East-Siberian coregonid fishes: their occurrence, evolution and present status*

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ABSTRACT

Coregonid fishes (coregonids) (Salmonidae, Coregoninae) of Siberia show immense morphological and ecological variability, what is reflected in their complex interspecific and intraspecific structure: *i.e.* occurrence of numerous species, forms and endemic species. Studies of the coregonids of Siberia is crucially important for understanding of their origin, taxonomy and evolution. We have analysed electrophoretically some 13 enzyme systems from over 20 samples of East-Siberian coregonids. This paper was intended as an introduction to a number of primary papers that are planned that will describe the biological and genetic characteristics of studied populations.

Names of coregonid species presented in this paper

Latin	Russian (transliterated)	English
Coregonus albula	evropejskaya ryapushka	European vendace
Coregonus autumnalis	omul	Arctic cisco
Coregonus autumnalis migratorius	bajkalskij omul	Baikal omul, omul
Coregonus baunti sp. *nova*	bauntovskaya ryapushka	Baunt least cisco
Coregonus lavaretus	obyknovennyj sig	European whitefish, whitefish
Coregonus lavaretus baicalensis	bajkalskij ozernyj sig	lacustrine whitefish of Lake Baikal
Coregonus lavaretus baunti	bauntovskij sig	Baunt whitefish
Coregonus lavaretus pidschian	sibirskij sig, sig-pyzhyan	Siberian whitefish; pidschian
"	ozerno-rechnyj pyzhyan	lacustrine-riverine Siberian whitefish
"	rechnyj pyzhyan	riverine Siberian whitefish
"	ozernyj pyzhyan	lacustrine Siberian whitefish
Coregonus lavaretus	teletskij sig	Teletsk whitefish pidschian nation smitti
Coregonus lavaretus pravdinellus	sig Pravdina	Pravdin whitefish
Coregonus sardinella	sibirskaya ryapushka	least cisco
Coregonus skrjabini sp. *nova*	bauntovskij sig pyzhyan	Baunt Siberian whitefish

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Geographical names appearing in this paper

Russian (transliterated)	English (listed alphabetically)
Bay	
Chivyrkujskij Zaliv	Chivyrkujskij
Gulf	
Gydanskaya Guba	Gydanskaya
Hollow (Vyrkin 1998)	
Barguzinskaya Kotlovina	Barguzinskaya
Charskaya Kotlovina	Charskaya
Mujskaya Kotlovina	Mujskaya
Tsipo-Tsipikanskaya Kotlovina	Tsipo-Tsipikanskaya (Baunt lakes)
Lake	
Ozero Bajkal	Baikal
Ozero Baunt	Baunt
Ozero Bolshoe Kapylyushi	Bolshoye Kapylyushi
Ozero Bolshoe Leprindo	Bolshoye Leprindo
Ozero Busani	Busani
Ozero Davatchan	Davatchan
Ozero Dorong	Dorong
Ozero Eravninskoe	Eravninskoye
Ozero Kulinda	Kulinda
Ozero Labaz	Labaz
Ozero Leprindokan	Leprindokan
Ozero Maloe Kapylyushi	Maloye Kapylyushi
Ozero Maloe Leprindo	Maloye Leprindo
Ozero Nichatka	Nichatka
Ozero Oron	Oron
Ozero Tajmyr	Tajmyr
Ozero Teletskoe	Teletskoye
Ozero Tsipikan	Tsipikan
Ocean	
Severnyj Ledovityj Okean	Arctic
Passage	
Maloe More proliv	Maloye Morye

Peninsula	
Poluostrov Tajmyr	Tajmyr
Region	
Rajon Mujskogo (nagorya)	Muya
River	
Reka Barguzin	Barguzin
Reka Bolshaya	Bolshaya
Reka Chara	Chara
Reka Irkut	Irkut
Reka Khatanga	Khatanga
Reka Kheta	Kheta
Reka Kirenga	Kirenga
Reka Lena	Lena
Reka Ob	Ob
Reka Selenga	Selenga
Reka Sibircha	Sibircha
Reka Toch	Toch
Reka Tsipa	Tsipa
Reka Tsipikan	Tsipikan
Reka Vitim	Vitim
Reka Enisej	Yenisei
Sea	
Karskoe More	Karskoye
Shoal	
Severo-Baikalskoe melkovodie	North-Baikal
Selenginskoe melkovodie	Selenga
Sibir	Siberia
System	
Sistema rek Kheta-Khatanga	Kheta-Khatanga Rivers
Tsipo-Tsipikanskaya ozernaya Sistema	Tsipo-Tsipikan Lakes
Zabajkale	Trans-Baikal
Upland	
Olekmo-Vitimskoe nagorye	Olekmo-Vitim

INTRODUCTION

Coregonid fishes (coregonids) constitute an important element of sea- and fresh-water ecosystems of the drainage basins of the Arctic Ocean in Asia, Europe and North America (Chereshnev et al. 2002; Reshetnikov 1980). Coregonids form the family Coregonidae according to some authors (Cope 1871; Reshetnikov 1980; Svetovidov et al. 1975), or the subfamily Coreguninae within the family Salmonidae according to others (superfamily *Salmonoidea*, suborder *Salmonoidei*, order Salmoniformes (Berg 1955; Nelson 1984)). Coregonids are adapted to lowland freshwaters and brackish parts of oceans in the cool and cold areas of the northern hemisphere (also high altitude lakes and rivers in more

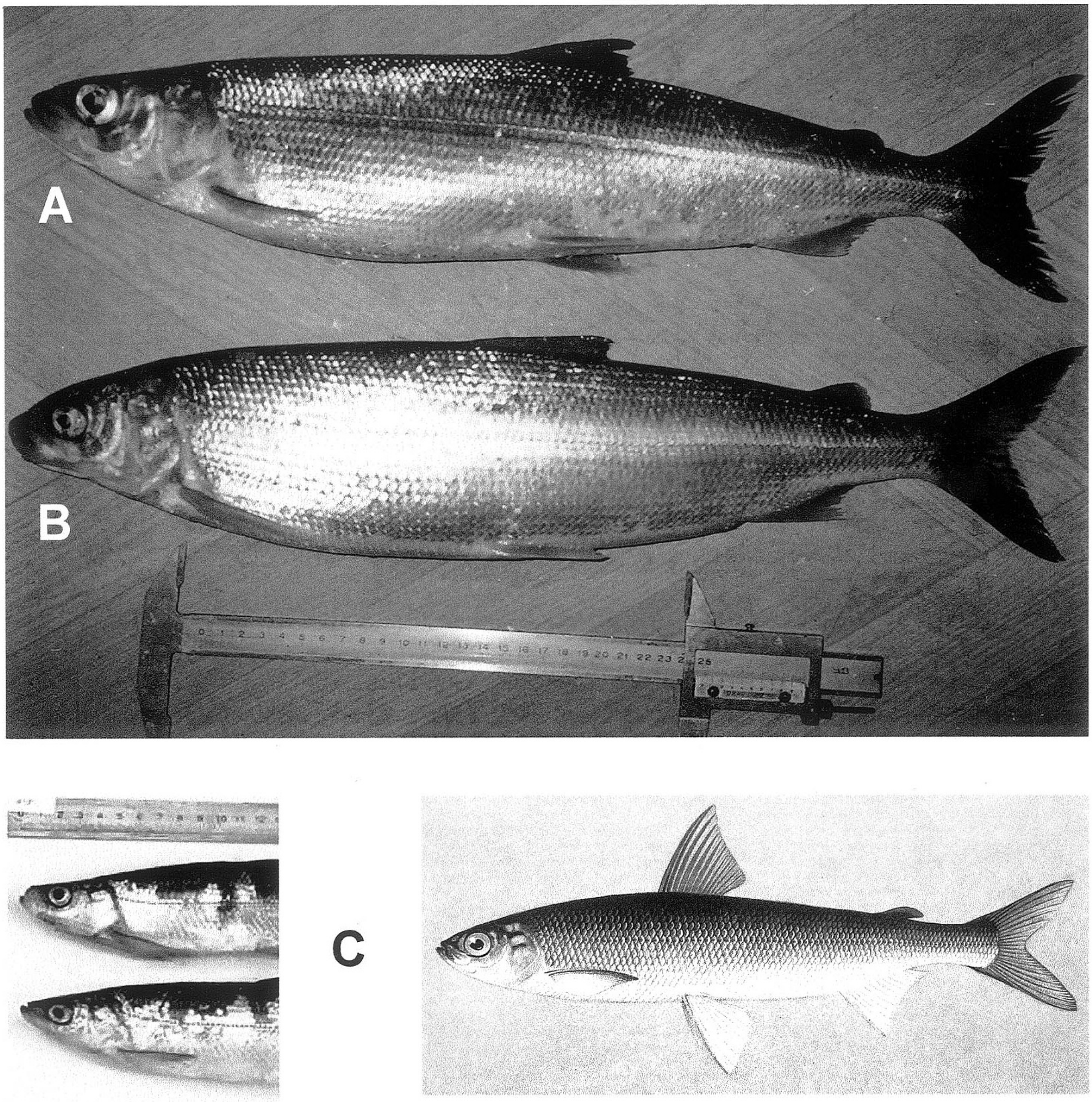


Figure 1. Examples of studied coregonids: A – omul (*Coregonus autumnalis migratorius*) (Lake Baikal), B – Siberian whitefish (*Coregonus lavaretus pidschian*) (Lake Baikal); C - least cisco (*Coregonus sardinella*) (Lena River). All photographs of fish were taken by A.M. Mamontov. *C. sardinella* drawing reproduced after Reshetnikov 2002.

temperate regions). The areas of occurrence of this evolutionary young group of fish were formed due to the succession of warm and cold (glacial) periods as well as to floods and droughts occurring over vast territories. During periods of dramatic climatic changes many of the largest lakes became refugia, *i.e.* species and stock preservation sites.

New forms of fish have been formed due to interactions between different species co-inhabiting the same refugium (Reshetnikov 1980, 1983; Sychevskaya 1988). Environmental conditions prevailing in the particular refugium have shaped the morphology, physiology and behaviour of the fish. Immense morphological variability and peculiar ecological characteristics mark indistinct boundaries between coregonid species (Berg 1948) and result in their complex intraspecific structure (Chereshnev et al. 2002; Lindsey 1981).

Among the coregonids of Siberia, whitefish (*Coregonus lavaretus*), least cisco (*C. sardinella*) and omul (*C. autumnalis*) (Figure 1) (Figure 2 and 3) are those whose phylogeny, evolution and taxonomy still remain controversial. In the system of Reshetnikov (1980), *C. lavaretus* (Linnaeus 1758) encompasses different forms with gill-raker numbers ranging from 15 to 64, and with the mouth opening ranging from sub terminal to terminal. There are migratory, riverine, riverine-lacustrine and lacustrine forms. In large water bodies they are further divided into coastal, deep-water and pelagic forms. In general, coregonid forms are described as the fish with low gill-raker counts (15-30 gill rakers), medium gill-raker counts (30-40) and high gill-rakered (more than 40 gill-rakers) (Reshetnikov 2002).

In accordance with criteria defining subspecies (precisely determined area of occurrence, ecological and morphological specificity), *C. lavaretus* complex of Siberia is composed of two subspecies: Siberian whitefish or pidschian, *C. l. pidschian* (Gmelin), including autumn spawning medium gill-rakered and low gill-rakered forms, and spring spawning medium-rakered Baunt whitefish (*C. l. baunti* Muchomedijarov 1948) (Anpilova 1967a, b; Reshetnikov 1980, 1998, 2002). Each large water body supports a unique population of Siberian whitefish (Reshetnikov 1980), and the riverine, riverine-lacustrine and lacustrine forms represent its ecotypes (Skryabin 1969, 1979).

According to Bogutskaya and Naseka (2004) numerous intraspecific coregonid forms are described as species, and this concerns also Baikal omul (*C. migratorius*) and lacustrine whitefish of Lake Baikal (*C. baicalensis*), Teletsk whitefish (*C. smitti*), Siberian whitefish (*C. pidschian*) and Baunt witefish (*C. baunti*). On the other hand Bogutskaya and Naseka (2004) do not report the occurrence of spring-spawning least cisco (*C. sardinella*) of Baunt Lake.

Siberian coregonids presently inhabiting large lakes are often descendants of populations which have originated from locations very distant to the contemporary ones. This accelerated ecological-morphological transformations of coregonid populations and their further divergence into the new local forms. Because of that, different forms of coregonids often occur sympatrically or parapatrically, showing various degrees of reproductive isolation between them. In Lake Baikal there is a persistent hybridisation between Baikal omul and Siberian whitefish (Mamontov 1995, 2000; Skryabin 1969), whereas in Baunt Lake there is no hybridisation between Siberian whitefish and least cisco. In Teletskoye Lake hybridisation between low-rakered and medium-rakered whitefish does not happen (or it has already been accomplished) (Mamontov 2000; Skryabin 1969).

However, lakes are usually inhabited also by coregonid forms with the gill-raker counts typical for interspecific hybrids, sometimes including backcrosses (Mamontov 2000). It has been postulated that due to the hybridisation the hypothetic ancestral high-rakered whitefish has evolved into the relic form of the medium-rakered type (Gundrizer 1978; Ostroumov 1951; Reshetnikov 1980).

Baikal omul has been considered by different authors to be:

- a subspecies *C. autumnalis migratorius* Georgi, belonging to the species *C. autumnalis* (Berg 1948; Reshetnikov 1980, 1998, 2002);
- a subspecies *C. autumnalis autumnalis* (Berg 1948) of the Arctic cisco, or
- a separate species (*C. migratorius*) (Bogutskaya and Naseka 2004).

According to molecular phylogenetic studies (Politov et al. 2000, 2004; Sukhanova 2004; Sukhanova et al. 2002, 2004, 2005), the Baikal omul would constitute a pelagic form of the lacustrine whitefish of Lake Baikal (*C. lavaretus baicalensis* Dybowski). It has been hypothesized that omul inhabiting Kulinda Lake is a relic of the Baikal omul (Sukhanova 2004). Kulinda Lake lost its connection with Lake Baikal during the last glacial period, some 11,300 – 9,500 years ago (Sukhanova et al. 2005). According to the molecular studies, the Baikal omul differs considerably from the Arctic omul (Politov et al. 2002, 2004; Sukhanova 2004; Sukhanova et al. 2002, 2004). Allozyme and mitochondrial DNA studies suggest that the Baikal omul is related to the form ancestral to the Arctic omul complex (Politov et al. 2002, 2004).

Least cisco (*Coregonus sardinella* Valenciennes) also encompasses lacustrine and riverine as well as residential and migratory forms. It has been hypothesized that the uniform fauna of Siberian ciscoes had been divided into several groupings, isolated from each other in different locations during the Pleistocene glaciation. The vast range of the least cisco occurrence was due to the river connections between lakes extending towards north-east Asia and, to a lesser extent, towards the west across the Ural Mountains (Pirozhnikov et al. 1975; Politov et al. 2000; Sendek 2000, 2002; Shaposhnikova 1976). The least cisco has not formed any subspecies, although there is substantial intraspecific differentiation (Reshetnikov 1980, 2002). Genetic studies revealed similarities between west-Siberian and east-Siberian forms of *C. sardinella* (Politov et al. 2000; Sendek 2000, 2002). The migratory forms of *C. sardinella* show morphological traits of the Siberian cisco, whereas the lacustrine resident forms are of the European vendace (*Coregonus albula*) type (Romanov 2000). Morphologically, local groups of least ciscoes are very similar to each other (Maksimov et al. 1995). The only exception is the spring-spawning least cisco in Baunt Lake, which is the tiniest form of this species (Anpilova 1956). Values of numerous traits make it more closely related to the European vendace (Skryabin 1977), however, the taxonomic status of the least cisco of Baunt Lake has not been determined yet (Reshetnikov 1980). Due to that it may be considered:

- a population of the least cisco (Skryabin 1977), or
- a separate species (Baunt least cisco (*C. baunti* sp. *nova*) (Karasev 1987), or
- its taxonomic status should not be discussed at all (Bogutskaya and Naseka 2004; Reshetnikov 2002), which would demand ignoring its spring-spawning behaviour as well as its morphological (Skryabin 1977) and genetic (Yakhnenko and Mamontov 2002) characteristics.

Summarising the above, answering the key questions of coregonid taxonomy will require more studies on their origin, distribution, phylogeny and relationships between the variety of species and populations (such as sympatry, isolation, migrations, etc.). Also, the evolutionary history of coregonid fishes should be studied in connection with the history of water bodies which they inhabit.

GEOLOGICAL HISTORY AND FORMATION OF SIBERIAN WATER BODIES

The origin of Baikal rift lakes, as well as their fauna and flora, is related to the history of the development of the Baikal rift depression (Bazarov 1986; Florensov 1968; Florensov et al. 1982; Karabanov 1999; Logachov et al. 1974; Lut 1978; Mats 1993; Mats et al. 2001; Popova 1981; Popova et al. 1989). Stages of the development of the Baikal rift depression and of the Baikal basin have been described by Mats et al. (2001):

1. archaic Baikal basins of the criptorift stage in a contour of the Baikal basin (70-27 million years before present (mybp)),
2. northern and southern pre-Baikal, large deep lakes in the southern and northern basins during the early rift stage (27-10? mybp),
3. pre-Baikal, large deep (several hundred meters) lakes in southern-middle Baikal and north-Baikal basins, connected by water overflow in an area of the future (underwater) Akademicheskij ridge (10.0-3.5 mybp),
4. palaeo-Baikal, a large deep lake (depths down to 1,000m in a southern basin), composed of three basins: southern, middle and northern, possessing water outflow to the Lena River (3.5-1.0 (0.5?) mybp),
5. contemporary Lake Baikal, a large, ultra deep lake (depths down to 1,000-1,300m) with the water outflow to Yenisei River (0.5? mybp).

The rift (3rd) stage of the development of the zone began with the uplifting of the whole Baikal structure and with a lowering of valleys, in the Middle Pliocene (2.8-2.5 mybp). Those were accompanied by a cooling climate and continued until the beginning of Quaternary (1.9-1.5 mybp) when glaciers developed (Florensov 1968; Logachov et al. 1974). By the end of the early Pleistocene (1.2 mybp) the group of young basins had been formed. Tectonic activity during the second half of the Pleistocene ended with the basic formation of the deep Lake Baikal and other lakes of the rift.

In the Pleistocene, not less than 30 periods of climatic cooling and warming occurred at and around Lake Baikal. This knowledge is based on the examination of Lake Baikal sediments, which showed changes of the content of biogenic silica and diatom algae (Grachev et al. 1998; Karabanov 1999). During the last 900,000 years there were nine glacial periods, when the climate became dry and the level of lake waters lowered. The most recent period of climatic cooling happened 11,000-9,500 years before present (ybp) (Karabanov 1999).

A contemporary network of Siberian lakes and rivers was established close to the end of the Pleistocene (some 450,000 ybp). In the system of the Vitim River, huge water-ice aggregations were formed beneath the surface of the flowing waters. Lakes Tsipikan, Baunt and Busani, Eravninskoye and others, have been formed due to thawing of glaciers and immersion of separate parts of the Baunt valley (Endrikhinskij 1982). During the Holocene (about 100,000 ybp) the area of these lakes has been reduced.

Palaeo-lakes like Nichatki, Bolshoe Leprindo, Maloe Leprindo and others were located in large intermountain Muya and Charskaya valleys of the region Olekmo-Vitim Upland (Figure 3). The surface topography of this region was related to the uplifting of the Baikal arch. Tectonic movements during the Upper Quaternary caused a reduction of the middle Quaternary lake, which bordered with Leprindo Lake, as well as the reorganisation of the network of lakes and rivers and drying of the palaeo-lakes basins. During this time another climatic cooling occurred (Muzis 1968).

The above description of the geological events does not allow precise explanations of the ways that some organisms entered Lake Baikal. Phylogenetic studies on relationships between the seals of Lake Baikal (nerpa *Phoca sibirica*), and the seals of the Pacific Ocean (spotted seal *Phoca largha*) and of the Atlantic Ocean (harbor seal *Phoca vitulina*) based on genetic markers led to the conclusion that nerpa has populated Lake Baikal along the Lena River about 2-1 mybp (Malikov et al. 1997; Pastukhov 1993). Disconnection of Lake Baikal from the Lena River and opening of the water discharge from Lake Baikal to Yenisei River through Irkut River (0.8-0.5 mybp), development of the array of endemic cottid fishes (Cottidae) (2.5-1.8 mybp) (Kirilchik et al. 1995) and of other groups of animals (more than 3-5 mybp) (Ogarkov et al. 1997) are not consistent with the absence of Lake Baikal endemics in the basin of Lena River, but they are consistent with the wide distribution of the above taxons in the system of Yenisei River, Tajmyr Lake and Gydanskaya Gulf of the Karskoye Sea (between the mouths of the Ob River and the Yenisei River (Kozhov 1962). Therefore, the history of the immigration of coregonids into Lake Baikal remains unclear.

CHARACTERISTICS OF SIBERIAN WATERS AND THEIR COREGONIDS

Lake Baikal

Lake Baikal is located almost in the centre of Asia. Its volume, the largest in the world, is 23,015km^3 and it is 636km long and 20-80km wide. The basin of the lake is composed of three parts: southern (maximum depth 1,446m, mean depth 843m), middle (1,642m, 854m) and northern (903m, 576m), which are separated by bottom elevations rising to the depths of 200-300m. The territory around the lake is taiga with severe continental climate, which is a little milder in the vicinity of Lake Baikal shores.

The lake has never been directly connected to the sea, although its waters have always flowed to the Arctic Ocean, at first through the Lena River, and later on (after geological changes) through the Yenisei River. Isolation of a great and extremely deep lake combined with climatic changes resulted in a development of an array of new species. Great depths provided conditions for development of new fish and invertebrate species. As a result, among over 1,500 animal species occurring in Lake Baikal, some 75% are endemics (Galazij 1993; Timoshkin 1995). There are also immigrants from the sea: the seal "nerpa" (*Phoca sibirica*), Baikal omul (*Coregonus autumnalis migratorius*) (Kozhov 1962) and a number of other fish species inhabiting northern oligotrophic mountain lakes: "golec davatchan" (*Salvelinus alpinus erythrinus* Georgi) (Berg 1948) and a recently identified form of grayling "kharius" (*Thymallus arcticus baicalensis* subsp. nov., Salmoniformes, Thymallidae) (Matveev et al. 2005). The timing and routes of their immigration into the Lake Baikal system remain debatable.

Coregonids inhabiting Lake Baikal are autmn-spawning and encompass high-rakered Baikal omul (*C. autumnalis migratorius* Georgi), medium-rakered lacustrine whitefish (*C. lavaretus baicalensis* Dybowski) and riverine-lacustrine Siberian whitefish (*C. lavaretus pidschian* Gmelin).

Differences between lacustrine whitefish (*C. l. baicalensis*) and riverine-lacustrine Siberian whitefish (*C. l. pidschian*) of Lake Baikal include numerous morphological and behavioural features, such as the number of gill-rakers as well as time and site of spawning. Probably spawning behaviour enables reproductive isolation between the two whitefish subspecies. Each subspecies is composed of a number of populations (Mamontov 1988; Mamontov and Yakhnenko 1995; Skryabin 1969). Overlapping spawning ecology enables hybridisation between the Baikal omul (*C. autumnalis migratorius*) and the Siberian whitefish (*C. lavaretus pidschian*) (Mamontov 1988; Skryabin 1969). But in general, Siberian whitefish of Lake Baikal (*C. l. pidschian*) is a reproductively riverine subspecies, whereas the lacustrine whitefish of Lake Baikal (*C. l. baicalensis*) is a reproductively lacustrine subspecies.

The lacustrine whitefish of Lake Baikal (*C. l. baicalensis*) (Krogius 1933) has synonymous names: *C. l. lavaretus* (Skryabin 1969) and *C. l. pidschian baicalensis* (Dybowski) (Karasev 1987). Bogutskaya and Naseka (2004) consider this fish a separate species *Coregonus baicalensis* Dybowski. It is composed of five populations (1-Chivyrkuiskij autumn; 2-Chivyrkuiskij winter; 3-Maloye More autumn; 4-Maloye More winter; 5-Selenga) differing in site and time of spawning, number of gill-rakers (Krogius 1933; Mamontov 2000; Skryabin 1969) and genetic characteristics (Yakhnenko et al. 1992). However, this species has not been listed by Reshetnikov (1998).

Omul (*C. autumnalis migratorius*) is a riverine-lacustrine form of pelagic whitefish (Misharin 1958) which encompasses three eco-morphological groups: benthic-deepwater, coastal-pelagic, and pelagic (Smirnov and Shumilov 1974). Each group is represented by several populations which spawn in different rivers and show morphological peculiarities developed in response to the respective ecological conditions. Within the given water body the three groups almost do not interbreed (Smirnov 1992; Smirnov and Shumilov 1974; Smirnov et al. 2005). Populations inhabiting large rivers are composed of numerous subpopulations. In Lake Baikal the omul inhabits waters down to 350-400m depths (Mamontov et al. 2004).

Baunt whitefish

Whitefish inhabiting lakes of the system Tsipo-Tsipikan Lakes (Figure 3) constitute the group of "Baunt whitefish".

Tsipo-Tsipikan (Baunt) lakes are located in the north-eastern part of Trans-Baikal in the system of Tsipa River (54-55° northern latitude and 112-113° eastern longitude) at altitudes higher than 1,100m. In the past, Lake Baikal has been connected to the basin of Lena River and to the system of Baunt lakes through a complex of hollows and valleys (like: Barguzinskaya, Muyskaya and Charskaya) (Endrykhinskij 1982; Kozhov 1962; Logachev et al. 1974; Skryabin 1977). The Baunt lakes are interconnected by a system of rivers and they are also joined with the Vitim and Lena rivers.

Baunt Lake is the largest one in this complex. There is no high-rakered whitefish, but there is a spring-spawning lacustrine least cisco (*C. sardinella*) (Anpilova 1956) and spring-spawning lacustrine Siberian whitefish (*C. lavaretus pidschian*) (Skryabin 1977). Baunt least cisco differs morphologically from lacustrine and riverine forms of least cisco (Skryabin 1977).

The Baunt Siberian whitefish differs from the Siberian whitefish of other Siberian lakes by its spring-spawning, high number of gill-rakers (mean 23.2) and by other morphological characteristics. All these features prove its considerable isolation from other Siberian whitefish (Skryabin 1977). In 1987, Karasev postulated that the Baunt Siberian whitefish should constitute a new species, *Coregonus skrjabini* sp. nova.

The least cisco of Baunt Lake is geographically distant (about 1,000km) to the sites of occurrence of the least cisco inhabiting the Lena River. According to Reshetnikov (1998) Baunt least cisco is a population belonging to *C. sardinella* species. However, the Baunt least cisco differs morphologically and ecologically from *C. sardinella*, whereas it is similar to the European vendace (*Coregonus albula*) (Skryabin 1977). Karasev (1987) describes the Baunt least cisco as a new species

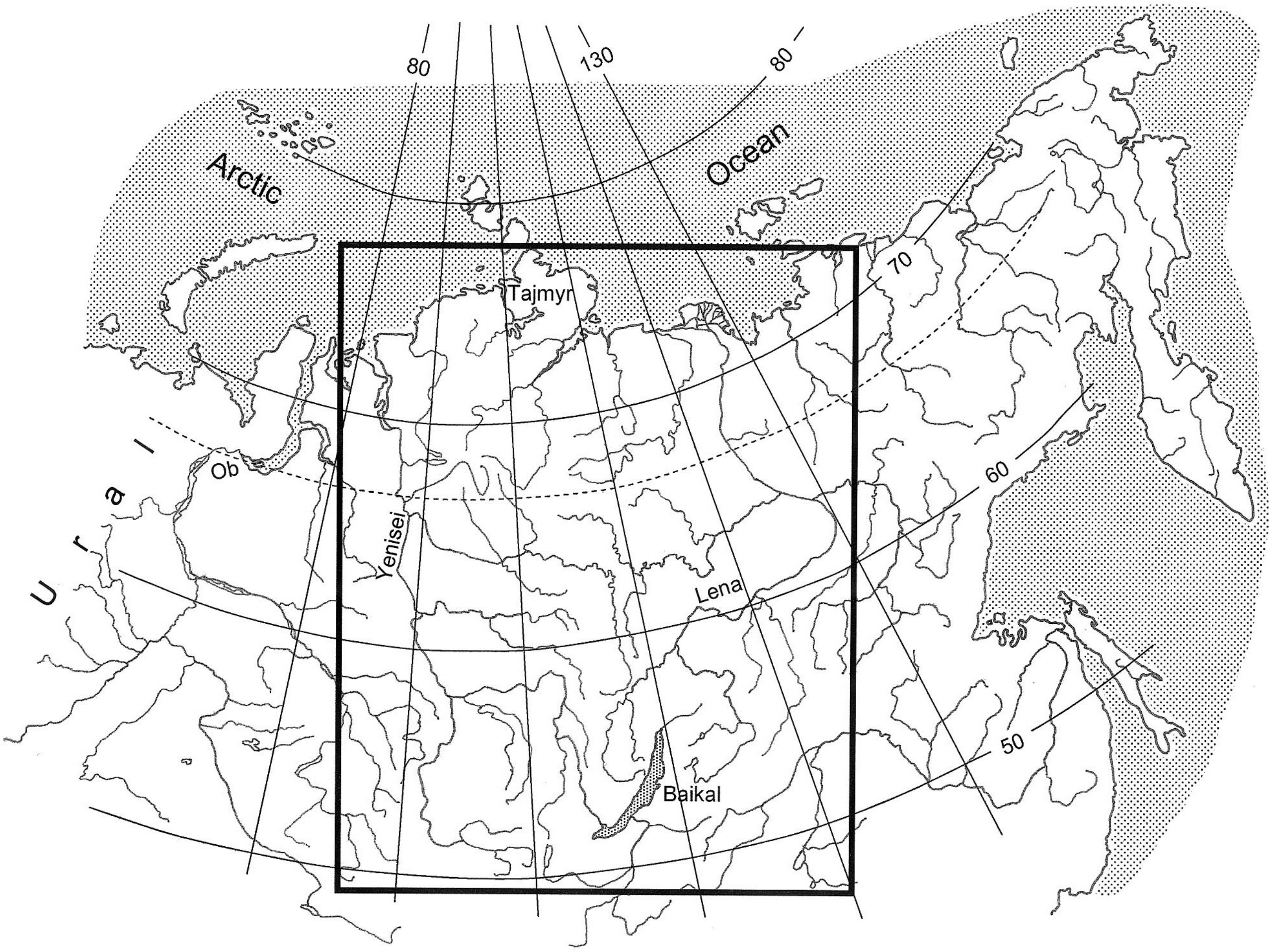
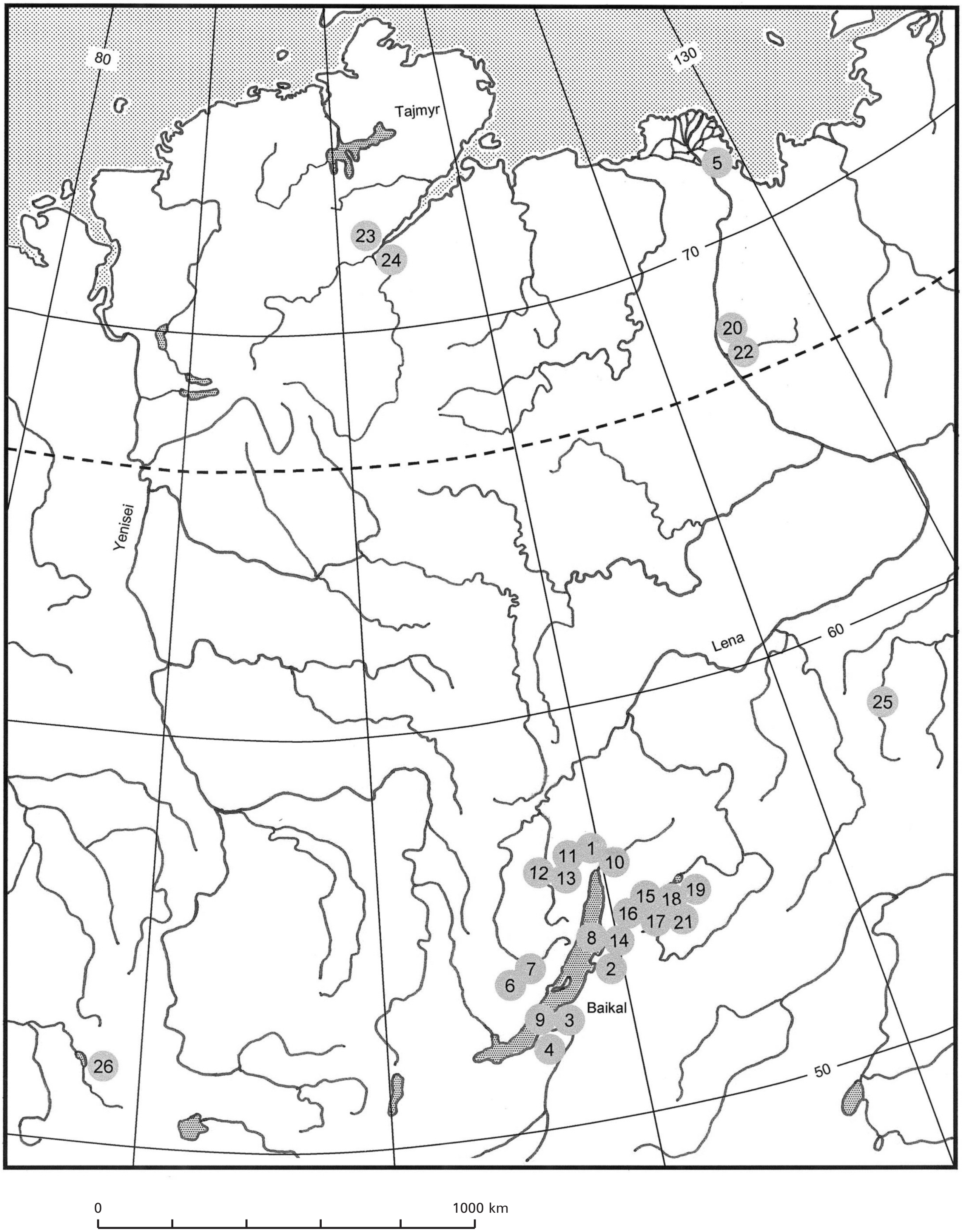


Figure 2. General map of Siberia with area of studies stretching between Yenisei River and Lena River.

Figure 3. Area of studies with fish sampling sites:

1 – omul (*Coregonus autumnalis migratorius* Georgi) (*C. a. m.*) – Churo River,
2 – omul (*C. a. m.*) – Barguzin River,
3 – omul (*C. a. m.*) – Selenga River,
4 – omul (*C. a. m.*) – Bolshaya River,
5 – Arctic cisco (*Coregonus autumnalis* Pallas) (*C. a.*) – Arctic part of Lena River,
6 – lacustrine whitefish of Lake Baikal (*Coregonus lavaretus baicalensis* Dybowski) (C. l. b.) – Maloye More [MM1],
7 – lacustrine whitefish of Lake Baikal (*C. l. b.*) – Maloye More [MM2],
8 – lacustrine whitefish of Lake Baikal (*C. l. b.*) – Chivyrkujskij Bay,
9 – lacustrine whitefish of Lake Baikal (*C. l. b.*) – Selenga Shoal,
10 – Siberian whitefish (*Coregonus lavaretus pidschian* Pallas) (*C. l. p.*) – Churo River,
11 – Siberian whitefish (*C. l. p.*) – North-Baikal Shoal,
12 – hybrid F_1 [*C. a. m.* X *C. l. p.*] – North-Baikal Shoal,
13 – backcross BC_1 {F_1 [*C. a. m.* X *C. l. p.]* X *C. l. p.*} – North-Baikal Shoal,
14 – Siberian whitefish (*C. l. p.*) – Barguzin River,
15 – Baunt whitefish (*Coregonus lavaretus baunti* Muchomedijarov) – Maloye Kapylyushi Lake,
16 – Siberian whitefish (*C. l. p.*) – Bolshoye Kapylyushi Lake,
17 – Siberian whitefish (*C. l. p.*) – Maloye Kapylyushi Lake,
18 – Siberian whitefish (*C. l. p.*) – Baunt Lake,
19 – Siberian whitefish (*C. l. p.*) – Busani Lake,
20 – Siberian whitefish (*C. l. p.*) – Lena River,
21 – Least cisco (*Coregonus sardinella* Valenciennes) (*C. s.*) – Baunt Lake,
22 – Least cisco (*C. s.*) – Lena River,
23 – Siberian whitefish (*C. l. p.*) – Labaz Lake (Tajmyr Peninsula),
24 – Siberian whitefish (*C. l. p.*) – Khatanga River,
25 – Siberian whitefish (*C. l. p.*) – Leprindo Lake,
26 – Siberian whitefish (*C. l. p.*) and Pravdin whitefish (*C. l. pravdinellus* Dulkeit) – Teletskoye Lake.


80
130
Tajmyr
70
60
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Yenisei
Lena
Baikal
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Coregonus baunti sp. nova. Electrophoretic analysis of enzymes proved that the differences between the Lake Baunt and the Lena River least cisco are of the subspecific magnitute (Yakhnenko and Mamontov 2002).

Kapylyushi Lakes

Lakes Bolshoye Kapylyushi and Maloye Kapylyushi are located on the left side of Tsipikan River (Figure 3), and they are connected to the river through a channel. The lakes are inhabited by the high-rakered spring-spawning Baunt whitefish (*C. lavaretus baunti*) and sparsely-rakered autumn-spawning Siberian whitefish (*C. lavaretus pidschian*). These two whitefish clearly differ from each other ecologically and morphologically (Skryabin 1977). The subspecific status of *C. lavaretus baunti* is supported by the characteristics of its embryogenesis (Chernyaev and Pichugin 1999).

Dorong Lake

Lake Dorong is inhabited by high-rakered lacustrine spring-spawning Baunt whitefish (*C. lavaretus baunti*) and low-rakered riverine-lacustrine Siberian whitefish (*C. l. pidschian*). Riverine-lacustrine Siberian whitefish spawn in Toch River and then they migrate to their feeding areas in Dorong Lake (Skryabin 1977).

Khatanga River system

The Khatanga River flows into the Arctic Ocean (Figure 3). The river is 227 km long and the area of its basin is about 364,000km^2. There are 112,000 of lakes (Lukyanchikov 1967) whose total area is about 11,600km^2. Among those Labaz Lake is the largest one (Lukyanchikov 1962). Coregonids of the Khatanga River are represented by the Siberian whitefish (*C. l. pidschian*), which encompasses three ecotypes: riverine, riverine-lacustrine and lacustrine. There is also one isolated population of least cisco (*C. sardinella*) and one of omul (*C. autumnalis*) (Lukyanchikov 1967).

Labaz Lake is located to the north-west of Kheta River (Figure 3). Small rivers connect Labaz Lake to a large number of lakes. There is also an outflow from Labaz Lake to Sibircha River, which flows to Kheta-Khatanga River. The climate of the area is polar-continental with a mean annual temperature of -14.4 °C. Food resources for fish are poor and due to that the fish grow slowly and mature late in their life. Labaz Lake is inhabited by a common bottom feeding Siberian whitefish (*C. l. pidschian*). The riverine-lacustrine form of this fish has 18 (15-24) gill-rakers and 81 (73-89) scales along the lateral line (Lukyanchikov 1967). The growth of this fish is slower than that of whitefish in other Siberian rivers. The lacustrine form has 19 (18-23) gill-rakers and 84 (74-92) scales in the lateral line and grows faster. The Siberian whitefish (*C. l. pidschian*) of Labaz Lake differs genetically from the Siberian whitefish of other Siberian lakes.

Teletskoe Lake

Teletskoe Lake is located between 51°21'46" and 51°48'36"N latitude in the north-eastern part of the Upper Altaj Mountains (Figure 3). The lake has been created by tectonic and glacial processes some 150,000 ybp after the most severe glaciation of Altaj (Egorov 1981; Shmidt 1964). Age of the lake has been determined as about 250,000-80,000 years on the basis of the bottom sediments thickness (450-500m) (Luzgin and Baryshnikov 2000). The lake has more than 70 inflows of different sizes. It is a deep oligotrophic lake located in high mountains.

The commonest coregonid of this lake is low-rakered bottom-feeding Teletsk whitefish (*C. l. pidschian* nation *smitti* Warpachowski). Among all pidschian-like whitefish, this form has the highest number (mean 27.3) of gill-rakers (Bochkarev 2000; Egorov 1981). There are also riverine-lacustrine forms of this Siberian whitefish.

Pravdin whitefish (*C. lavaretus pravdinellus* Dulkeit) is the smallest among the coregonids, being an endemic planktivore with a medium gill-raker count (mean 34.12) (Bochkarev 2000; Egorov 1981; Gundrizer 1962). There are lacustrine and riverine-lacustrine forms of the Pravdin whitefish. With regard to the number of gill-rakers, the Pravdin whitefish is similar to the whitefish of Dorong Lake and Oron Lake.

Leprindo Lakes

Lakes Bolshoye Leprindo and Maloye Leprindo (as well as Leprindokan Lake and Davatchan Lake) constitute a part of the basin of the Vitim River (Figure 3). They have been created by tectonic and glacial processes. In general, lakes Bolshoye Leprindo and Maloye Leprindo are separated by the mountains, by they are connected via a channel. Bolshoye Leprindo Lake is connected to Vitim River via the Chara River. Both lakes are oligotrophic with quantitatively and qualitatively poor fauna.

Before the construction of the Baikal-Amur railway (in 1970's), the coregonids of Leprindo Lakes were represented by lacustrine, riverine-lacustrine and riverine forms of Siberian whitefish *C. l. pidschian* nation *brachymystax* Smitt. Biological and parasitological data support the existence of a local lacustrine form of Siberian whitefish in Bolshoye Leprindo Lake (Pronin 1977). Cluster analysis based on morphological data showed probable similarity between Siberian whitefishes of Chara River, of Kirenga River and Oron Lake (Knizhin et al. 2001).

CONCLUDING REMARKS

We have analysed electrophoretically some 13 enzyme systems from over 20 samples of coregonids from Lake Baikal, from the System of Tsipo-Tsipikan Lakes, from Labaz Lake (Tajmyr Peninsula), Bolshoye and Maloye Leprindo Lakes, from the Lena River and from the Khatanga River (Figure 3). In each case the geographical location of waters, their geological age and conditions of their formation were different, and we have found that this was reflected in the taxonomical structure of coregonid fishes inhabiting these waters. This paper is intended as an introduction to a number of primary papers that are planned that will describe the genetic taxonomy of Siberian coregonid fishes.

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