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The Caddisfly Fauna of Four Great Asian Lakes: Baikal, Hovsgol, Khanka, and Biwa

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Abstract. The biodiversity of four great Asian lakes (Baikal, Hovsgol, Khanka, and Biwa) is considered, including results of recent faunistic investigations and lists of species. A comparison of the Trichoptera faunas of the four lakes is reviewed on specific and generic levels and it is concluded that Khanka and Biwa caddisfly faunas are more closely related (about 30% similarity on the specific level and 69% on the generic level). Conversely, the faunas of Baikal and Hovsgol, which are much closer geographically, are very different (about 6% similarity among species and 9% among genera). Possible reasons for the similarity of Khanka and Biwa faunas may include their similar geological history and their origin from the same basin. Strong differences between Baikal and Hovsgol caddisfly faunas may be explained by the comparatively ancient geological age of Baikal and the relative isolation of these faunas over a very long time. The reasons for this isolation remain poorly understood, despite the close proximity of Baikal and Hovsgol.
Key words. Biodiversity, Endemic species, Faunal similarity, Geological history

Introduction

The ancient lakes of Asia are centers of biodiversity for the freshwater biota of the continent, often harboring unique, endemic organisms (Timoshkin, 1997). Baikal is inhabited by at least 2565 animal species and subspecies (Timoshkin, 1995, 1999); Hovsgol has at least 290 animal species (Kozhova et al., 1994; Kozhova & Izmest'eva, 1998); Khanka is inhabited by about 550 invertebrate species (Vshivkova et al., 1997; Vshivkova et al., 1998; Vshivkova & Sushizkii, 2002); and Biwa has 595 animal species (Mori & Miura, 1990).

We are still far from knowing all species of these lakes, however, and suspect that many more species could be discovered with intensive exploration. Such exploration could have very strong positive impact on theoretical biology (modes of speciation, rates of evolution, pattern of phylogeny, and biogeography); on practical ecology (biomonitoring of water quality and lake health); and on biodiversity conservation.

Geography and Geology

Three of these lakes are located on the continental part of the East Palearctic Region (Russia, Mongolia), and Lake Biwa is on an insular part of the Region, on Honshu Island (Japan), separated from the continent by about 550 km (Fig. 1). Baikal and Hovsgol are located in mountainous areas and are very close geographically – about 600 km by way of the Selenga River channel and about 200 km by the shortest geographical distance. Lake Biwa is in hilly terrain, and Lake Khanka occurs in the broad Khanka Valley, surrounded by numerous small lakes and marshes. Some hydrological, chemical, and biological characteristics of the lakes are in Table 1.

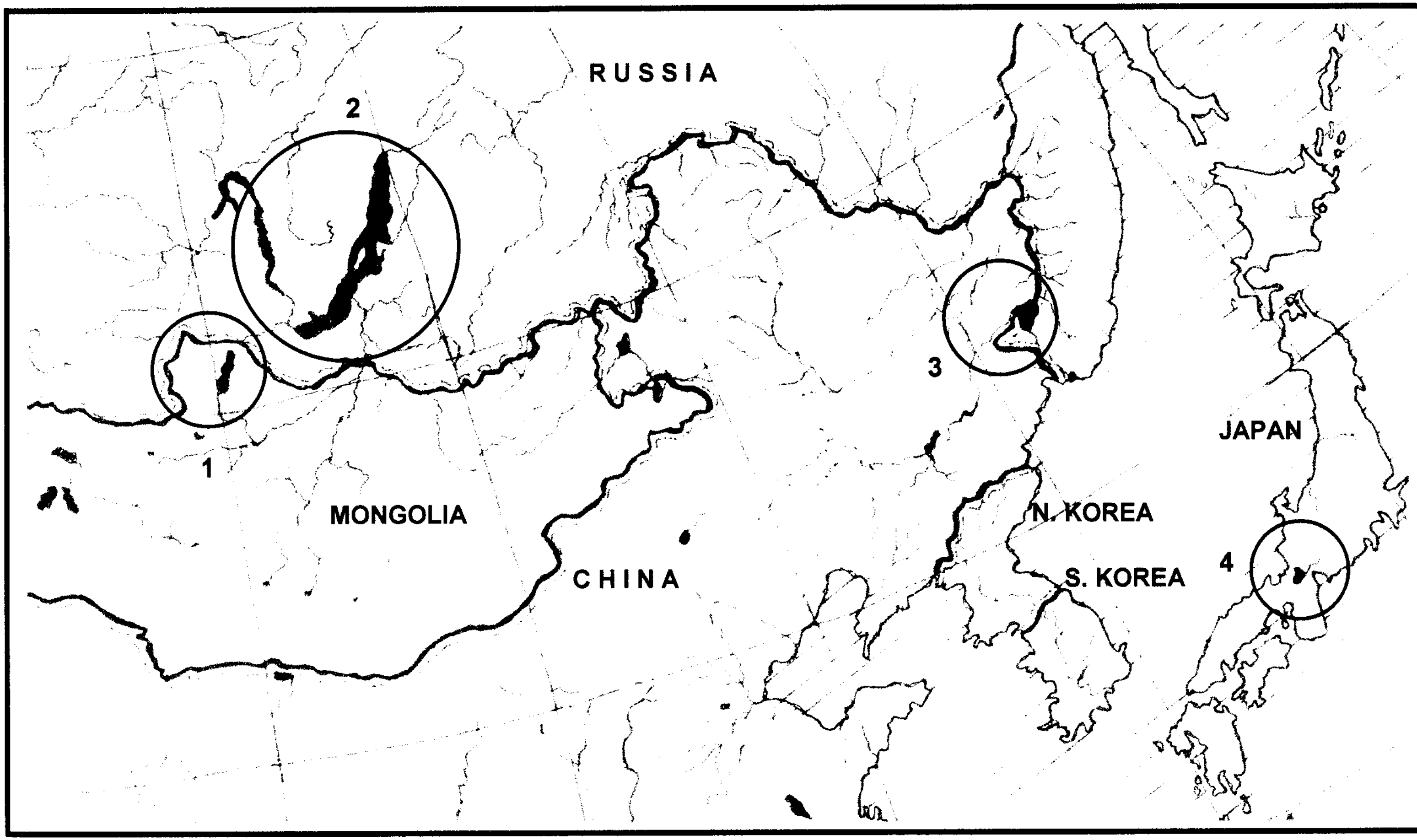

Fig. 1. Location of the four lakes: 1. Hovsgol, 2. Baikal, 3. Khanka, and 4. Biwa.

Baikal. "Lake Baikal is the deepest lake in the world [The total depth from the lake surface is 1,741 m]. The bottom of the lake lies 1,285 m below sea level, and is the deepest continental rift on the earth. Its water volume is approximately equal to the total volume of the Great Lakes of North America, or about 20% of the total freshwater on the earth. It is also known as one of the most ancient in geological history, and there are few lakes in the world to compete with this lake in biotic diversity." (World Lakes Database, 2002a). It is oxygenated to the bottom and has underlying sediments amounting locally to a depth of at least 7-8 km (Hutchinson et al., 1992). Having existed continuously in one form or another for at least 30 million years, it is the oldest lake on Earth (Kozhova & Izmest'eva, 1998). Geological debate persists over the origin of the Lake, whether it is a graben lake or a syncline (Kozhova & Izmest'eva, 1998). The lake consists of three distinct basins that originated at different times, with the southern basin being the oldest; the long-term history of Lake Baikal is characterized with prolonged periods of isolation from adjacent water bodies (Kozhova & Izmest'eva, 1998).

Hovsgol. Lake Hovsgol is located in northern Mongolia. Although its northern end is only about 200 km southwest of Lake Baikal, the surface of Lake Hovsgol is at an altitude of 1,645 m, in contrast to Baikal's surface level of 456 m above sea level (World Lakes Database, 2002b). These two lakes are separated by the Eastern Sayan Mountains and connected by the Selenga River with length of about 600 km. The river from Lake Hovsgol is the major source of water entering Lake Baikal (Kozhov, 1963). Both Lake Hovsgol and Lake Baikal are located in taiga forest, with Lake Hovsgol in its southern border. The Hovsgol Lake basin has been estimated between 2.5 - 4 million years old and thus appears to be similar in age to the central and northern basins of Lake Baikal (Goulden et al., in preparation). Lake Hovsgol was formed as a geological fault graben lake (Goulden et al., in preparation). Although it is not as deep as Baikal, only 262.4 meters maximum (Goulden et al., in preparation), it is much deeper than the other lakes considered here.

Khanka. This lake is "great" only because of its surface area, but holds much less water than any of the other three lakes. In fact, it is unique in being so shallow among the world's great lakes, with maximum depth only 6.5 m (World Lakes Database, 2002c). Lake Khanka is located in the southern part of the Russian Far East and is a part of the Amur River Basin, connected with the Ussuri by the Sungacha River and then the Amur River. The northern part of the Lake is located in China, but most of the lake is situated in Russian territory. The bottom of the lake is composed mainly of soft silt sediments with sand; gravel is not common. Because of the soft sediments and shallow depth, the water of the Lake is turbid, with transparency not exceeding 0.5 m (Korotky, 1990). Riparian and littoral vegetation is represented partially by broad-leaf deciduous forest, but mainly by wetlands with rich grass and shrubs (Belaya, 1995). The lake is surrounded by the large Khanka Valley, which was formed in the late Cretaceous period (Kulakov, 1972).

The Khanka depression is represented by a slight synclinal fold that arose in the Cenozoic Period (Kulakov, 1972). Originally it was covered by a very well-developed river system that was part of the Paleo-Amur basin. Then, in the middle of the Pleistocene, in the region of the Ussuri-Khanka depression, a system of small shallow lakes began to develop. To the end of the Middle Pleistocene, the Paleo-Khanka lake occupied all of the valley of the Sungacha River in the eastern part of the modern lake. The lake size was strongly changed during Middle, Late Pleistocene and Holocene. The modern boundary of the lake was formed about 3, 000 years ago (Kulakov, 1972).

Biwa. The largest freshwater lake in Japan is located in the center of Honshu, Shiga Prefecture. It is divided into a North Lake and South Lake with the average depth of the North Lake being

Table 1. Some characteristics of the Asian lakes

Characteristics	Baikal	Hovsgol	Khanka	Biwa
Age (y b.p.t.)	30,000,000	2.5 - 4,500,000	3,000 - 1,000,000	ca. 4.3 - 5,500,000
Country of location	Russia (Southern Siberia)	Mongolia (northern part)	Russia/China (Russian Far East, southern part)	Japan central Honshu)
Location	$51^0 29'$ - $55^0 46'$ N, $102^0 50'$ -110^0 40 E	$50^0 30'$-$51^0 35'$ N, $100^0 15'$-$100^0 40'$ E	$44^0 8'$-$45^0 5'$ N, 132^0-133^0 E	$35^0 1'$ – $35^0 6'$ N, $135^0 07'$ – $136^0 25'$ E
Relief	mountainous	mountainous	lowland	hilly terrain
Altitude (m a.s.l.)	454.5	1,645	69-72	85.6
Area (km^2)	31,500	2,760	4,070	674
Length (km) maximal	636	136	90	63.5
Width (km) maximal	81	36.5	67	16
minimal	25	20	40	1.35
Depth (m) maximal	1,741	267	6.5	103.8
mean	740	138	4.5	41
Volume (km^3)	23,670	380.7	18.3	27.5
Catchment area (km^2)	540,000	4,920	15,370 – Russian territory; 1,520 - Chinese	3,174
Maximum thickness of sediments (km)	7-8	0.5	> 0.5	?
Transparency by Secchi disk (maximum) (m)	40-41	25-27 (near shore 15-18)	0.5	4-9
Tributaries	> 300	96	15 in Russian territory; 9 in China	> 400
Outflow rivers	Angara	Selenga	Sungacha	Seta-gawa
Temperature regime	thermally uniform	dimictic	dimictic	monomictic
Maximal surface water temperature (summer) (C^0)	open Baikal: 12.0	14-20 (usually 12-14)	25.5	27.2
Maximum deep water temperature C^0)	250 m: 3.5	near bottom 2-4	1.5 m: 17.7; 6 m: 15.3	near bottom: 7
Water chemistry	poor mineralized soft water of the hydrocarbonate class, Calcium group	poor mineralized soft water of the hydrocarbonate class, Calcium group	?	?
Number of animals	2,565 (64 % - endemics)	290	ca. 550 (invertebrates)	595
Number of lake caddisflies	16 (15 endemics)	18 (2 endemics)	46 (no endemics)	36 (2 endemics)

50 meters and that of the South Lake, 5 meters. The deepest part is about 100 m from the water surface. The two basins differ considerably in water quality, physical conditions, flora, and fauna. The forest vegetation consists mostly of secondary forests of Japanese cedar and mixed deciduous hardwoods, covering about 60% of the surrounding landscape (World Lakes Database, 2002d).

"The Old Biwa Lake was established as a small shallow lake (Lake Ohyamada) about 5-6 million years before present, 50 km south of the present location of the lake, at the time of the Ueno-Shimogawara Formation. Around 3.5 million years ago, at the time of the Iga-Aburahi Formation, the lake expanded northeastward into areas where subtropical organisms lived, and then mostly filled up. From 3.0 to 2.6 million years ago Lake Ayama was formed again as a shallow but large lake, moving northward, with its fauna related to Chinese elements (e.g., Nakajima, 1986, 1994; Nakajima & Nakai, 1994), but not to subtropical Afro-Chinese ones. Between 2.6 and 2.2 million years ago Lake Koga was established as a large and deepwater lake. Later, however, the lake (Lake Gamo) became shallower again but expanded northwest to form the shoreline of the present lake. Then, about 1 million years ago, Lake Katata was formed at the present southern basin site and since 0.8 million years ago the southern part of the present northern basin has also been filled with water. A deeper lake almost similar to the present lake existed at least since 0.3 mybp. Most endemic fishes exist also since that time" (Kawanabe, 1996).

The bottom of the Lake has been and still continues to subside due to diastrophism, and so the Lake has avoided being choked with sediments that rivers carry into it. The Lake fills the bottom of an oblong tectonic basin; it was formed about 5 million years ago in the region of the North Lake and then moved gradually southward. The present basins were formed about 0.43 million years ago; among other great lakes of the world, it is one of the oldest insular lakes (Tanida et al., 1999).

Trichoptera Investigations

Baikal. The caddisfly fauna of Baikal has been studied for much longer and more extensively than those of the other three lakes. Early information on Baikal caddisflies was recorded by Hagen (1858, 1864), McLachlan (1872), Martynov (1914a, b; 1924, 1934), Levanidova (1941, 1948), Schmid (1953, 1954), and Lepneva (1964, 1966). Modern investigators, who added new species, provided new records, or re-considered older taxonomic information have been Mey (1981, 1994), Menshutkina (1967, 1986), Ivanov and Menshutkina (1996), and Rozhkova (1994, 1996). Kozhova and Izmest'eva (1998) summarized results of investigations of the Baikal biota, including freshwater insects, in their monograph. The list of caddisflies of the Baikal Basin (including the both the endemic fauna of the open lake and the more widely distributed fauna of northwestern coastlines and tributaries) now includes 122 species, but inhabitants of the open lake are not numerous, totaling only 16 species (Table 2).

Hovsgol. Records concerning Hovsgol caddisflies were provided by Martynov (1909, 1914a, 1914b), Levanidova (1947), Batraeva & Putyatina (1977), Rozhkova (1983, 1984, 1998), Erbayeva et al. (1977, 1982, 1986, 1989), and Morse (1999). Recent international studies supported by the Mongolian Academy of Sciences, the Academy of Natural Sciences of Philadelphia, and Clemson University (South Carolina) brought new information and discoveries of new species and records in Hovsgol Lake basin (Morse et al., in preparation). The list of Mongolian caddisflies included at least 119 valid, extant species, while Lake Hovsgol inhabitants included 18 species (Table 2).

Table 2. List of caddisflies species of Four Great Asian Lakes

+ = lake inhabitants; (+) = inhabitants of lower parts of tributaries or their shallow bays; * = endemic species

Species	Baikal	Hovsgol	Khanka	Biwa
Glossosomatidae				
Anagapetus schmidi (Levanidova, 1979)		(+)		
Glossosma altaicum (Martynov, 1914)		+	(+)	
Glossosoma intermedium (Klapalek, 1892)		(+)	(+)	
Glossosoma nylanderi McLachlan, 1879		(+)		
Agapetus inaequispinosus Schmid, 1970		(+)		
Agapetus sibiricus Martynov, 1918			(+)	
Padunia sp.		(+)		
Hydroptilidae				
Agraylea multipunctata Curtis, 1834			+	
Hydroptila angulata Mosely, 1922		(+)		
Hydroptila chinensis Xue & Yang, 1990			(+)	(+)
Hydroptila itoi Kobayashi, 1977			+	+
Hydroptila matsuii Kobayashi, 1974				(+)
Hydroptila oguranis Kobayashi, 1974				(+)
Hydroptila ornitocephala Yang & Xue, 1992			+	
Hydroptila sp. N (female)			(+)	
Hydroptila sp. 1		+		
Hydroptila sp.				+
Orthotrichia costalis (Curtis, 1834)?			+	
Orthotrichia tragetti Mosely, 1930			+	
Orthotrichia sp. A			(+)	
Orthotrichia sp.				+
Oxyethira ecornuta Morton, 1893			+	
Oxyethira sp. 1			(+)	
Oxyethira flavicornis (Pictet, 1834)		+		
Oxyethira josifovi Kumanski, 1990			(+)	
Oxyethira sp. n.			(+)	
Tricholeiochiton aff. *fagesii*			+	
Philopotamidae				
Philopotamidae gen.? sp. A		*		
Hydropsychidae				
Ceratopsyche kozhantschikovi (Martynov, 1924)		(+)	(+)	
Ceratopsyche lianchiensis (Li & Tian, 1990)			(+)	
Ceratopsyche nevae (Kolenati, 1858),		(+)		
Ceratopsyche valvata (Martynov, 1927		(+)	(+)	
Cheumatopsyche amurensis Martynov, 1934			+	
Cheumatopsyche brevilineata (Iwata, 1927)				+
Cheumatopsyche daurensis Ivanov, 1996			(+)	
Cheumatopsyche infascia Martynov, 1934			(+)	(+)
Potamyia chinensis (Ulmer, 1915)			(+)	

(Table 2, continued)

*Potamyia czekanovskii (*Martynov, 1910)			(+)	
Potamyia echigoensis (Tsuda, 1949)				(+)
Amphipsyche proluta McLachlan, 1872			(+)	
Macrostemum radiatum (McLachlan, 1872)			(+)	(+)
Polycentropodidae				
Cyrnus nipponicus Tsuda, 1942			(+)	
Neureclipsis bimaculata Linneus, 1758			+	
Neucentropus mandjuricus Martynov, 1907			+	+
Dipseudopsidae				
Dipseudopsis alba (Iwata, 1927)				+
Hyalopsyche sachalinica Martynov, 1910			+	+
Ecnomidae				
Ecnomus tenellus (Rambur, 1842)			+	+
Ecnomus yamashironis Tsuda, 1942			+	+
Psychomyiidae				
Paduniella amurensis Martynov, 1934				+
Paduniella uralensis Martynov, 1914	(+)		+	
Psychomyia flavida Hagen, 1861			(+)	
Psychomyia minima (Martynov, 1910)		(+)		
Psychomyia pusilla (Fabricius, 1781)	(+)			
Phryganeidae				
Agrypnia colorata (Hagen, 1873)		(+)		
Agrypnia czerskyi (Martynov, 1924)		(+)	(+)	
Agrypnia obsoleta (Hagen, 1864)	(+)	(+)		
Agrypnia picta Kolenati, 1848		+	+	
Agrypnia sahlbergi (McLaclhan 1880)			+	
Phryganea bipunctata Retzius, 1783	(+)	(+)		
Phryganea (C.) japonica McLachlan, 1866				+
Phryganea rotundata (Ulmer, 1905)	(+)			
Phryganea(C.) sinensis (McLachlan, 1862)			+	
Phryganopsychidae				
Phryganopsyche latipennis (Banks, 1906)			(+)	(+)
Limnephilidae				
Anabolia sp.		(+)		
Arctopora sp.		(+)		
Asynarchus amurensis (Ulmer, 1905)		+	+	
Asynarcus iteratus McLachlan, 1880		(+)		
Chaetopteryx sahlbergi McLachlan, 1876		(+)		
Hydatophylax nigrovittatus (McLachlan, 1872)		+		
Hydatophylax sp.	(+)			
Grammotaulius sibiricus McLachlan, 1874		(+)		

(Table 2, continued)

Limnephilus correptus McLachlan, 1880			+	
Limnephilus fenestratus (Zetterstedt, 1840)		(+)		
Limnephilus fuscovittatus Matsumura, 1904		(+)		+
Limnephilus hovsgolicus Morse, 1999		*		
Limnephilus nigriceps Zetterstedt, 1840	(+)			
Limnephilus orientalis Martynov, 1935				+
Limnephilus picturatus McLachlan, 1875		(+)	(+)	
Limnephilus quadratus Martynov, 1914		(+)	(+)	
Limnephilus rhombicus (Linnaeus, 1758)	(+)	+		
Limnephilus sericeus (Say, 1824)			(+)	
Limnephilus stigma Curtis, 1834			(+)	
Limnephilus sp. 1		+		
Limnephilus sp. 2		(+)		
Nemotaulius admorsus (McLachlan, 1866)		+	+	+
Nemotaulius mutatus (McLachlan, 1872)	(+)	(+)	(+)	
Nemotaulius puctatolineatus (Retzius, 1783)	(+)			
Nothopsyche nigripes Martynov, 1914			+	
Nothopsyche pallipes Banks, 1906				+
Nothopsyche ruficollis (Ulmer, 1907)				+
Philarctus bergrothi McLachlan, 1880		(+)		
Limnephilidae gen.? sp.		+		
Goeridae				
Goera japonica Banks, 1906				+
Goera squamifera Martynov, 1909			(+)	
Goera kawamotonis Kobayashi, 1987			(+)	
Goera tungisensis Martynov, 1909		(+)	(+)	
Apataniidae				
Apataniini				
Apatania biwaensis Nishimoto, 1994				*
Apatania doehleri Schmid, 1954		+		
Apatania majuscula McLachlan, 1872	+	+		
Apatania stigmatella Zetterstedt, 1840		+		
Apatania tsudai Schmid, 1953				+
Apatania zonella (Zetterstedt, 1840)		(+)		
Baikalini				
Baicalina bellicosa Martynov, 1914	*			
Baicalina levanidovae Ivanov & Menshutkina, 1966	*			
Baicalina reducta Martynov, 1924	*			
Baicalina tallingi Rozhkova, 1996	*			
Baicalina thamastoides Martynov, 1914	*			
Protobaicalina hageni Ivanov & Menshutkina, 1996	*			
Protobaicalina nigrostriata (Martynov, 1914)	*			
Protobaicalina multispinosa (Mey, 1994)	*			
Protobaicalina spinosa (Martynov, 1914)	*			
Thamastini				
Protoradema baicalensis (Martynov, 1914)	*			

(Table 2, continued)

Protoradema setosum Martynov, 1924	*			
Radema infernale Hagen & McLachlan, 1872	*			
Baicalinella foliata (Martynov, 1914)	*			
Baicalodes ovalis Martynov, 1914	*			
Thamastes dipterus Hagen, 1858	*			
Lepidostomatidae				
Goerodes bipertitus (Kobayashi, 1955)				(+)
Goerodes japonica (Tsuda, 1936)				+
Goerodes orientalis (Tsuda, 1942)				(+)
Goerodes tsudai (Tani, 1971)				(+)
Sericostomatidae				
Gumaga sp.				+
Molannidae				
Molanna moesta Banks, 1906			+	+
Calamoceratidae				
Anisocentropus pallidus Martynov, 1935			(+)	
Ganonema extensum Martynov, 1935			(+)	
Georgium japonicum (Ulmer, 1905)				+
Leptoceridae				
Ceraclea alboguttata (Hagen, 1860)			+	+
Ceraclea annulicornis (Stephens, 1836)	(+)		(+)	
Ceraclea ensifera (Martynov, 1935)			+	
Ceraclea excisa (Morton, 1904)			(+)	
Ceraclea gigantea Kumanski, 1991			+	
Ceraclea globosa Yang & Morse, 1988			+	
Ceraclea lobulata (Martynov, 1935)		(+)	+	+
Ceraclea nigronervosa (Retzius, 1783)			+	+
Ceraclea riparia (Albarda, 1874)			(+)	
Ceraclea superba (Tsuda, 1942)				+
Ceraclea sp. 1		(+)		
Ceraclea sp. 2		(+)		
Ceraclea sp. n.			+	
Leptocerus biwae (Tsuda, 1942)				+
Leptocerus valvatus (Martynov, 1935)			+	
Mystacides absimilis Yang & Morse, 1997			(+)	
Mystacides azurea (Linnaeus, 1767)				+
Mystacides bifidus Martynov, 1924	(+)	+	+	
Mystacides dentata Martynov, 1924			+	
Mystacides interjecta (Banks, 1914)			+	
Mystacides sp. (Hovsgol)		+		
Mystacides sp. (Biwa)				*
Oecetis bullata Yang & Morse, 1997			+	
Oecetis furva amurensis Martynov, 1935			+	
Oecetis lacustris (Pictet, 1834)			+	

(Table 2, continued)

Oecetis minima (Martynov, 1935)			+	
Oecetis morii Tsuda, 1942			+	+
Oecetis nigropunctata Ulmer, 1905			+	+
Oecetis ochracea (Curtis, 1825)	(+)	(+)	(+)	
Oecetis paxilla Yang & Morse, 2000?			+	
Oecetis testacea orientalis Kumanski, 1991			+	
Oecetis tripunctata (Fabricius, 1793)				+
Oecetis tsudai Fischer, 1970				+
Oecetis yukii Tsuda, 1942				+
Parasetodes aquilonius Yang & Morse, 1997		(+)	(+)	
Parasetodes respersellus (Rambur, 1842)			+	
Setodes amurensis Martynov, 1935			+	
Setodes sp.		(+)		
Triaenodes pellectus Ulmer, 1908			+	
Triaenodes rufescens Martynov, 1935			+	
Triaenodes unanimis McLachlan, 1877			+	
Triaenodes yamamotoi Tsuda, 1942				+
Triaenodes sp.		(+)		
Triplectides misakiana (Matsumura, 1931)				+
Ylodes reuteri (McLachlan)		+		
Number of species (total):	29	54	84	47
Number of lake species:	16	18	46	36
Number of endemic species:	15	2	0	2

Khanka. The history of investigation of Khanka caddisflies is not as rich as that of the other three lakes and can be divided into two periods: early (Martynov, 1910, 1914b, 1934, 1935), and recent (Mey, 1991; Vshivkova, 1995; Vshivkova et al., 1997; Vshivkova et al., 1998). Recent international expeditions to Khanka basin supported by the Russian Academy of Sciences, the US National Science Foundation, and the Japanese Society for Promotion of Science during 1992-1999 allowed discovery of new and interesting records, including several taxa new to science. The list of species in the Khanka Basin now includes 125 species, of which 46 species are Lake inhabitants (Vshivkova, Morse, and Tanida, unpublished).

Biwa. The Trichoptera larvae and adults of Lake Biwa were investigated by Iwata (1927), Tsuda (1942a, b; 1971), Kuwayama & Tsuda (1950), Nishino (1987a,b), Tanida & Nishino (1992), Uenishi (1993), Nishimoto (1994), and Tanida (1997). A summary of previous investigations, as well as original data with discussion of biogeographical and ecological aspects, was published recently by Tanida et al. (1999); the list of caddisflies species recorded by them includes 48 species, with true lake inhabitants represented by 36 species.

Results and Discussion

New Records

Recent international studies have brought many interesting discoveries for the caddisfly fauna of these four lakes and their basins.

Baikal. The Baikal fauna is well investigated and description of new taxa or new records here are rare events (Mey, 1994; Rozhkova, 1996). However, recent studies in the other three lakes have shown that our knowledge about caddisflies of these regions is very far from being completed.

Hovsgol. From Lake Hovsgol a new species *Limnephilus hovsgolicus* Morse, 1999, was recently described, and a possible new genus of Philopotamidae has been recorded (but not yet described, Morse et al., in preparation). Ten species new to Mongolia also were reported: *Rhyacophila depressa* Martynov, *Anagapetus schmidi* Levanidova, *Potamyia* sp., *Hydroptila angulata* Mosely, *Oxyethira flavicornis* Pictet, *Allomyia* sp. (probably *A. sajanensis* Levanidova), *Arctopora* sp., *Limnephilus quadratus* Martynov, *Parasetodes aquilonius* Yang & Morse, *Triaenodes* sp. (Morse et al., in preparation).

Khanka. Two new species, *Oxyethira*, sp. n., and *Ceraclea*, sp. n., have been discovered for the Lake. Four species are new to Khanka Lake Basin: *Oxyethira josifovi* Kumanski, *Mystacides absimilis* Yang & Morse, *Oecetis brachiura* Yang & Morse, and *Parasetodes aquilonius* Yang & Morse. Five species are new to Russia: *Hydroptila chinensis* Xue & Yang, *Hydroptila itoi* Kobayashi, *Hydroptila ornitocephala* Yang & Xue, *Tricholeiochiton* aff. *fagesii* (Guinard), *Oecetis paxilla* Yang & Morse.

Biwa. A list of caddisflies of Lake Biwa was published a few years ago (Tanida et al., 1999). Now we add some new findings as well: a new species for Japan - *Hydroptila chinensis* Xue & Yang, and two species new for the Biwa Lake basin - *Hydroptila matsuii* Kobayashi and *Hydroptila oguranis* Kobayashi.

Comparison of Caddisfly Faunas

In comparing the faunas of these four lakes we limit ourselves strictly to lentic caddisfly species and genera, although our faunistic lists (Tables 2, 3) include also inhabitants of lower parts of tributaries and shallow bays. The number of lake-inhabiting caddisfly species varies strongly from lake to lake: Khanka Lake has 47 species, no endemics (0% endemics); Biwa – 36, two endemics (5.5%); Hovsgol – 18 species, two endemics (11%), and Baikal – 16 species, 15 endemics (93.8%).

Analyses of faunal similarity were accomplished by calculating Sörensen (1948) and Jaccard (1912) coefficients and inferring UPGMA clusters (Legendre and Legendre, 1983) for both species and genera. Dendrograms of species similarity are provided in Figs. 2a, b and of generic similarity in Figs. 3a, b; matrices of Sörensen (1948) coefficients of similarity for species and genera are provided in Tables 4 and 5, respectively.

A comparison of the caddisfly fauna at the species level (Figs. 2a, b) emphasizes the unique Baikal Trichoptera - almost all of them are endemic and belong to endemic Baikalian genera and tribes. Interestingly, where all 15 endemic species in Baikal belong to Apataniidae, apataniids are much less common in the other three lakes: at least three widespread East Palearctic *Apatania* species occur in Lake Hovsgol, two *Apatania* species occur in Lake Biwa (one of them is endemic to the lake, the other is endemic to Japan), and no Apataniidae occur in Lake Khanka. On the other hand, often-lentic Hydroptilidae and Leptoceridae are absent from Baikal, but very numerous in Khanka (especially Hydroptilidae) or in Khanka and Biwa (especially Leptoceridae). Hovsgol so far is known to have only two peculiar endemic species (*Limnephilus hovsgolicus* and Philopotamidae gen.? sp.n.) and the fauna is common, consisting of typical East Palearctic species and genera of cold or cold-temperate waters; strictly potamophilous representatives are absent.

Table 3. List of caddisfly genera of Four Great Asian Lakes

+ = lake inhabitants; (+) = inhabitants of lower parts of tributaries or their shallow bays;
* = endemic genera

Genera	Baikal	Hovsgol	Khanka	Biwa
Anagapetus		(+)		
Glossosoma		+	(+)	
Agapetus		(+)	(+)	
Padunia		(+)		
Agraylea			+	
Hydroptila		+	+	+
Orthotrichia			+	+
Oxyethira		+	+	
Tricholeiochiton			+	
Philopotamidae gen.? sp. A		+		
Ceratopsyche		(+)	(+)	
Cheumatopsyche			+	+
Potamyia			(+)	(+)
Amphipsyche			(+)	
Macrostemum			(+)	(+)
Cyrnus			(+)	
Neureclipsis			+	
Neucentropus			+	+
Dipseudopsis				+
Hyalopsyche			+	+
Ecnomus			+	+
Paduniella	(+)		+	+
Psychomyia	(+)	(+)	(+)	
Agrypnia		+	+	
Phryganea	(+)	(+)		
Phryganea (Colpomera)			+	+
Phryganopsyche			(+)	(+)
Anabolia		(+)		
Arctopora		(+)		
Asynarchus		+	+	
Hydatophylax	(+)	+		
Grammotaulius		(+)		
Limnephilus	(+)	+	+	+
Nemotaulius	(+)	+	+	+
Nothopsyche			+	+
Philarctus		(+)		
Limnephilidae gen.? sp.		+		
Goera		(+)	(+)	+

(Table 3, continued)

Apatania	+	+		+
Baicalina	*			
Protobaicalina	*			
Protoradema	*			
Radema	*			
Baicalinella	*			
Baicalodes	*			
Thamastes	*			
Goerodes				+
Gumaga				+
Molanna			+	+
Anisocentropus			(+)	
Ganonema			(+)	
Georgium				+
Ceraclea	(+)	(+)	+	+
Leptocerus			+	+
Mystacides	(+)	+	+	+
Oecetis	(+)	(+)	+	+
Parasetodes		(+)	+	
Setodes		(+)	+	
Triaenodes		(+)	+	+
Triplectides				+
Ylodes		+		
Number of genera, collected in lakes	8	14	25	24
Total number of genera, collected in lakes, lower parts of their tributaries, and their shallow bays	17	29	37	27

In spite of their freshwater connection through the Selenga River and in spite of their close proximity and similar geological origins, Lakes Baikal and Hovsgol have only one common species (*Apatania majuscula* McLachlan) and their coefficient of similarity is very low (CS = 0.059). On the contrary, the Lake Hovsgol fauna is closer to that of Lake Khanka (CS = 0.125) than to Baikal. Khanka has no endemic species at all, and its fauna generally consists of lentic and potamophilous species; Leptoceridae and Hydroptilidae represent about 70% of all species present and Polycentropodidae are very numerous also. The fauna of Lake Biwa is rich with Leptoceridae (about 38% of its caddisfly species composition). However, both rithrophilous and potamophilous genera are also present here. There are two endemic species here: *Apatania biwaensis* Nishimoto and *Mystacides*, sp.n. (*Mystacides longicornis* Group). The closest relationships are between these two lakes, Biwa and Khanka, with about 30% similarity (12 common species, CS = 0.293).

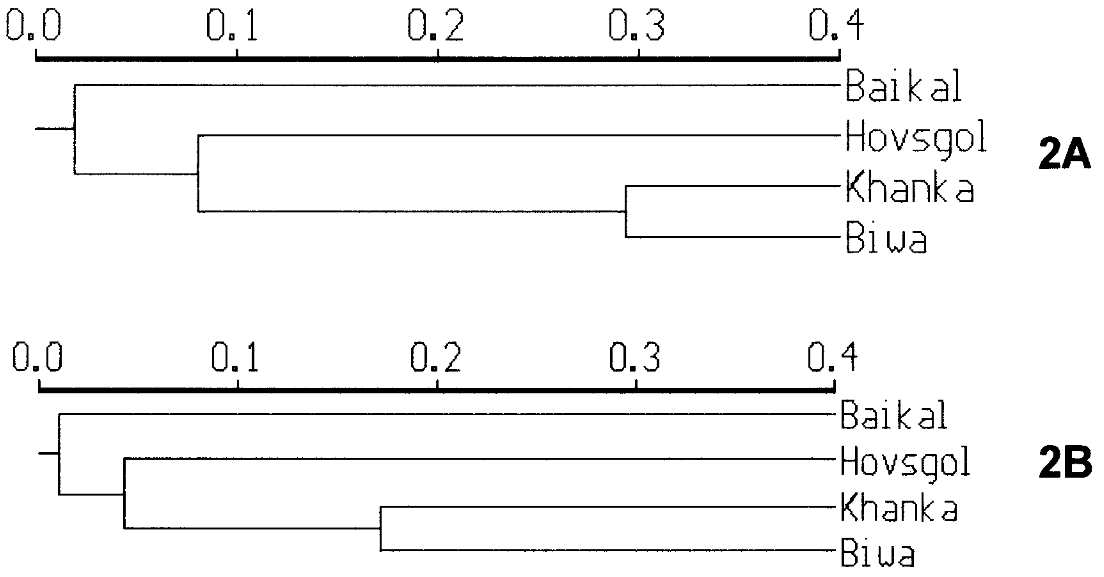

Fig. 2. Dendrogram of caddisfly species composition similarity level:
A – Sörensen coefficient, B – Jaccard coefficient

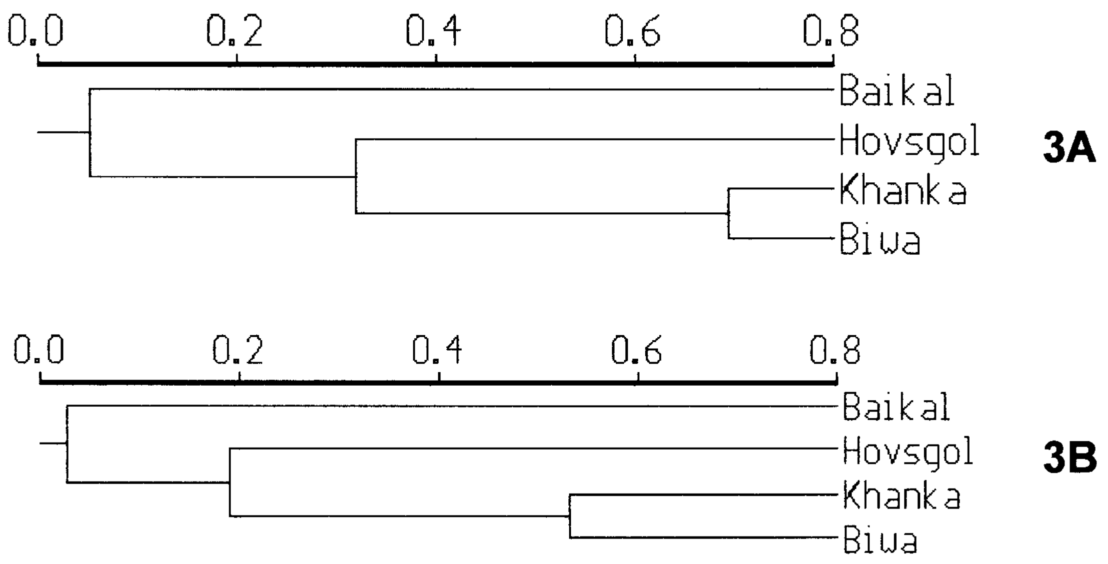

Fig. 3. Dendrogram of caddisfly generic composition similarity level:
A – Sörensen coefficient, B – Jaccard coefficient

We report here an interesting peculiarity. *Hyalopsyche sachalinica* Martynov is an East Asian endemic, but until recently it was known only from South Sakhalin and the lower Amur River (Martynov, 1910, 1934). It has not been reported since Martynov's original descriptions. Now, more than 60 years later, we have found it in both Lake Khanka and Lake Biwa (Tanida, 1997; Vshivkova, Morse, Tanida, unpublished).

Comparison of faunas at the generic level (Fig. 3a, b) more precisely demonstrates the ecological relationships of the faunas and is a more powerful instrument for biogeographical analysis, according to Kryzhanovskii (1965). Concurring with the species-level data, a comparison of caddisfly faunas of the four lakes on the generic level shows the closest connections between the Khanka and Biwa faunas (about 70% of generic composition similarity; CS = 0.694). The similarity is high, in spite of the large distance (1,060 km) between these water bodies and the barrier of the marine Japan Sea between them. Whereas Hovsgol and Baikal have only two common genera (CS = 0.095), Hovsgol and Khanka have 8 common genera (CS = 0.368).

High faunal similarities between Khanka and Biwa, and relatively high similarities between Khanka and Hovsgol (CS = 0.368) suggest ancient connections of their faunas; the Khanka-Biwa similarity suggests they have a common origin. In contrast, we wonder about the great differences between the Hovsgol and Baikal faunas in light of their proximity and the apparent geological similarities of their habitats.

Ancient connections between the Khanka and Biwa faunas seems possible in light of the geological history of their lakes. Before the Pleistocene Epoch, a large, shallow, freshwater lake was located in the basin of the modern Japan Sea. At that time, a common community of the freshwater lake and its inflowing rivers may have developed. An ancient proto-Amur River flowed into this lake in the Late Pliocene Epoch, before the glacial period, and an outlet connected the faunas of the proto-Khuan and proto-Janzhy Rivers. During the first major glacial period of the Pleistocene, this freshwater lake persisted, but the direction of flow for the proto-Amur River changed, turning to the Okhotsk Sea. Beginning in the first interglacial period the shallow basin was flooded by saltwater through breaches, first across central Sakhalin, then across the Shantar Strait and later the Laperuza Strait. Despite some periods of isolation, expansion, contraction, and deepening, the lake always remained a saltwater sea after that first major glaciation (Lindberg, 1972; Kulakov, 1972). So, we can say that the similarity of the Khanka and Biwa faunas probably resulted from a similar origin that persisted into the Lower Pleistocene Epoch. This hypothesis invites phylogenetic testing with various taxa to discover whether Lakes Khanka and Biwa have an unusually high number of sister lineages. If found, these sister lineages would support the inference that their allopatric vicariance is congruent and can be dated relatively precisely to yield some interesting conclusions about comparative rates of evolution.

Consider, in contrast, the historical geology of Baikal and Hovsgol. Baikal and its fauna apparently originated 30-20 million years ago, at least in the southern basin of the lake. Hovsgol originated much later, 4.5-4.0 million years ago, long after Baikal and its fauna were established. The question we ponder is this: with two lakes so near each other (200 km), formed by similar processes, belonging to the same river system, and having at least 4 million years to integrate biotas, why are they still so different? Both lakes are cold, deep, highly oxygenated, apparently similar in most ecological aspects. Although several of their endemic species are brachypterous and not able to move far from the larval habitat, others have normal-size wings and can fly or be blown across the landscape occasionally. Obviously, there have been some other mechanisms of isolation, which are not yet understood completely.

It is our plan to investigate the historical biogeography of these four lakes further, using additional taxa of animals and plants and modern cladistic methods of analysis (e.g., component analyses, three-area statement analyses; Humphries and Parenti, 1999).

Table 4. Matrix of Sörensen (1948) similarity for caddisfly species composition of four great Asian lakes (number of common species in parentheses)

	Baikal	Hovsgol	Khanka	Biwa
Baikal	-	0.059 (1)	0 (0)	0 (0)
Hovsgol		-	0.125 (4)	0.037 (1)
Khanka			-	0.293 (12)
Biwa				-
Number of species	16	18	46	36

Table 5. Matrix of Sörensen (1948) similarity for caddisfly generic composition of four great Asian lakes (number of common genera in parentheses)

	Baikal	Hovsgol	Khanka	Biwa
Baikal	-	0.095 (1)	0 (0)	0.063 (1)
Hovsgol		-	0.368 (8)	0.270 (6)
Khanka			-	0.694 (17)
Biwa				-
Number of genera	8	14	25	24

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