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To cite this article: O T Rusinek and I V Fefelov 2019 *IOP Conf. Ser.: Earth Environ. Sci.* **274** 012129

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The role of natural processes in the formation of the fauna of water and ground organisms of Baikal Lake

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Abstract. The relationship between the paleogeographic events of the Neogene and the Quaternary period on Lake Baikal with the formation of the faunistic complexes of fish, birds, and their parasites is analyzed in the article. The composition of fish parasites confirms that the representatives of endemic Baikal *Cottoidei* passed the most prolonged isolation in Baikal, and the fish of the boreal lowland complex settled the lake relatively recently and may have penetrated here repeatedly. The current composition of aquatic birds indicates the tense conditions of their habitat in the Baikal region in the Quaternary and the significant variability of their fauna in the Pleistocene climatic cycles due to the periodic colonization of Baikal by birds.

1. Introduction

In recent years, numerous new data have appeared on geological, climatic, and paleogeographic events that took place on Baikal and in the Baikal region over long historical periods, as well as on the evolution of the flora and fauna of Baikal. The authors of this article considered it very interesting to compare these events with the history of the formation of the fauna of fish, birds, and their parasites. Since there are close connections between these groups of animals, it was very important to assess when and under what conditions they could form and which of the natural processes can be attributed to.

Therefore, we set the following goal: to evaluate the nature of the influence of natural processes on the formation of modern faunas of fish, birds and their parasites. To achieve it, the following tasks were defined:

1. To provide an overview of literature data on geological and climatic events in the Baikal region;
2. To characterize the fauna of fish and their parasites and present the history of their formation;
3. To characterize the fauna of birds and their parasites and present the history of their formation;
4. To evaluate the structure of the parasitic systems of Lake Baikal.



2. Materials and Methods

Own materials of parasitological studies of fish of Lake Baikal, collected during the years of 1984-2015. Based on the work, 47 species and subspecies of Baikal fish were surveyed, which accounts for 4/5 of the entire ichthyofauna of the lake. The results were also used by the second author's own observations on the distribution, biology, and ecology of birds in the Selenga River delta and in Southern Baikal, which were conducted in 1984-2015.

3. Results and Discussion

3.1. Geological and climatic events

According to the literary data on geological [40; 38; 12; 1; 52; 50; 34; 48; 25; 9; 29; 41; etc.] and climatic events [51; 52; 48; 37; 5; 6; 28; 2; 75; 69; 8; 13; 47; 3; 4; 82; 79, etc.] in the Baikal region during the Paleocene-Holocene, the main of them are as follows.

Geological events:

- Paleocene (60 million years ago): the beginning of the formation of the rift system;
- Late Oligocene (25 million years ago): the beginning of the formation of the Southern and Middle Baikal basins;
- The second half of Miocene (10 million years ago): the formation of the Northern basin and the formation of Baikal as a single reservoir;
- Late Pliocene (2-1.5 million years ago): the formation of the Pra-Manzursky Baikal flow to Lena;
- Early Pleistocene (700-400 thousand years ago): closing of the Pra-Manzursky flow;
- Middle Pleistocene: Baikal water flow through the Kultucho-Ilchinskaya valley in the Irkut river, the connection of Baikal with the Yenisei;
- The second half of Late Pleistocene: the closure of the flow through Irkut, the formation of the Listvennichnyy Bay and the opening of the Angarsk flow (18-14 thousand years ago).

Climate events:

- The end of Cretaceous-Paleogene: the climate is close to humid tropical and subtropical;
- Oligocene-Miocene: the climate is warm;
- Middle Miocene: gradual decrease in temperature and degree of moisture;
- Late Miocene-Pliocene is characterized by multiple alternations of arid and humid phases with a general increase in aridization;
- Middle-Late Pleistocene was accompanied by climatic changes that led to the periodic development of mountain-valley glaciers and to interglacial conditions; the last glaciation on the territory of Eastern Siberia was 22(23)-14 thousand years ago;
- Late Pleistocene-Holocene is characterized by periods of warming (interglacial) and cold snaps of varying degrees.

3.2. General and zoogeographic characteristics of the fish parasites of Lake Baikal

The parasite fauna of 47 species and subspecies of fish of Lake Baikal is represented by 255 species and subspecies belonging to 13 types: Kinetoplastida, Polymastigota, Sporozoa, Microspora, Cnidosporidia, Ciliophora, Cnidaria, Plathelminthes, Nematelminthes, Acanthocephales, Annelida, Mollusca, Arthropoda, and 18 invertebrate classes: Kinetoplastidea – 16, Diplomonadea – 2, Coccidea – 5, Microsporea – 3, Myxosporidia – 45, Cyrtostomata – 1, Hymenostomata – 28, Hydrozoa – 1, Monogenea – 53, Amphilinida – 1, Cestoda – 26, Trematoda – 29, Aspidogastrea – 1, Nematoda – 13, Acanthocephala – 7, Hirudinea – 4, Bivalvia – 2, Crustacea – 15. In addition, *Saprolegnia* mushrooms are noted. Aboriginal parasitic fauna consists of 241 species and subspecies. The parasitic fauna of

invading fish, which appeared in Baikal as a result of artificial introduction over the past 70 years, has 47 species and subspecies; 14 of them belong to the fauna that is not characteristic of Baikal and is specific to these species of fish. Due to the introduction of new fish species, the fish parasites of Lake Baikal expanded the range of their intermediate and final hosts, changing the original structure of the parasitic systems. At the same time, the transition of parasites from introduced fish to the aboriginal ichthyofauna was not observed. Among the parasites of Baikal fish, organisms developing without intermediate hosts (63%) dominate: protozoans, monogenes, leeches, and crustaceans.

As a result of a zoogeographic analysis conducted in accordance with modern requirements [55; 56], it was established that out of a total of 255 species and subspecies of Baikal fish parasites, 198 taxons, or 77.6% of the entire parasite fauna, are distributed into the faunal complexes (Fig. 1). The remaining species were included in the group with an uncertain position due to the lack of data on their biology. Endemics: 38 species, or 14.9% of the entire fauna. The rank of endemism corresponds to the species and subspecies levels.

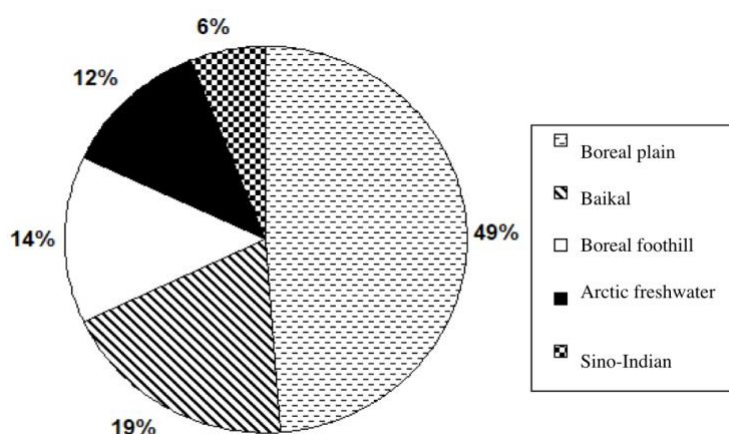


Fig. 1. The ratio of the faunistic complexes of fish parasites in Lake Baikal.

The boreal lowland parasite complex is represented by 97 species. The dominant position in it is occupied by the simplest 50 species; hydroids – 1 species, monogeneans – 16, cestodes – 11, trematodes – 5, nematodes – 6, scrubs – 1, leeches – 2, crustaceans – 5 species. The greatest morphological diversity is characterized by the monogenic fauna, dominated in it by representatives of the order Dactylogyridea – parasites of carp, perch, pike, and sturgeon fish.

The Baikal faunistic complex unites 38 endemic species and subspecies of parasites, among which protozoans make up 25, monogenes – 4, nematodes – 2, scratchers – 1, leeches – 3, crustaceans v 3. These are mainly fish parasites of the suborder Cottoidei, with the exception of 2 species of nematodes and scraping, which are noted in many Baikal fish.

The boreal foothill faunistic complex consists of 27 species and subspecies of parasites: the simplest – 2, monogenes – 22, cestodes – 1, nematodes – 1, crustaceans – 3. These are mainly parasites of lenka *Brachymystax lenok*, taimen *Hucho taimen*, grayling *Thymallus arcticus*, and minnow *Phoxinus phoxinus*, narrowly specific to hosts.

The Arctic freshwater faunistic complex unites 24 types of parasites, among which are the simplest – 5, the monogeneans – 1, the cestode – 7, the trematode – 3, the scratchers – 4, and the crustaceans – 4. All of them are the parasites of the whitefish *Coregonidae* and burbot *Lota lota*. The Sino-Indian faunistic complex consists of 12 species, among which 9 are monogenes, 1 – aspidogastrea, and 2 – types of cestode.

All current assumptions about the origin of Baikal fish belong either to individual species (sturgeon *Acipenser baeri baicalensis*, burbot, grayling, omul *Coregonus autumnalis migratorius*), or to the group

of catastrophe fish *Cottoidei* [36; 19; 20; 32; 62; 66; 60; 61; 80, etc.]. The ichthyofauna as a whole, formed in the process of a certain historical time, was not considered.

The correspondence of the faunistic complexes (FC) of parasites to the faunistic complexes of fish in Baikal allowed us to form a synthetic hypothesis of the origin of the modern Baikal ichthyofauna [59], according to which not individual species of fish were settled in the lake but rather faunal complexes.

It is known that in the evolution process of the Earth's surface and climate, not only individual species were settled, belonging to different systematic groups, but the entire fauna was formed in similar ecological conditions of certain physiographic zones. Different systematic groups evolved and settled together. At the same time, it is known that closely related species with different ecological needs can develop and evolve as a part of different faunal complexes [74; 46; 14; 64; 16; 55; 56; 57; 22; 76; 77, etc.]. Correspondence of FC to the fish parasites of FC suggests that the appearance in Baikal should correspond to the time of their formation and penetration possibilities.

In the Oligocene-Miocene period, in reservoirs where modern Baikal is located, a thermophilic fauna existed, represented by the fish of the boreal plain FC. In the Pliocene, due to climate change, in the waters of Eurasia, the warm-water fauna of fish was replaced by cold-water ones. Presumably, in the Pliocene-Pleistocene period, the infestation took place in Baikal of the ancestors of modern rogue-fish (cold-water marine origin) as part of the boreal foothill FC. Perhaps this happened through the Pra-Manzurka river, which was connected to the Lena river, which, like now, flowed into the Arctic Ocean, as well as through other watercourses, including the eastern ones, which could well be the paths of penetration of these fish into Baikal. *Cottoidei* in Baikal were able to realize their sea potential and, having successfully evolved in accordance with the ecological features of the lake, formed endemic families, genera and species [65; 60; 61]. The existence of endemic taxa in fish of the boreal foothill FC (Siberian grayling, with its endemic forms or subspecies) and the arctic freshwater FC (Baikal omul and whitefish) may indicate that these fish inhabited Baikal earlier than representatives of the modern boreal plain FC, among which there are no endemic taxa. Fish of the boreal foothill FK could easily penetrate Baikal in the Pleistocene period, when migrations to the mouths of Baikal tributaries and Baikal itself for feeding were possible for them. Note that in the fish of this FC, there are actually no endemic parasites. The settlement of Baikal with fish from the freshwater FC of the Arctic could have happened at the end of the Pleistocene-Holocene period, i.e. along the Yenisei river through the Angara river. The formation of the oligotrophic ecosystem of Baikal by this time contributed to the successful development of the reservoir by omul-planktophagus. Fishes of boreal plain FC settled Baikal at the end of the Pleistocene-Holocene, when favorable conditions for their habitat were formed here due to climate warming.

Thus, the Baikal FC of fishes is the most ancient, being formed in Baikal as a result of prolonged isolation in the lake of roageous fishes. Data obtained by [30] indicate a relatively young age (2.5–2 million years ago) of the evolution of *Cottoidei* in Baikal, based on molecular biological studies.

According to the proposed hypothesis, the modern parasitic fauna of Baikal fish could have been formed as a result of the settlement of the lake by various FCs of host fish in accordance with the timing of their formation and the possibilities of penetration into Baikal. Among the parasites of Baikal fish, representatives of the boreal plain complex prevail, the owners of which are sturgeon, pike *Esox lucius*, cyprinid fish Cyprinidae, *Perca fluviatilis* perch, and *Gobitis melanoleuca* spined loach. In fish of this FC, only 3 endemic parasites are noted; these are the blood parasites of the *Leuciscus leuciscus* perch and dace (the main stages of their life cycle take place in leeches, from which these parasites could get to the fish), as well as *Sphaerospora rota* myxosporidia – its zoogeographic status needs to be clarified [72].

The depletion of the composition of specific parasites of fish of the boreal plain and arctic freshwater FC reflects that all of these fish (except for the goldfish *Carassius auratus gibelio*) are on the edge of their range. Endemic taxa of parasites are found mainly in endemic fish, such as roageous fish, Baikal omul and grayling, as well as in a water mammal, Baikal seal, or seal, *Phoca sibirica*.

The parasites of the *Cottoidei* sub-order fish, which develop with the participation of intermediate hosts, are represented by parasites of salmonid fish and burbot. Probably, parasites of salmon-shaped fish are still only developing rogameous fish as a specific group of hosts. Cestodes of the genus *Proteocephalus* do not develop in these fish and use them as reservoir hosts. Plerocercoids difillobotriid do not form a typical thick-walled capsule (cysts) like that formed in the body cavity of salmonid fish, which may indicate the recent inclusion of *Cottoidei* in the life cycle of these cestodes. *Comephoronema werestschagini*, which is most common in burbot and rogameous fish, probably came to Lake Baikal during the introduction of burbot and is unlikely to be endemic due to its findings in the Far East [22].

These facts suggest that the fish of the boreal plain complex began to colonize the coastal zone of Baikal, when ecological conditions favorable for their habitat were formed here (perhaps this happened many times). At the same time, fish lost some specific types of parasites characteristic of them in other water bodies (for example, in Western Siberia).

The following groups of endemics are distinguished among vertebrates in Baikal:

- Numerous species-specific rogameous fish with endemism at the level of families, genera, species and subspecies;
- Baikal subspecies omul (*Coregonus autumnalis migratorius*);
- 2 subspecies (or forms) of Baikal grayling (*Thymallus arcticus baicalensis* and *T. arcticus brevipinnis*);
- Baikal seal.

In these animals, endemic species and subspecies of parasites are mainly noted; Species rank of endemism is characteristic of the parasites of the fish of the suborder *Cottoidei* and omul, and for the parasites of whitefish and grayling, subspecies. These data, in our opinion, are evidence that it was the ancestors of the rogameous fish, omul, grayling, that were among the first in the Baikal settlement process, which made it possible to form an endemic parasite fauna. A variety of free ecological niches could contribute to this. The parasitic fauna of fish of the boreal plain and boreal foothill faunal complexes has undergone very minor changes (generally in the direction of depletion), which can be explained by the recent penetration of their owners into Baikal. Significant (compared with other groups of fish) endemism of parasites of rogameous fish (*Cottoidei*) suggests that their owners were isolated longer than others in Baikal and, from this point of view, are the most ancient inhabitants of the lake. The absence of endemic parasites with a complex life cycle in rogameous fish may indicate that in the process of catastrophic events and climate change on Baikal the fish fauna died or moved to more favorable conditions for them, like sponges, mollusks and diatom flora. Settlement Baikal lake of fish at the end of the Pleistocene - Holocene led to the formation of new coenotic links, in which parasites were also involved. Ro gameous fish, as a link in the food chains of deep-water Lake Baikal, have become reservoir, intermediate and definitive owners of the parasites of the boreal piedmont, boreal plain and arctic freshwater FC. Therefore, it can be stated that the endemic parasitic systems associated with the *Cottoidei* sub-order fish are the most ancient in Lake Baikal, formed here as a result of the prolonged isolation of their hosts.

3.3. The composition and origin of the bird fauna and bird assemblages in the Baikal region: General characteristics of the avifauna of the Baikal region

The principle of typification of the fauna of birds of Northern Eurasia by the origin of the species was proposed by [71]. The structure and ornithogeographic zoning of the Baikal region was examined by [10; 11], and the classification of the bird ranges in this territory according to geographical complexes in the light of the concept of Shtegman is by [17]. According to these works, it is obvious that the regional avifauna, with the prevalence of representatives of the Siberian faunistic complex (38%), is represented by genera and species of different origin: connections with Central, Minor, West, South-East, Northern Asia, Beringia and Africa are traced. It is considered generally accepted that the modern avifauna of the region was formed in the Quaternary. The origin of taxa of birds above the genus on a

large time scale (Neogene and previous geological epochs) speaks little about the history of individual genera and species in a particular region due to the flight ability of birds and the dynamism of their ranges.

The formation of the avifauna of the Baikal region was considered earlier and the main attention was paid to forest and mountain complexes of birds [42; 18]. Analysis of the fauna of birds of the Baikal region related to water has not yet been available. The fundamental work [35] is devoted to waterfowl. The moderate and high latitudes of Western Asia from the Volga to the Ob region are considered in it.

We believe that in order to understand the processes that contributed to the formation of the modern composition of birds, it is necessary to pay attention to the assessment of landscape-cenotic bonds of nesting birds.

363 species of birds are currently registered on Lake Baikal [54]. 237 species nests (65%). Note that 35 non-breeding species migrate regularly through Lake Baikal to the north of Western and Eastern Siberia. The remaining species are rare migrants and stray.

Dorzhiev and Elaev in their work [17], based on the ecological connections of the birds of the Baikal Siberia, divide them into 5 groups: forest, open spaces, alpine, water and near-water, synanthropic. In our version of the classification of birds of Lake Baikal, on the one hand, the association of species with natural areas and altitudinal zonality, and on the other hand, with respect to the aquatic environment, since almost all birds, regardless of their connection with a particular geographical area, are clearly separated on water and non-water.

The analysis showed that of the nesting birds, 58 species inhabit several natural zones, 4 - urbanophilous, 12 - mountainous (rock, mountain-tundra, sub-hollow). The remaining 163 have an area confined to a certain natural zone. They are represented by 3 groups: species typical of the taiga zone - 94 species; "forest-steppe" (including types of typical forest-steppe, deciduous forests and forest edges) - 49; birds of steppes and steppe territories - 20. Although representatives of the forest-steppe group come from different geographic zones, on Baikal they prefer biotopes with a similar landscape structure, which complicates the classification of the elements of this group.

Species that are directly related to the aquatic environment or nest in coastal and waterlogged stations in the region are 79 (33%), non-aquatic - 158.

The geographic regions in which the Quaternary avifauna were formed are clearly distinguished. In relation to Baikal, they are located in the north, east, west and south. The northern complex in the Baikal region is represented mainly by taxa of the holarctic taiga biome and individual species inhabiting the tundra and meadow stations. In the taxonomic composition of the eastern and western regions there are representatives of various biomes - both forest species and forest-steppe and meadow-steppe species; they are united by the need for a moderately humid climate with a low degree of continentality. Desert-steppe and mountain-steppe species are found in the Baikal region on the northern boundary of distribution; there are fewer of them than representatives of the previous groups. Regional division fits well with "biome".

A different composition of avifauna elements is inherent in the high-altitude zones. Many mountain species have a fragmented transpalearctic range. The links of the Baikal alpine forms with relatives from Central Asia and, rarely, Beringia, inhabiting not only mountains, but also zonal tundras or steppes are traced. Weakening of the zonal aspect also occurs in aquatic species, since their mosaic distribution is associated with similar placement of water bodies.

It is important to note that among the birds of the Baikal region there are not only endemic species, but also endemic subspecies. Even in those mountainous subspecies that are characteristic of the Baikal region, the ranges are far away either in the Altai-Sayan mountainous country (the tundra partridge *Lagopus mutus nadezdae* Serebrowsky 1926), or in the Stanovoi highland (mountain reel *Leucosticte arctoa giglioli* Salvadori 1868) [63]. In the Baikal region, 111 species of birds (one third of the regional avifauna) have the periphery of their range [21].

In 74 species of birds nesting in Central Siberia, there are meridional discontinuities of the range or contact zone of the eastern and western populations, passing in the area of the Yenisei and the Sayans or in the Baikal rift. Most often, these populations are attributed to different subspecies, but sometimes

- to species-specific forms as part of the superspecies complex. It is assumed that they experienced adverse climatic conditions in the refugia located in the south-east and south-west of the modern range [42; 44]. Judging by the degree of their divergence, the periods of their isolation were rather long.

The range of birds living in the taiga zone is often more complete: the range of a single subspecies or a chain of several contact subspecies stretches across Eurasia. This can be considered a consequence of the periodic fragmentation of the taiga zone in the Pleistocene and Early Holocene. The modern ornithological population of the taiga was formed in the Holocene. In the Pleistocene, this process probably took place repeatedly following the dynamics of climate and changes in ecosystems [35; 18].

The share of species in which there is a junction of the subspecies ranges in the Baikal region is 17% for aquatic and non-aquatic birds. The number of species that have special subspecies in Central Siberia is smaller in the former than in the latter, 3% versus 12%. The number of species that have an interrupted area here, on the contrary, is much larger in the former - 21% compared with 0.5%. This is particularly interesting in light of the fact that aquatic birds generally have fewer subspecies than non-water ones. Mayr [39] connects the less fractional intraspecific structure of aquatic birds with the formation of their high ability to change nesting sites due to the instability of the aquatic habitat.

Thus, a certain "faunistic vacuum," noted by Nazarenko [44] for birds of deciduous and dark coniferous forests of Eastern Siberia, is also shown by us for birds associated with the water bodies of the region. This is caused both by the existence of zoogeographic barriers (Baikal and mountain ranges) and landscape reorganizations in the Pleistocene [42], and by the continental climate with reduced moisture.

3.4. *The history of the formation of the modern ornithological fauna of Baikal*

The origin of most modern genera and bird species belongs to the Pliocene and Pleistocene [31]. The evolutionary role of ecological conditions in birds is manifested primarily in behavioral change, while their morphology and embryogenesis are conservative [43]. Therefore, during the Quaternary period, the landscape and zonal preferences of modern species could vary significantly, but the requirements for the type of habitats (open, bush, water bodies, etc.) did not change much. The dynamics of the fauna and population of birds in the Baikal region primarily reflects the dynamics of their distribution, and not speciation.

According to studies of recent years [48; 3; 80, etc.], during the periods of Pleistocene cold spells in the Baikal region, birch-larch woodlands and grassy landscapes prevailed, but the taiga remained in separate refugia. Local glaciations had a mountain-valley character. Deep freezing of the soil favored the existence of permanent and temporary reservoirs. Such conditions are acceptable for nesting birds of tundra and grassy landscapes, many aquatic and near-water species, some forest-steppe species. In warm or moderately cold wet periods, different types of dark-coniferous taiga with the participation of broad-leaved species were common, but due to the strongly dissected mountainous terrain, undoubtedly, there were areas of steppes of various types. The composition of the birds was apparently close to the modern. In warm dry interglacial light coniferous forests and steppes spread. This creates conditions for the habitat of birds, associated by origin with the southern taiga, forest-steppe and steppe zone, including aquatic.

Climatic reconstruction [70] showed that the end of the Sartan cooling, between 16 and 11 thousand years ago, was characterized by deep thermal cycles that had no analogues in the Holocene, with a frequency of about 1 thousand years. At the maxima of the cycles, the temperatures approached modern; in minima they were lower by 4-6 °C, and the duration of the ice-free period on Baikal decreased to 120-140 days. Under these conditions, there could well be populations of migratory birds associated with water, they could be limited only by the trophic factor. Thus, many Charadrii waders (feeding on invertebrates), Anserinae geese (phytophages), a number of Laridae gulls (ichthyophages) are perfectly adapted to modern tundra conditions, it only takes 2-3 months to raise their young. V. G. Degtyarev [15] came to the conclusion that in Central Yakutia even during periods of cold snaps populations of waterfowl and near-water birds could live. Indeed, from the cave on the Duktay River (right tributary of the Aldan), the remains of the *Anser anser* gray goose, *Anas strepera* gray duck, *Anas*

formosa cloctuna, *Sterna hirundo* common tern, *Larus ridibundus* black-headed gull from the Late Pleistocene layers are identified [49]. An overview of the paleontological finds of birds from the Baikal region shows that they are dominated by representatives of the genera of terrestrial and aquatic birds, which are typical for lowland and mountain shrub-steppe stations, as well as for rocky biotopes [49].

In the Quaternary, high seismic activity was characteristic of the Baikal basin, which caused fluctuations in the lake level with an amplitude of more than 100 m [23]. The estuaries of the rivers, in particular, the Selenga, changed the flow regime and configuration not only due to changes in the level of Baikal, but also directly under the influence of tectonic events [80; 58]. Although the Baikal deltas and shallow waters existed in the same areas for hundreds of thousands of years, they were periodically subjected to drastic changes. This is equivalently reflected in aquatic bird populations: the littoral is important for them, but not the deep-water pelagial of Baikal.

As the history of the formation of the Selenga delta avifauna [68] shows, colonial species require from several years to several decades to create a small breeding group. With a favorable situation, a group is supposedly able to reach the rank of an independent population over several centuries. But even in these insignificant periods of time the birds had to change nesting sites within and Baikal region for the reasons mentioned above. Most of the species were supposed to leave the region during cold periods, returning here to the warm. Therefore, not only speciation, but also the formation of subspecies here was impossible. The exceptions were only a few species that do not have direct links with water, mostly sedentary and inhabiting rocky, tundra and mountain-steppe biotopes. They could form subspecies due to mountain isolates - a process that is widespread on a global scale. However, the modern mountain avifauna is composed mainly of newcomers from the north / northeast and from the south.

The settlement of Baikal by migratory birds nesting in Western or East Asia and wintering in tropical latitudes is limited by the geographical position of the lake. On the shortest route between Lake Baikal and wintering areas, the vast high mountains and deserts of Central Asia are located, unfavorable for both migrations stops and the formation of new winterings. The tagging by satellite radio transmitters of the black stork *Ciconia nigra* [78] and the burial eagle *Aquila heliaca* [81] showed that birds wintering in South Asia during migrations are forced to round the Central Asian region from the east or west. Not all species are capable of lengthening the span, faced with a lack of time in the annual life cycle [24]. This limits the species composition of the Baikal birds, at least for the time being.

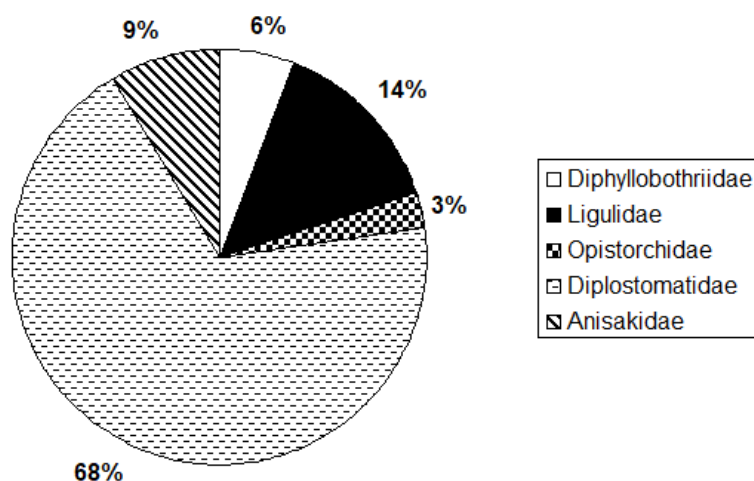


Fig. 2. Groups of bird parasites, which life cycle in the larval phases of development takes place in fish.

In the Pleistocene landscape-climatic conditions, populations of such birds as the tern, lakebird, and many anseriformes could almost always exist in the Baikal region. The gull *Larus argentatus* (sensu lato) could constantly inhabit Baikal due to its behavioral adaptations and euryphagia [26]. But this

species prefers the coast of productive reservoirs and, possibly, periodically left the lake when it became ultra-oligotrophic and not having shallow waters. Birds of grassy and tundra spaces, for example, sandpipers of the subfamily Calidridinae, as well as mountain species, were to become common during cold periods, but disappear or form local mountain populations during periods of climatic optimum. On the contrary, species of more southern genesis, such as the white tern *Chlidonias leucopterus*, the marsh sandpiper *Tringa stagnatilis*, could form here numerous temporary groups during warming events, but disappeared when cold snaps. Species that prefer reservoirs in late succession stages (a large bittern of *Botaurus stellaris*, red-headed pochard *Aythya ferina*) probably occupied the Baikal region only during periods of mild and stable climate. The primary way of forming the near-water avifauna of Baikal and Baikal region was undoubtedly the path of colonization / recolonization by birds from adjacent regions.

Given current knowledge of the distribution of birds, the dynamism of their habitats, and their association with characteristic types of habitats, it can be assumed that in each subsequent interglacial, the species composition of birds in the region differed from the previous interglacial, as it was formed from a few components that survived the cooling and new invaders. Biocenotic relations were re-formed. It is legitimate to speak not so much about the extinctions of the faunas, but rather about the "extinctions" and the revival of ecosystems. The frequency of landscape-climatic changes in the Pleistocene (especially in the later) probably played a greater role than their amplitude. Today's landscape-ecological complexes of birds are of precast, heterochronic origin.

Thus, the modern composition of the Baikal ornithological fauna was mainly formed in the Holocene in accordance with changes in the landscape-climatic situation, but due to the mountainous relief in the bird fauna, there are also species characteristic of the last Ice Age.

According to the literature, the composition of parasites of 96 bird species of Lake Baikal, examined by parasitological methods, includes 300 species of helminths [45]. There are no endemic taxa among them. In fish, only 35 species of bird parasites pass through the larval phase of development (Fig. 2). Among avian parasites, introduced species predominate over native species. Thus, out of 45 species of helminths of the gray-eyed gull, *Larus canus*, 27 species (60%) were found in adult phases in the spring, that is, brought from other regions [67]. The above may indicate a relatively recent time for the settlement of modern bird fauna of the coast of Baikal, which did not lead to the formation of parasitic systems specific to this lake.

4. Conclusion

1. The data on geological and climatic events on Baikal indicate that the formation of modern fish fauna, bird fauna, and their parasites was influenced by these processes and in accordance with the possibilities of animal exploration of this region.
2. The modern ichthyofauna was formed during the long evolution of this reservoir, but the fauna of rogue fish can be attributed to the most ancient in Baikal in terms of the duration of its isolation in this lake, which led to the formation of endemic taxa of various systematic rank. Among endemic Baikal species and subspecies of parasites, parasites of rogue-like fish significantly dominate (32 out of 38 known ones), which also indicates the long evolution of this group of fish in Baikal.
3. The structure of the modern avifauna of Baikal contains elements of different geographical origin (with a predominance of boreal and widespread species). The absence of endemic taxa in birds and their parasites is noted. A large number of meridional boundaries between populations of one species or closely related species, primarily in aquatic birds, indicate the tense ecological conditions of birds living on Lake Baikal in the Quaternary period.
4. Periodic colonization from contiguous regions should be considered the main way of forming the Baikal avifauna. Only few Palaearctic bird species could inhabit Baikal during the entire Pleistocene-Holocene, most species had to leave the region at certain times due to unfavorable habitat conditions.

5. Acknowledgments

The work was done on the topic “Study of Some Ecosystem Elements of the Territory of Eastern Siberia Based on the Results of Field and Experimental Studies as a Reflection of Changes in Abiotic Environmental Factors.” State registration number AAAA-A16-116051910013-0.

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