HYDROPORINAE								
Allopachria flavomaculata Kamiya, 1938							+	East Palearctic
Hydroglyphus japonicus Sharp, 1873						+	+	East Palearctic
Hydroporus acutangulus Thomson, 1856	+				+	+		Palearctic
Hydroporus aenescens J. Sahlberg, 1880[4]	+							East Palearctic
Hydroporus angusi Nilsson, 1990						+		East Palearctic
Hydroporus bergmani Nilsson, 1995	+	+						East Palearctic
Hydroporus breviusculus Poppius, 1905					+	+		East Palearctic
Hydroporus elongatulus Sturm, 1835	+							Palearctic
Hydroporus erythrocephalus Linnaeus, 1758	+							Palearctic
Hydroporus fuscipennis Schaum, 1868	+	+			+	+	+	Holarctic

Table 1. Continued

Species	Region							Distribution
	NEA	KAM	NKR	SKR	SAK	PRM	HOK	
Hydroporus glabriusculus Aubé, 1838	+							Holarctic
Hydroporus lapponum Gyllenhal, 1808	+							Holarctic
Hydroporus laticollis Zimmermann, 1922		+			+	+		East Palearctic
Hydroporus morio Aubé, 1838	+	+	+	+	+	+	+	Holarctic
Hydroporus nigellus Mannerheim, 1853	+	+	+		+			Holarctic
Hydroporus notabilis LeConte, 1850	+	+	+					Holarctic
Hydroporus picicornis J. Sahlberg, 1875	+							Palearctic
Hydroporus saghaliensis Takizawa, 1933				+	+		+	Japano-Kurilian
Hydroporus sibiricus J. Sahlberg, 1880	+							East Palearctic
Hydroporus submuticus Thomson, 1874	+	+	+		+	+	+	Palearctic
Hydroporus tristis Paykull, 1798	+	+		+	+		+	Holarctic
Hydroporus uenoi Nakane, 1963	+	+		+	+	+	+	East Palearctic
Hydroporus umbrosus Gyllenhal, 1808		+	+			+		Palearctic
Hygrotus chinensis Sharp, 1882						+	+	East Palearctic
Hygrotus enneagrammus Ahrens, 1833	+							Palearctic
Hygrotus impressopunctatus Schaller, 1783	+	+		+	+	+	+	Holarctic
Hygrotus inaequalis Fabricius, 1777	+	+			+	+	+	Palearctic
Hygrotus marklini Gyllenhal, 1813	+	+						Holarctic
Hygrotus mongolicus Jakovlev, 1899[5]	+							East Palearctic
Hygrotus novemlineatus Stephens, 1829	+							Palearctic
Hygrotus quinquelineatus Zetterstedt, 1828	+							Palearctic
Hygrotus semenowi Jakovlev, 1899						+		East Palearctic
Hyphydrus falkenstromi Gschwendtner, 1939						+		East Palearctic
Hyphydrus japonicus Sharp, 1873							+	East Palearctic
Nebrioporus anchoralis Sharp, 1884							+	Japanese
Nebrioporus hostilis Sharp, 1884						+		East Palearctic
Nebrioporus simplicepes Sharp, 1884				+	+		+	Japano-Kurilian
Oreodytes alpinus Paykull, 1798	+	+			+	+		Palearctic
Oreodytes kanoi Kamiya, 1938							+	Japanese
Oreodytes natrix Sharp, 1884						+	+	East Palearctic
Oreodytes okulovi Lafer, 1988		+				+		East Palearctic
Oreodytes sanmarkii C. R. Sahlberg, 1826	+	+		+	+	+	+	Holarctic
Stictotarsus multilineatus Falkenström, 1922	+	+	+					Palearctic
LACCOPHILINAE								
Japanolaccophilus nipponensis Kamiya, 1939							+	Japanese
Laccophilus difficilis Sharp, 1873						+	+	East Palearctic
Laccophilus lewisioides Brancucci, 1983						+		East Palearctic
Laccophilus minutus Linnaeus, 1758						+		Palearctic
Laccophilus sharpi Regimbart, 1889							+	Oriental
Laccophilus vagelineatus Zinnermann, 1922						+		East Palearctic
Number of species	62	38	23	17	39	64	50	

[1]probablly synonym of *Agabus congener* Thunberg, 1794.
[2]probablly synonym of *Agabus erichsoni* Gemminger and Harold, 1868.
[3]probablly synonym of *Ilybius chishimanus* Kôno, 1944.
[4]probablly synonym of *Hydroporus acutangulus* Thomson, 1856.
[5]probablly synonym of *Hygrotus unguicularis* Crotch, 1874.

rence in 1000 dendrograms resulting from bootstrap samples was calculated. The obtained value gave the statistical confidence level for each cluster of the regions.

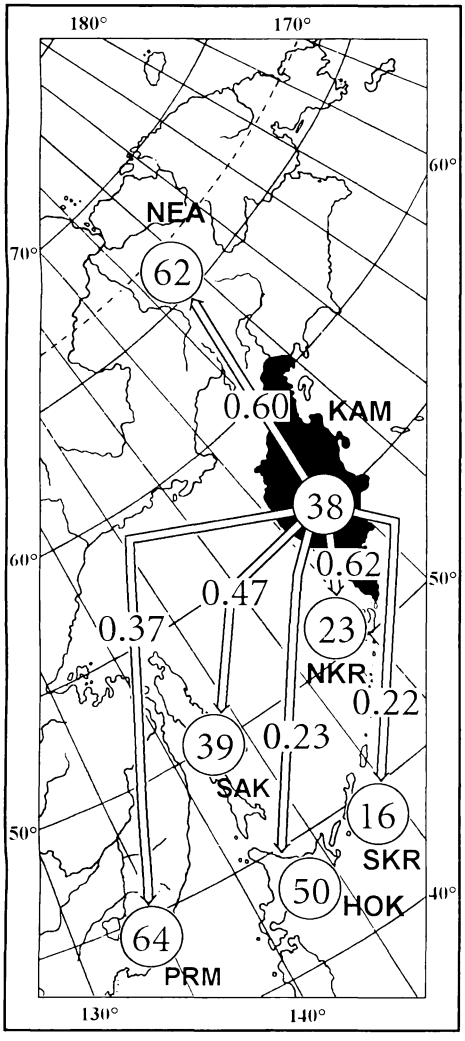

Fig. 1. Schematic presentation of dytiscid faunal similarities between Kamchatka and adjacent regions. Faunal similarity calculated using Sorensen's coefficient are given by the arrows. The number of the species recorded from each region is given within circles. KAM, Kamchatka; NEA, northeasternmost part of Asia; NKR, North Kurils; SKR, South Kurils; SAK, Sakhalin; PRM, Primorye; HOK, Hokkaido.

Results and Discussion

Altogether 38 species of Dytiscidae have been recorded from Kamchatka (Nilsson et al., 1999; Table 1). Sakhalin and the Kuril Archipelago have comparable numbers of species, 39 and 36, respectively (Fig. 1). About twice as many species, 64, are known from Primorye. A total of 94 species of Dytiscidae are known from these four regions.

Figure 1 shows the results obtained from this analysis of Kamchatka and six surrounding regions. Two regions (NEA and NKR) are most closely allied with Kamchatka. The very low values of similarity between Kamchatka and the South Kurils and Hokkaido are notable.

Figure 2 shows the results of cluster analysis for the faunal similarities among Kamchatka and six adjacent regions. The frequency of appearance of different branches in the bootstrap-estimated dendrograms supports the stability of the original chaining of the regions. The regions are divided into two major clusters according to geographic position (south and north regions). The three northern regions (NEA, KAM and NKR) formed a stable cluster (bootstrap value = 98.1%). The southern regions (PRM, SAK, SKR and HOK) were clustered into another branch (also with a stable bootstrap value, 95.5%). The mainland fauna of Primorye showed low similarity with the insular faunas of Sakhalin, the South Kuriles and Hokkaido.

Based on their distribution pattern (Table 1), the species found in the Far East were classified into three chorological groups: Holarctic, Palearctic and Japano-Kurilian. The Holarctic and Palearctic elements are well represented in Kamchatka (three of five and one of four species found in the peninsula, respectively). The fauna of northeasternmost Asia and the North Kurils are also characterized by the predominance of Palearctic and Holarctic elements. For example, in Primorye only one of six species has a Holarctic distribution, whereas East Palearctic elements are more important (three of five species). The Japano-Kurilian fauna includes a high proportion of the lotic species that are absent from Kamchatka. No species endemic to Kamchatka is known. Levanidova (1982) and Tshistjakov (2000) noted the same situation for amphibiotic insects and Heterocera (except Geometridae and Noctuidae).

The dytiscid fauna of Kamchatka is characterized by dominance of boreal species, with relativly low species diversity. We suggest that the relativly low diversity of species in Kamchatka is a result of its origin, and the high geographic isolation of the peninsula.

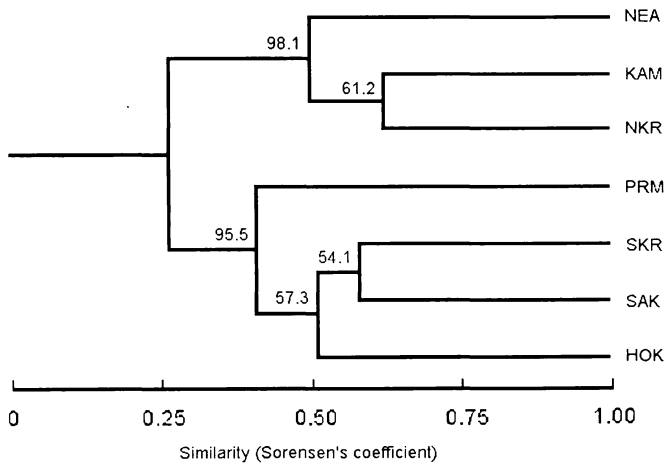

Fig. 2. Dendrogram of the dytiscid faunal similarity among seven regions of Far East Asia resulting from UPGMA cluster analysis (evaluated by Sorensen's coefficient). The bootstrap confidence level (from 1,000 replicates) is indicated at the node of each cluster. KAM, Kamchatka; NEA, northeasternmost part of Asia; NKR, North Kurils; SKR, South Kurils; SAK, Sakhalin; PRM, Primorye; HOK, Hokkaido.

The absence of species endemic to Kamchatka suggests a rather young age of its dytiscid fauna, which was possibly formed after the last glacial epoch. The occurrence in Kamchatka of Nearctic species such as *Ilybius discedens* Sharp and *Graphoderus perplexus* Sharp indicates a possible relationship of the area with North America, especially Beringia. However, the taxonomy and fauna of the Dytiscidae in these regions still require considerable study, 92 species being known so far from Alaska and the Aleutian Islands (Bosquet, 1991). Future studies will eventually clarify the biogeography of dytiscids in Eurasia and North America and their origin and formation.

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カムチャッカ半島のゲンゴロウ科の生物地理学：予備的考察

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カムチャッカ半島からは，38種のゲンゴロウ科が知られている．極東各地域間（シベリア，サハリン，沿海州，北千島，南千島，および北海道）のゲンゴロウ相の類似性についてクラスター分析を行った結果，カムチャッカ半島のゲンゴロウ相は，北千島およびシベリアのゲンゴロウ相と類似度が高いことが示された．これらの地域のゲンゴロウ相は，全北区要素が卓越することが特徴的である．カムチャッカ固有種は現在のところ知られていない．アジア北東部のゲンゴロウ科の生物地理学を解明するには，さらなる研究が必要である．