

Review

# Fresh- and Brackish-Water Cold-Tolerant Species of Southern Europe: Migrants from the Paratethys That Colonized the Arctic

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**Abstract:** Analysis of zoogeographic, paleogeographic, and molecular data has shown that the ancestors of many fresh- and brackish-water cold-tolerant hydrobionts of the Mediterranean region and the Danube River basin likely originated in East Asia or Central Asia. The fish genera *Gasterosteus*, *Hucho*, *Oxynoemacheilus*, *Salmo*, and *Schizothorax* are examples of these groups among vertebrates, and the genera *Magnibursatus* (Trematoda), *Margaritifera*, *Potomida*, *Microcondylaea*, *Leguminaia*, *Unio* (Mollusca), and *Phagocata* (Planaria), among invertebrates. There is reason to believe that their ancestors spread to Europe through the Paratethys (or the proto-Paratethys basin that preceded it), where intense speciation took place and new genera of aquatic organisms arose. Some of the forms that originated in the Paratethys colonized the Mediterranean, and overwhelming data indicate that representatives of the genera *Salmo*, *Caspiomyzon*, and *Ecrobia* migrated during the Miocene from the region of the modern Caspian through the Araks Strait, which existed at that time. From the Ponto-Caspian and the Mediterranean regions, noble salmon, three-spined stickleback, European pearl mussel, seals, and mollusks of the genus *Ecrobia* spread to the Atlantic Ocean and colonized the Subarctic and Arctic regions of Europe and North America. Our study indicates that the area of the former Paratethys retains its significance as a center of origin of new species and genera and that it has been the starting point of migration “corridors” up to the present time.

**Keywords:** evolution; zoogeography; Eurasia; phylogeography; colonization; Paratethys; Arctic; Subarctic



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## 1. Introduction

The dispersal of aquatic organisms from one waterbody to another is a suitable model for studying patterns of evolution and faunogenesis. Terrestrial and marine species usually disperse gradually, and the disappearance of physical barriers that impede this process, e.g., a mountain range destruction, takes a long time; therefore, different species usually do not disperse simultaneously. Only rare unique phenomena, such as a connection between hitherto isolated landmasses, stimulate simultaneous dispersal of many terrestrial species and trigger the evolutionary processes accompanying such events [1].

The connections and separations of the basins of different seas are also quite rare events in Earth's history. At the same time, they drive long-term processes of evolution of many aquatic species simultaneously conquering a new basin or becoming simultaneously isolated in it. At the same time, these events are not as rare as the connections of continents, which allows researchers to trace the evolution of a number of groups of aquatic organisms during more than one cycle of colonization and isolation. It becomes possible to assess the evolutionary consequences of such processes on time scales much larger than in the case of using the traditional model, evolution on islands [2].

Tracing the evolution of an entire group of organisms allows making well-grounded assumptions about their possible fate in the rapidly changing modern world: whether they risk going extinct when their habitat changes or join the cohort of rapidly spreading invasive species.

The freshwater fauna of the European Mediterranean and the Ponto-Caspian basin includes several cold-tolerant fish and invertebrate species belonging to various taxa. These species occupy specific habitats, including those of mountainous regions, and it is believed that there is a real risk of disappearance of these organisms in a considerable part of their ranges due to global warming [3–7]. Noble salmons (genus *Salmo* Linnaeus, 1758), three-spined sticklebacks (genus *Gasterosteus* Linnaeus, 1758), planarians of the genus *Phagocata* Leidy, 1847 and some other groups are typical representatives of cold-water taxa in the freshwater biota of the Mediterranean.

The origin of cold-water species inhabiting Southern Europe in the Mediterranean and the Black Sea basins has been discussed for a long time. The currently dominant hypotheses relate to the appearance of the cold-water component of the Southern European aquatic fauna with the invasion of the ancestors of these organisms from high latitudes during the Pleistocene glaciations (from about 2.5 Mya to 12 Kya).

About a century ago, Regan [8] put forward his assumption about the origin of the populations of noble salmons (*Salmo*) inhabiting Southern Europe from the anadromous brown trout, which migrated there from Northern Europe during one of the ice ages or shortly before the first glaciation. This was a purely hypothetical opinion, but it has been entrenched in science for a long time. Moreover, in addition to the brown trout, other cold-tolerant species inhabiting the Mediterranean and the Ponto-Caspian region have begun to be viewed as descendants of Northern invaders who spread to the south in the Pleistocene. It should be noted, however, that the assumption on this migration route, while seemingly correct, contradicts numerous facts. Among others, modern molecular genetic approaches and new paleontological findings have shown that cold-tolerant southern forms do not always originate from the northern ones: in many cases, southern mountain forms are the ancestors of northern ones, and not vice versa (see [9,10]).

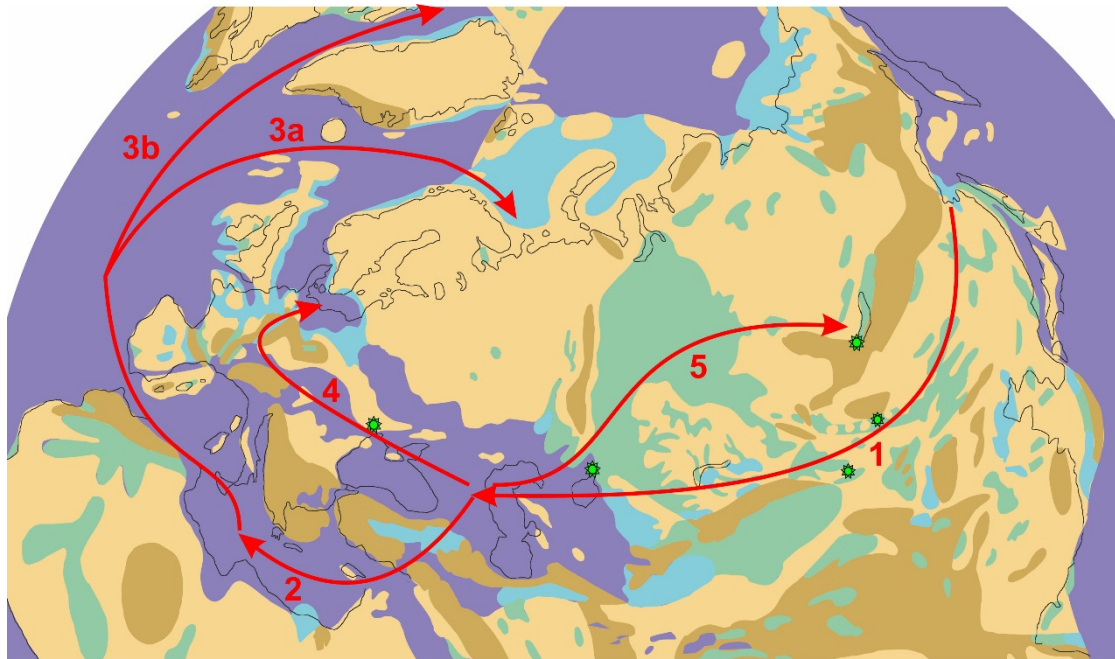
Another hypothesis explaining the origin of the cold-tolerant species of the Southern European mountainous areas is that they are remnants of a much more ancient, preglacial fauna, although there were no convincing data in favor of this assumption until recently. For a long time, reconstructions of animal migration routes were based on scant paleontological material and outdated paleogeographic reconstructions, and the lack of genetic data precluded testing morphology-based hypotheses on phylogenetic relationships between different forms.

Specifically, as early as the first half of the 20th century, it was hypothesized that faunal exchange between the Atlantic and the Pacific oceans could occur via the Tethys Ocean, which was located between the continents of Gondwana and Laurasia from the Triassic to the Pliocene (see [11–13] for reviews). However, after Berg [14], biogeographers believed for a long time that only tropical taxa participated in this faunal exchange, whereas the cold-tolerant elements of the Southern European fauna were a priori considered to be of northern origin.

For example, Kosswig [15] made an important inference about the possibility that some fish species that currently inhabit fresh waters have migrated into the Mediterranean through the Tethys. However, Kosswig considered it necessary to make a reservation that this seems not to apply to sticklebacks and the brown trout (*Salmo trutta* Linnaeus, 1758), which are “secondary fresh-water fishes of northern origin” that “entered the Mediterranean during the Pleistocene” [15] (p. 319).

The situation was not altered essentially even after the first studies that demonstrated the important role of the Paratethys, an ocean (or sea) in Western Eurasia that was separated from the Tethys in the late Eocene, about 37 Mya, played in the formation of the fish and mollusk fauna of Europe ([16,17]; Figure 1). Bianco’s [18] review convincingly substantiated the importance of the Paratethys as an intermediate habitat in the dispersal

of Asian cyprinids to the Mediterranean region. The author concluded that these fishes migrated “via the ‘Mediterranean seaway’ rather than by ‘river captures’ from northern Europe” [18] (p. 181); however, the Pleistocene “river captures or inversion of flow direction . . . could explain the presence of similar or identical cold-adapted freshwater fishes (*Phoxinus phoxinus*, *Cottus gobio*, genus: *Salmo*, genus: *Salvelinus*) in the upper courses of river drainages” [18] (p. 179).



**Figure 1.** The hypothetical migration routes of aquatic animals via Paratethys. 1—from the Far East to Paratethys; “Pearl Way” (Oligocene); 2—from Paratethys to the Mediterranean region (Miocene); 3—from the Mediterranean to the Atlantic (3b) and Arctic (3a) oceans; 4—from the Black Sea basin to the Atlantic Ocean (through the watershed); and 5—from Paratethys to the north-east. Purple denotes oceans and seas, blue—brackish water reservoirs, turquoise—fresh water reservoirs, yellow—plains, and brown—mountains. Dark lines mark the modern boundaries of large waterbodies. Green stars—localities of fossil margaritiferid mussels. The paleogeographic setting corresponds to the period of 30 Mya; after [16].

Nonetheless, to date, numerous data have been accumulated that support the hypothesis on antiquity of cold-water taxa inhabiting the basins of the Mediterranean, Black, and Caspian seas. For example, a monograph on the living organisms of the ancient Balkan mountain lake Ohrid [19] presents evidence that the most ancient inhabitants of this lake, including cold-water ones, are directly related to the fauna that was widespread in Eurasia in the Neogene. Paleontological studies confirm that there was a transitional faunistic sub-region in the Neogene that represented “a latitudinal belt stretching from the Amur basin in the east to Western Asia and the southern Mediterranean in the west” [20] (pp. 36–37).

At different times, hypotheses have been put forward about the Tethys Ocean and adjacent waterbodies as the places of origin of several taxonomic groups containing many cold-water forms, notably pinnipeds [21], noble salmon [22], and continental calanoid copepods [23].

A number of recent molecular genetic studies have shown that many sister taxa inhabiting the Arctic Ocean and Caspian Sea basins have greatly diverged genetically; hence, they migrated to the Caspian basin long before the Pleistocene (see [24] for review). In addition, analysis of both the species content of the faunas and the genetic diversity of populations inhabiting Southern Europe shows that these characteristics have not been changed significantly during the Pleistocene glaciations [25,26]. Interestingly, data on terrestrial animals also show that the populations of the southernmost mountain regions of Europe, the Pyrenees, and the Balkan Mountains are significantly different genetically from

more northern populations and appear to have formed before the Pleistocene (reviewed by [27]). Some of these populations served as sources for the resettlement of northern Europe after glaciation [28].

It is characteristic that the pathways of penetration of ancient cold-water relict forms into the Mediterranean basin are rarely discussed in the current literature. At the same time, there is every reason to believe that most of these forms have migrated to the Mediterranean from the Paratethys and, moreover, that these forms have given rise to a number of typical inhabitants of the Arctic and Subarctic.

In this review, we summarize the available factual data on the modern distribution, taxonomic positions, paleontological findings, and phylogeography of cold-water aquatic organisms of the Mediterranean and the Danube basin. Furthermore, we use paleogeographic data to clarify the routes of their dispersal and assess the contribution of the Paratethys (and the preceding proto-Paratethys) to the formation of the modern freshwater biota of Southern Europe.

## 2. Material and Methods

The primary data for this review were obtained from the Web of Science database ([www.webofknowledge.com](http://www.webofknowledge.com) accessed date: 21 April 2021) using the following names of cold-tolerant taxa and the key regions of their distribution as the search entries: *Ecrobia*, *Jaera*, *Magnibursatus*, *Notocotylus atlanticus* (invertebrata), *Caspiomyzon*, *Eudontomyzon helenicus* (lampreys), *Oxynoemacheilus*, *Phoxinus*, *Pungitius* evolution, *Schizothorax prophyllax*, stickleback Mediterranean, *Thymallus*, *Turcinoemacheilus* (fishes), Ohrid evolution, Ohrid origin, Paratethys, and Xining basin.

Here, we used the term Central Asia in its classical meaning, following von Richthofen's definition: "vom Hochland von Tibet im Süden zum Altai im Norden, und von der Wasserscheide am Pamir im Westen zu derjenigen der Riesenströme von China und dem Gebirge Khingan im Osten" ("from the highlands of Tibet in the south to the Altai in the north, and from the watershed on the Pamir in the west to those of the great rivers of China and the Khingan Range in the east") [29] (p. 7). Thus, this region includes Western China, Mongolia, and the southern mountains of Asian Russia, but it does not include Kazakhstan, Turkmenistan, Kyrgyzstan, Tajikistan, and Uzbekistan. The latter countries are collectively called Middle Asia [30], except for Northwestern Kazakhstan, which belongs to Europe.

We defined the boundary between Europe and Asia according to the Encyclopedia Britannica (<https://www.britannica.com/place/Europe>; accessed date: 21 April 2021): it runs along the Mediterranean Sea, the Black Sea, the Kuma-Manych Depression, the Caspian Sea, the Emba (Zhem) River, and the Ural Mountains.

Abbreviations used: Kya, thousands of years ago; Myr, millions of years; and Mya, millions of years ago.

## 3. Factual Data

### 3.1. Schizothoracine Fishes (Subfamily Schizothoracinae)

The schizothoracines represent a characteristic element of the ichthyofauna of the mountainous areas of Central Asia. Most species of the subfamily occur here, and this region is reasonably considered to be the place of origin of this group [31–35]. According to the fossil record, the earliest representatives of the schizothoracines lived in the Oligocene in waterbodies of the Zaisan Depression, eastern Kazakhstan [36], and in the Qaidam Basin, northeastern Tibetan Plateau [37].

However, one extant species of this group, the Egerdir marinka (*Schizothorax prophyllax* Pietschmann, 1933), is known from Lake Egerdir in Southwestern Asian Turkey [38], and several other species inhabit waterbodies of Iran [39].

The origins of these species and routes of their dispersal to Western Asia have not been discussed in the literature, and data on the genetic characteristics of the populations of Turkish and Iranian waterbodies are lacking. At the same time, it is known that, at the beginning of the Oligocene in the Tarim Basin, north of the modern Tibetan plateau, a bay

of Paratethys still existed [40] and that, in the Late Oligocene, the Paratethys reached the Junggar Basin [41]. Therefore, it seems very likely that the schizothoracine fishes used the Paratethys and associated freshwater systems for their westward migration.

This assumption is supported by the fact that the schizothoracines can adapt to an increased water salinity: *Gymnocypris przewalskii* (Kessler, 1876) lives in the salt lake Kuku-nor [42] and has genetic adaptations to an increased salinity [43].

### 3.2. Nemacheiline Loaches (Subfamily Nemacheilinae)

Along with Schizothoracinae, the nemacheiline loaches are the most characteristic inhabitants of the Central Asia mountain waterbodies. Analysis of zoogeographic, paleontological, and morphological data suggests that this group arose in the area of the modern Southern China [44].

On the other hand, several genera of this subfamily occur in Western Asia [45], and two members of the genus *Oxyzomacheilus* Banareescu and Nalbant, 1966 even reached the Balkan Peninsula waterbodies [46]. Another genus, *Turcinoemacheilus* Banareescu and Nalbant, 1964, is distributed mainly in the basins of the Tigris and Euphrates rivers, but one member of this genus, *T. himalaya*, has been described from Nepal [47]. Note that Prokofiev [44] considers this species to be the most morphologically primitive in the genus.

According to Prokofiev [44] (p. 286), the westward spread of the nemacheiline loaches took place during the early Neogene sea regression, when “the Tethys–Paratethys basin lost its connection with the Indian Ocean”. Probably, large-scale phylogenetic studies of this group of fish would help to solve this question more precisely, but genetic studies of the Nemacheilinae in Western Asia and Europe have so far dealt only with interspecific differences [48] and the short-distance dispersal of representatives of some genera [46].

As in the case of the Schizothoracinae, it is important to note that the nemacheiline loaches can live in salt water: they were found in the salt lake Dalai-Nur in Northeastern China [42]. Thus, the physiological characteristics of this group of fish agree with the assumption that they used Paratethys for their dispersal.

### 3.3. Sticklebacks (Family Gasterosteidae)

*Nine-spined sticklebacks* (*Pungitius* Costa, 1848): The representatives of this genus, which, according to different authors, includes two to eight species, are extensively represented in the ichthyofauna of Northern Eurasia and North America. The species *Pungitius pungitius* (Linnaeus, 1758) has the widest range, covering the entire Northern Eurasia; two other species are endemic to the Far East; one species, to North America; and one more species, to Western Europe. In the basins of the Black, Caspian, and Aral seas, the species *Pungitius platygaster* (Kessler, 1859) occurs, and the endemic species *P. hellenicus* Stephanidis, 1971, is known from Greece (see [49] for review).

More than a half-century ago, Münzing [50] (p. 231) put forward the assumption that the nine-spined sticklebacks migrated to the Ponto-Caspian basin from the north, “at latest during the penultimate (=Riss) glaciation”, which is dated to 190–130 Kya. However, a recent study on the phylogeny of the genus *Pungitius* using nuclear and mitochondrial markers [51] has shown that *P. platygaster* and *P. hellenicus* have significantly diverged genetically from the other members of the genus. Hence, Guo and al. [51] concluded that the ancestor of these two species entered the Ponto-Caspian basin from the Arctic in the Miocene or Pliocene.

The oldest fossil remains of nine-spined sticklebacks (the extinct species *Pungitius hexacanthus* Schtylko, 1934) were found in Western Siberia and dated to the Miocene period [52,53]; therefore, the scenario of the introduction of the genus *Pungitius* into the Ponto-Caspian basin in the Miocene from Siberia seems more likely. However, analysis of the median-joining network of mitochondrial haplotypes of fishes of the genus *Pungitius* [54] shows that the closest extant relatives of *P. platygaster* are the Far Eastern endemic species *P. kaibarae* Tahaka, 1918 and *P. tymensis* (Nikolsky, 1889).

Therefore, with a considerable degree of confidence, it can be assumed that the ancestors of *P. platygaster* entered Paratethys from the Far East no later than in the Miocene and then moved into the Mediterranean, where *P. hellenicus* evolved. However, *P. hellenicus* was unable to spread widely over the Mediterranean, unlike its more thermophilic relative, the three-spined stickleback.

*The three-spined sticklebacks* (*Gasterosteus aculeatus* Linnaeus, 1758): The modern range of this species is very broad: it embraces the northern part of the Pacific Ocean basin, the east of North America, almost the entire Europe, including the Black Sea basin, Turkey, and even part of Northern Africa [55].

Most finds of fossil representatives of the genus *Gasterosteus* have been made in the northern part of the Pacific Ocean basin, the earliest of which is 16 Myr old. The oldest remains of *G. aculeatus* in the Atlantic Ocean basin date back to the Pliocene–Pleistocene, about 1.9 Mya (reviews: [55–58]).

In the Mediterranean and Black Seas basins, a number of phylogenetic lineages of the three-spined stickleback, including endemic ones, have been identified; however, most researchers still hold the hypothesis of the northern origin of this species [59–63].

Our analysis of the diversity of the cytochrome b mitochondrial gene (*Cyt b*) has shown that, among the haplotypes of *G. aculeatus* in Europe, those found in the populations of the Black and Mediterranean seas are the closest to the Pacific ones [64]. The rest of the European stickleback phylogenetic lineages originate from each other, and their ancestor carried a haplotype close to modern Mediterranean ones [64]. The phylogenetic lineages of *G. aculeatus* of the Baltic, White, and Barents seas are the youngest, as judged by the network structure.

This is a strong argument in favor of the assumption that the dispersal of the three-spined stickleback from the Pacific Ocean to the modern Mediterranean basin took place via the Paratethys. Further dispersal of this species occurred, apparently, through the area of the modern Strait of Gibraltar and along the coast of Europe; at an early stage of this process, the so-called transatlantic lineage of haplotypes emerged, representatives of which are found both in Europe and on the Atlantic coast of North America.

The spread of the three-spined stickleback from the Pacific Ocean into the Black Sea and then to Northern Europe explains a “zoogeographic anomaly” discussed by Gibson and Køie [65]. Specifically, the trematode *Magnibursatus caudofilamentosa* (Reimer, 1971), has been found to parasitize *G. aculeatus* living in the seas off the northern and eastern coasts of Denmark, whereas the other representatives of the genus *Magnibursatus* inhabit the Black Sea, Mediterranean Sea, and the Bay of Biscay [66,67]. Moreover, trematode genera that are close to *Magnibursatus* occur in regions that were once parts of the Tethys Ocean: the basins of the Mediterranean Sea, the Caspian Sea, and water bodies of India, China, and Japan [65].

### 3.4. Salmonids

*The noble salmon* (genus: *Salmo*): This genus includes the brown trout, widely distributed in Western Eurasia, a range of endemic forms occurring in the Mediterranean area and the Caucasus, and the Atlantic salmon (*Salmo salar* Linnaeus, 1758) spawning in the rivers of Northeastern North America and Western and Northern Europe (see [22] for review).

It should be noted that, as early as the end of the 19th century, the description of an extinct Miocene fish, *Salmo* (?) *immigratus*, found in the environs of Zagreb, Croatia, was published [68]. This fossil was unearthed from the Sarmatian Sea deposits, dated 10–14 Mya. Unfortunately, the fish was poorly preserved and could not be identified accurately; therefore, this find did not attract attention of scientists, especially because the vast majority of experts considered noble salmon until recently to be a group of northern origin.

For example, Regan [8] held the opinion that the noble salmon separated from Pacific salmon in the Miocene, when Asia and America were joined. According to Regan, a group of fish isolated in the Arctic from the main range, gave rise to the genus *Salmo*, which

later disappeared in the rivers of Siberia after the cooling of the climate but survived in Northern Europe. This hypothesis states that, much later, in “pre-glacial times”, the noble salmon gained a foothold in the basins of the Black and Caspian seas, and then, during the last ice age, in the Mediterranean region. Tortonese [69] also considered the brown trout of the Black and Caspian seas to be an “old resident”, and the Mediterranean one, an invader of the Ice Age. A similar point of view was expressed by Balon [70], who believed that the brown trout entered the basins of the Mediterranean and Black seas during the Ice Age. Kydersky [71] (p. 204) wrote: “... there is no reason to doubt that *S. trutta* is a northern species. The northern origin of *S. trutta* is illustrated by the very pattern of the range of fish of the genus *Salmo* as a whole”.

However, other authors, who thoroughly studied a number of morphological, karyological, and paleontological data on the brown trout of the Caucasus and the Balkan Peninsula, concluded that the populations of these regions are considerably old ([72–74] and references therein).

Dorofeeva [22], after detailed analysis of morphological, karyological, and zoogeographic data, came to the conclusion that noble salmon originated from the group of salmonid fish that dispersed westward from the Pacific Ocean along the shores of the ancient Tethys Sea. In Dorofeeva’s opinion, the brown trout evolved somewhere in the region that includes the basins of the Mediterranean, Black, Caspian, and Aral seas.

For a long time, ichthyologists and molecular geneticists could not reach an agreement on the place of the brown trout origin (see [75] for review). However, a study of the mitochondrial *COI* gene diversity of noble salmon throughout almost the entire range of the genus *Salmo* was recently carried out. Median-joining haplotype network analysis entirely confirmed the opinion of Dorofeeva [22]: the most ancient haplotype of the brown trout was found in the population of the Aral Sea basin, but it also occurred in the basins of the Caspian and Adriatic seas [76].

*The taimen* (genus: *Hucho* Günther, 1866): Three extant species of *Hucho* are known: the huchen, *Hucho hucho* Linnaeus, 1758, inhabiting the Danube basin; the Siberian taimen, *Hucho taimen* (Pallas, 1773), broadly distributed in northern Asia and the basins of European rivers adjacent to the Urals; and the Sichuan taimen (*Hucho bleekeri* Kimura, 1934), which is endemic to the mountain streams of the Yangtze River basin [77]. The earliest known member of this genus was found in Transbaikalia, in deposits dated between the Oligocene and the middle Miocene [78].

A monograph by Holčík et al. [79] summarizes paleogeographic evidence to conclude that the ancestors of the three extant species of *Hucho* diverged as early as in the Miocene. A recent finding of fossil taimen in the Late Miocene deposits in Ukraine [80] supports this conclusion.

Molecular genetic data do not contradict this hypothesis as well. The analysis of two regions of mitochondrial DNA (the D-loop region and a *Cyt b* gene fragment) have shown that the three *Hucho* species have almost equally diverged from each other, and the differences between nucleotide sequences within each species are comparable with the interspecific ones [77,81].

Some intriguing results have been obtained during the network analysis of the variants of the amino acid sequence of the cytochrome oxidase *c* subunit I in salmonids. It has turned out that taimen, noble salmon, and lenok (*Brachymystax* Günther, 1866) species form a common phylogenetic branch of the network, whereas Pacific salmonids do not belong to this branch [82]. Proceeding from this and taking into account the paleontological and phylogeographic data presented above, we can soundly assume that this entire branch evolved in the Paratethys basin. From this paleobasin, *Salmo* migrated westward to Europe; *Brachymystax*, northward to Siberia and eastward to the mountains of central China; and *Hucho*, in all three directions, to form the three extant species of this genus.

As it will be shown in the next section, freshwater pearl mussels of the genus *Margaritifera* Schumacher, 1816, whose larvae parasitize the gills of salmonids, migrated through the Paratethys basin together with these fish.

### 3.5. Freshwater Pearl Mussels of the Genus *Margaritifera*

The European pearl mussel *Margaritifera margaritifera* (Linnaeus, 1758) is broadly distributed in Western and Northern Europe, including Northern Portugal and Southern France [6]. Its larvae parasitize salmonids, the most suitable hosts for them being the brown trout and Atlantic salmon, and less suitable, the European taimen (see [83] and references therein). The extinct species *M. arca* Tshepalyga, 1964, which inhabited the Black Sea basin in the Upper Pliocene and Early Pleistocene, is considered to be the ancestor of *M. margaritifera* [84–86].

Judging by paleontological and genetic data, the genus *Margaritifera* originated in the Pacific Ocean basin, where most members of this genus (four species) still live [87]. *Margaritifera dahurica* (Middendorff, 1850), inhabiting the Amur basin and adjacent aquatic systems, is the closest to *M. margaritifera* according to molecular genetic data [87]; the main hosts of the glochidia of *M. dahurica* are lenoks (*Brachymystax*) [88].

Close relationships between the two species can also be traced using paleontological data (Figure 1). Fossil shells of pearl mussels close to the currently existing *M. dahurica* are known from the Cenozoic deposits of Middle and Central Asia. One of these forms is *Margaritifera martinsoni* Modell, 1964 (formerly known as *M. elongata* Martinson, 1951) lived in the Early to Middle Oligocene in the modern Aral Sea area; the same species is known from the Miocene of the Baikal region [89]. Bogachev [90] mentioned the finds of shells similar to *M. elongata* in the Miocene–Pliocene fauna of Dzhungaria (Northwestern China). Several species of margaritiferid mussels are known from the Pliocene of Western Mongolia. One of them has been named *M. praedahurica* Tshepalyga, 1971 due to its resemblance to the extant *M. dahurica* [91].

At the same time, the Aral Sea area was inhabited, in the Early to Middle Oligocene, by another species of pearl mussels, *M. occulta* Maderni, 1990. This species was somewhat similar to *M. arca*, which later occurred in Europe and the Caucasus [89]. Note that, according to paleogeographic data [17], the locality of *M. occulta* was at the shore of the Paratethys Sea, and the pearl mussel may have been transferred on the gills of salmonid fish, to modern Europe and the Caucasus: it is known that margaritiferid glochidia can survive not only in freshwater, but also in saltwater [92].

Thus, numerous data indicate that freshwater pearl mussels lived in water bodies of the Paratethys basin for a long time together with their salmonid hosts belonging to the *Salmo*–*Brachymystax*–*Hucho* clade. A number of forms of *Margaritifera* arose here, apparently including the ancestors of the modern *M. dahurica* and *M. margaritifera*, which parasitize precisely salmonids belonging to this group of fish [83,88].

### 3.6. Unionid Mussels (Family Unionidae)

This bivalve family evolved in East Asia in the Middle Jurassic [93,94], most probably, simultaneously with Margaritiferidae [95]. Researchers agree that both families had the same ancestor, a representative of the Triassic family Shifangellidae described on the basis of paleontological findings in Eastern China [94].

Judging from molecular genetic data, three different phylogenetic lineages of Unionidae simultaneously dispersed from the east to the west of Eurasia, having been differentiated even before dispersal [93,94].

For example, the unionid genus *Potomida* Swainson, 1840 is now widespread in the mountain and semimountain streams of the Mediterranean region [96], whereas its sister group, which includes the genera *Lamprotula* Simpson, 1900 and *Pronodularia* Starobogatov, 1970, inhabits rivers of Eastern China, Korea, and Japan [97]. The most interesting fossil finds show that, during the Jurassic period, the area of modern China was inhabited by mollusks morphologically similar to the recent *Potomida* of European water bodies [98]. Even if the external similarity of their shells is accounted for by convergence, and they should be classified to a different genus, the fossil Jurassic mussels undoubtedly represent a sister group of the genus *Potomida*. A number of *Unio* species inhabits Europe and Western Asia [99–101], and the range of their sister group in East Asia, including the genus

*Nodularia* Conrad, 1853, stretches from Northern Vietnam to Northeastern Russia [97,100]. The presence of shells of *Unio* in the Jurassic of Dzungaria [102] is remarkable, indicating that these extinct *Unio* formed a stem group for the clade Unionini.

Finally, the species *Microcondylaea bonellii* (Férussac, 1827) is the only species of its genus, whose range is restricted to the river systems of the northern and eastern parts of the Adriatic Sea [99,103,104], and the genus *Leguminaia* Conrad, 1865, closely related to it, consists of two extant species that occur in Western Asia, in the Orontes and Euphrates river basins [101,105]. These two genera form a sister group to the genus *Sinosolenaia* Bolotov, Kondakov, Konopleva, and Vikhrev, 2021 widespread in East Asia [106,107].

Since paleontological data indicate that the dispersal of mollusks of the family Unionidae from East Asia to the Middle East and the Mediterranean occurred in the early Paleogene or even during the Cretaceous period, it can be safely assumed that this dispersal could go through a transcontinental system of water bodies, e.g., an extended lake–river system, the position of which, however, is still difficult to reconstruct, or through the shallow desalinated areas along the coast of Tethys/Proto-Paratethys [13,108,109].

Although not all European and Middle Eastern representatives of Unionidae can be classified as cold-water species, many of them tend to live in mountain streams (*Potomida*, *Microcondylaea*, *Leguminaia*, and some *Unio*) [99], and a number of species of the genus *Unio* even spread rather far northward, into the Subarctic [100,110]. However, these *Unio* species are likely to have invaded the Subarctic region relatively recently, in the Holocene [111].

### 3.7. Snails of the Genus *Ecrobia* Stimpson, 1865 (Family Hydrobiidae)

The gastropod genus *Ecrobia* has a vast range [112,113]. *Ecrobia truncata* (Vanatta, 1924) is widespread in the northeast of North America, the range of *E. ventrosa* (Montagu, 1803) covers Western and Northern Europe and the Mediterranean region. *E. maritima* (Milaschewitsch, 1916) is characteristic of the Black Sea and some parts of the Mediterranean Sea. *Ecrobia grimmeri* (Clessin, 1887) has long been considered a Ponto-Caspian endemic, and *E. spalattiana* (Radoman, 1973) is an endemic to the Mediterranean Sea. Not all representatives of this genus can be considered as cold water species, but some of them occur even in Arctic seas.

*Ecrobia grimmeri*, allegedly endemic to the Caspian Sea, was recently found in a lake in Iraq; it was assumed that the snails were transferred there by waterfowl [114]. Later, however, representatives of this species were found in the province of Hormozgan, Southern Iran [115]; hence, *E. grimmeri* may have lived in the Persian Gulf basin for as long as in the Caspian basin.

Recent paleontological finds confirm that representatives of the genus *Ecrobia* have lived in Western Asia since very ancient times. *E. grimmeri* is found in the Middle and Upper Miocene sediments on the southern coast of the Caspian Sea, in modern Iran [116]. *Ecrobia* sp. inhabited the northeastern Mediterranean in the Latest Miocene [117]. The extinct species *E. polysarca* (Cossmann and Peyrot, 1919) has been described from the Neogene deposits of Aquitaine, at the Atlantic coast of France.

Although *Ecrobia* is not the only representative of aquatic organisms that have spread throughout the Paratethys and the Mediterranean and then crossed the Atlantic Ocean (as noted above, the Atlantic salmon and three-spined stickleback also crossed the Atlantic), the mechanism and route of *Ecrobia* migration remain unknown. According to Vandendorpe et al. [112], genetic data allow three possibilities to be considered: (1) recent human-mediated dispersal, (2) historical transatlantic interchange, and (3) historical transpolar interchange, the last scenario being considered more probable by the authors of the cited paper.

### 3.8. Planarians (Order Tricladida)

The group of planarian species formerly included in the genus *Fonticola* Komárek, 1926 exhibits a very remarkable pattern of distribution. These animals occur in Central Asia, Northern Africa, and Central and Western Europe; the highest species richness of this

group is observed at the eastern coast of the Adriatic Sea. Most of the representatives in this group inhabit cold mountain brooks, but some species can live in the littoral zone of large lakes, where the water temperature sometimes reaches 27 °C [19].

At present, the genus *Fonticola* is considered to be a part of the genus *Phagocata*, which initially included species distributed in the temperate belt of North America; central, Western, and Southern Europe; Asia Minor; some parts of Southern Siberia (including Lake Baikal); Far East; Chukotka; and Alaska [118].

The range of the genus *Phagocata* s. lato (i.e., including the genus *Fonticola*) strikingly resembles that of the mussel genus *Margaritifera*. We concur with the opinion of Porfirieva [119], who believes that *Phagocata* was a member of the paleolimnic fauna that was formed in shallow Mesozoic basins stretching from Japan and South Korea through Manchuria and Mongolia to Central Asia. Unfortunately, the origin of European *Phagocata* has not yet been studied by molecular genetic methods.

### 3.9. Seals (Family Phocidae)

These mammals are common in the Arctic and Antarctic, most species of the group are closely associated with ice, and many researchers believed that they arose in the Arctic. However, as early as half a century ago, the hypothesis was put forward on the origin of all pinnipeds in the Tethys Sea or associated water basins [21]. Recently, data supporting this hypothesis have been rapidly accumulated.

Paleontological studies have shown that several seal species lived in the Paratethys; they were especially diverse in the Miocene. For instance, the earliest representatives of the subfamily Cystophorinae lived in the Paratethys, which, supposedly, is the homeland of this group. Later, this group migrated to the Atlantic Ocean, where they split into two genera. The hooded seal, *Cystophora cristata* (Erxleben, 1777) currently inhabits the North Atlantic and the adjacent Arctic regions, and the northern elephant seal, *Mirounga angustirostris* (Gill, 1866), has spread to the Pacific Ocean through the Arctic [120].

It is also assumed that the seal genus *Pusa* Scopoli, 1777 evolved in the Paratethys; one of its representatives, *P. caspica* (Gmelin, 1788), still lives in the Caspian Sea. Seals of this genus, having entered the Atlantic and reached the Arctic Ocean, gave rise to the ringed seal, *P. hispida* Schreber, 1775, a typical inhabitant of the Arctic and Subarctic [121]. Genetic data indicate a considerable divergence time between *P. caspica* and *P. hispida* [122–124]; apparently, these species had diverged before the beginning of the Pleistocene glaciations. Paleontological data also indicate the antiquity of the Caspian seal: a fossil seal similar to *P. caspica* in many respects has been found in the deposits of the Sarmatian Sea (Middle Miocene) in modern Azerbaijan [125].

### 3.10. Cold-Water Hydrobionts of Southern Europe Whose Ways of Dispersal Remain Insufficiently Studied

The origins and routes of dispersal of several other groups of Southern European cold-water aquatic organisms have not been studied sufficiently. However, they all have closely related (most likely, ancestral) groups in Asia, including those living in Lake Baikal or mountain water bodies.

For example, the oligochaete *Lamprodrilus pygmaeus* Michaelsen, 1901, a species originally discovered in Lake Baikal, occurs in Lake Ohrid [19]. Other species of this genus are found in different countries of Eastern Europe [19], but unfortunately, molecular genetic data on this group are still lacking.

At the same time, a study on the gene encoding the 18S ribosomal subunit [126] has shown that not only some other oligochaetes of this lake, but also the species *Trichodrilus diversisetosus* Rodriguez and Giani, 1986, which is known from water bodies (including cave ones) of France and Spain [127], are clustered together with the genus *Lamprodrilus*.

The diatom genus *Krsticiella* Levkov, 2007, previously known exclusively from lakes Baikal and Ohrid, has recently been found in several water bodies of Siberia and Alaska [128]. In addition, it is very likely that they are also present in the Pliocene deposits of the Volga basin, and in the Late Pliocene to Early Pleistocene deposits of the polar Urals [128].

The latest evidence makes it obvious that the lampreys (Petromyzontiformes) only recently gained a foothold at northern latitudes; most probably, this took place after the last glacier retreat. Molecular genetic analysis has shown that the residential forms of lampreys inhabiting these regions are not endemic species but rather recent derivatives of anadromous species [129,130]. On the other hand, both the Mediterranean and the Ponto-Caspian basins have their endemic species and even genera of lampreys [131,132], some of them share some morphological traits with the Far Eastern lampreys of the genus *Lethenteron* Creaser and Hubbs, 1922 [133]. At the same time, a species of the genus *Eudontomyzon* Regan, 1911 was described from the Korean Peninsula, while the rest of the species of this genus live in Southern Europe [134].

Exciting results have been obtained by Lang et al. [135] in their study on the complete mitochondrial *Cyt b* sequences of lampreys. The data show that the Caspian lamprey *Caspiomyzon wagneri* (Kessler, 1870) is closely related to *Eudontomyzon hellenicus* Vladykov, Renaud, Kott, and Economidis, 1982, endemic to Greece, and significantly differs from the other lamprey species.

The burbot *Lota lota* (Linnaeus, 1758) is widespread in cold waters of the Holarctic, including some aquatic systems of the Northern Mediterranean. Fossil remains of representatives of the genus *Lota* have been found in the Paratethys deposits, including rocks of the modern Aral Sea region formed in the mid-Tertiary time [136], and in the Lower Pliocene sediments in the area of modern Vienna [137]. These facts give strong support for the opinion by Van Houdt et al. [138] (p. 607): “Based on the genetic data and the fossil record we hypothesize that the genus *Lota* arose in the Middle Miocene and that a freshwater form evolved in Europe between 15 and 5 Myr ago”.

It is now generally accepted that the most likely place of origin of graylings (genus *Thymallus* Link, 1790) is in the southern parts of the river basins of Siberia and the Far East [139]. Most species of this genus occur in Asia, but the European grayling *Thymallus thymallus* (Linnaeus, 1758) is widespread in Europe (see [139] for review). It is noteworthy that this species (and the brown trout and three-spined stickleback) is characterized by the presence of several highly divergent genetic lineages in the Mediterranean region and in the Ponto-Caspian basin [139–145], and two forms from the Mediterranean Sea basin are justifiably considered to be endemic species [139].

Weiss et al. [142] have come to an important conclusion about the time of appearance of representatives of the genus *Thymallus* in Europe. According to the authors, “As there is no hypothesis of a freshwater connection between the Danube and Loire in the last 2 million years, a pre-Pleistocene expansion of *Thymallus* across Southern Europe is almost certain” [142] (p. 1402). The fact that graylings are very old inhabitants of the Mediterranean and the Black Sea basins is confirmed by the discovery of the fossil grayling *Thymallus latisulcatus* Rückert-Ülkümen and Kayam, 1993 on the coast of the Sea of Marmara in layers dating from the Upper Miocene to the Lower Pliocene [146]. It should be mentioned, however, that only otoliths of this fish have been found.

Minnows (*Phoxinus* Rafinesque, 1820) have the same pattern of distribution as lampreys, the brown trout, the three-spined stickleback, and graylings: several highly divergent genetic lineages of this genus occur in the basins of the Mediterranean and Black seas [147].

Recent studies have shown that *Gyrodactylus salaris* Malmberg, 1957, a monogenean parasite of salmonids, which was considered endemic to Northern Europe, also lives in the Danube basin and Lake Ohrid, and at least one of the widespread evolutionary lineages of this parasite originated from this lake [148].

During the past decade, a series of studies ([149–151], etc.) has revealed a new regional hotspot of the species diversity of hydrobiid snails (Gastropoda: Caenogastropoda) in the Caucasus and Transcaucasian region. This area is inhabited by tens of endemic genera and species, most of which occur in underground habitats, such as cave lakes and streams. Molecular taxonomy indicates that all endemic Caucasian taxa of hydrobiid snails belong to two subfamilies, Belgrandiellinae Radoman, 1983 and Sadlerianinae Radoman, 1973, widely distributed in the southern part of Eastern and Central Europe [152,153]. Thus, it can

be hypothesized that faunal exchange between the Caucasian area and Southern Europe, and even westward migration of the ancestral forms of the two subfamilies from the Ponto-Caspian basin to the Balkan Peninsula, occurred in the past. However, available data are still too scarce to prefer this assumption, and the migration in the opposite direction, i.e., from the Balkans to the Caucasus, remains a possible alternative.

Recent phylogenetic and taxonomic studies on radicine pond snails (Gastropoda: Lymnaeidae: Amphipepleinae) have confirmed the hypothesis on an important role of giant Miocene lakes in the evolutionary diversification of this group [154]. Earlier, this hypothesis was put forward on the basis of paleontological evidence [155]. Some endemic genera and species of radicine snails currently inhabit Central Asian mountains [154,156]. Molecular phylogenetic data on the gastropod family Valvatidae reported by Clewing et al. [157] assume interchange between the aquatic malacofaunas of Tibet, Siberia, and Europe in the past.

It should also be noted that several groups of aquatic insects are widespread in both Southern Europe and High Asia [158].

Thus, recent data on poorly studied species of cold-water aquatic organisms testify to the antiquity of their populations in the Mediterranean Sea and Ponto-Caspian basins. This further confirms the assumption that many species of Lake Baikal and Lake Ohrid are remains of the once widespread fauna preserved in these deep ancient lakes [19,159].

#### 4. Discussion

##### 4.1. The Routes of Invasion of Cold-Tolerant Hydrobionts from the Pacific Ocean Basin and Central Asia to the Paratethys Basin

It is well established that the recent aquatic fauna of Europe has largely been formed by ancient migrants from Asia. At the same time, until recently, most authors insisted that the spread of Asian hydrobiont species into Europe, with a probable exception of some aquatic insects, occurred through the Arctic Ocean basin (see [158,160] for review). However, long-term research made by Soviet paleontologists and paleogeographers (unfortunately, few, if any, of their papers have been translated into English) led to the conclusion that some representatives of the East Asian fauna have dispersed westward through Central and Middle Asia (see [159] for review).

As shown above, recent research has completely confirmed this conclusion. The results of studies on bivalve mollusks, whose large and durable shells have been preserved in rock strata for millions of years, are especially indicative. These studies allow, albeit with a certain degree of caution, to assume at least two time periods of active invasion of aquatic organisms from the Pacific Ocean basin through Central Asia to Middle Asia.

The finding of *Unio* shells in the Jurassic deposits of Dzungaria, located at the boundary between Central Asia and Middle Asia [102], suggests that some unionid genera (*Potomida*, *Microcondylaea*, *Leguminaia*, and *Unio*) and, according to Porfirieva [119], the planarian genus *Phagocata*, migrated from the Pacific Ocean basin to the area of the modern Ponto-Caspian and Mediterranean basins as early as the Mesozoic. This migration could occur through ancient water bodies that still remain poorly studied, mainly through the proto-Paratethys [108,109].

The localities of extinct margaritiferid mussels living in the Oligocene–Pliocene stretch from the Pacific Ocean, via Mongolia and Dzhungaria, to the modern Aral Sea (Figure 1). This indicates that the dispersal of this group through Central Asia occurred much later than the dispersal of Unionidae. The hosts of pearl mussel glochidia, including salmonid fish and, possibly, sticklebacks, obviously migrated via the same route and at the same time.

It is interesting that many groups of thermophilic aquatic organisms apparently used the same pathway during their dispersal in the past. For example, it was recently discovered that the catfish *Silurus soldatovi* Nikolsky and Soin, 1948, which currently inhabits exclusively the Amur River basin, in the occurred in the modern Western Mongolia and Tuva [78] and even Ukraine [161] in the Late Miocene and Pliocene.

Conclusions about the very old Central Asian origin of cold-water Ponto-Caspian species do not contradict the current views on the formation of the hydrofauna of this

region. For instance, Naseka [162] (p. 488) provides some facts in support of “a hypothesis on a relatively ancient age of the Caucasian fish fauna and its origin from the southern branch of the Oligocene East Asian fauna—Internal Asian fauna *sensu* Sychevskaya (1986)”.

Recent geological research has also made it possible to determine the location of the water bodies where this southern branch of the Oligocene Eastern Asian fauna lived. In the Oligocene and Miocene, extensive water systems consisting of large lakes existed both in the Tibetan Plateau [163,164] and in the modern Mongolia [165]. Until the end of the Miocene, there were also lakes, though temporary, in the Tarim Basin [166].

Apparently, these large aquatic systems provided many vacant and very diverse ecological niches, and, hence, intense generification and speciation took place there. In particular, the gradually rising Tibetan Plateau acted as an important center for the emergence, diversification, and dispersal of cold-tolerant organisms, including aquatic taxa (see [9,154] for review). In particular, the schizothoracine fish and loaches of the subfamily Nemacheilinae arose in this area.

The Central Asian lake systems, apparently, retained a connection with the Paratethys for a long time; therefore, the cold-water fauna that arose in the mountainous areas of Central Asia could in some cases migrate along the rivers of the southern hilly coast of the Paratethys. The desalination of the Paratethys that occurred in the Late Oligocene [167] could facilitate this process.

Thus, aquatic systems of Central Asia and the subsequent disappearance of these systems explains well the emergence of the disjunct ranges of many groups of freshwater aquatic organisms, and the localization of sister groups in Europe and eastern Asia.

#### 4.2. The Routes of the Spread of Cold-Water Species from the Paratethys to the Mediterranean Region

As paleogeographic reconstructions [17,108,109,168] have shown, the Paratethys and its predecessor the Proto-Paratethys have become connected with the Mediterranean Sea many times and in many places. At the Cretaceous–Paleogene boundary, when the Paratethys was beginning to become isolated, the two seas were separated by only a chain of islands, and aquatic organisms could disperse through numerous straits between them during this period (Proto-Paratethys Sea: [108,109]). Probably, the emergence of a number of Mediterranean genera of the family Unionidae (*Potomida*, *Microcondylaea*, *Leguminaia*, and *Unio*) that have sister groups in East Asia, the native land of this family, should be dated to this epoch.

However, the spread of cold-water aquatic organisms into the Mediterranean from the area of the present-day Black Sea in the later period (Neogene–Quaternary) was, apparently, difficult or even impossible. Most likely, this is why neither European taimen nor margaritiferid mussels parasitizing salmonids migrated to the Mediterranean, although both groups, according to paleontological data, already lived in the area of the modern Black Sea basin at that time [80,84–86]. Our study of the mitochondrial *COI* gene diversity has demonstrated that the brown trout populations of the Black and Caspian seas are characterized by different groups of haplotypes, whereas the Mediterranean populations of this species have the haplotypes found in the Caspian basin (or those directly originating from them). In turn, the haplotypes similar to those that are common in the Black Sea basin are found only in a few populations of the northern coast of the Mediterranean Sea, i.e., the haplotypes of the Black Sea group are not characteristic of this region [76].

We concluded from these data that the brown trout likely migrated to the Mediterranean through the Araks Strait directly connecting the northeast part of this sea with the modern Caspian Sea area in the Upper to Middle Miocene, 15–20 Mya (Figure 1, arrow 2).

Apparently, together with the brown trout, its parasite *Echinorhynchus baeri* Kostylev, 1928 (Acanthocephala) also crossed the area of the current watershed between the Caspian Sea and the Indian Ocean. *E. baeri* has been described as endemic to Lake Sevan (the Caspian Sea basin), but it has recently been discovered in the Euphrates River basin [169].

Obviously, the ancestors of the schizothoracine fish *Schizothorax prophyllax*, which lives in the south of the Asian part of Turkey and is absent both in the rest of the Mediterranean and in the Black Sea basin, also migrated via the Araks Strait.

Analysis of paleontological data shows that representatives of the gastropod genus *Ecrobia* also dispersed through this strait. As noted above, they are found in the Middle and Upper Miocene deposits of the southern coast of the Caspian Sea, in Iran [116], where the northeastern part of the Araks Strait was situated. Moreover, by the end of the Miocene, they appeared in the northeastern Mediterranean [117], i.e., in the southwestern part of the Araks Strait.

Interestingly, the Northeastern Mediterranean is inhabited by the bivalve mollusk that was previously considered an endemic species *Anodonta pseudodopsis* Locard, 1893; however, molecular genetic analysis revealed that it belongs to one of the phylogenetic lineages of the European duck mussel *Anodonta anatina* (Linnaeus, 1758) (Unionidae), which is also widespread in the Caspian Sea basin [101].

It is also remarkable that the endemic Greek lamprey *Eudontomyzon hellenicus* is genetically similar to the Caspian lamprey *Caspiomyzon wagneri* but differs significantly from the lampreys inhabiting the Black Sea basin [135], apparently, the ancestor of *E. hellenicus* also entered the Mediterranean through the Araks Strait.

According to Mordukhay-Boltovskoy [170], *Cornigerius lacustris* (Spand, 1923), a crustacean of Caspian origin, inhabits the Euphrates basin, which also agrees with the assumption that the ancestors of this species dispersed from the Caspian along the Araks Strait.

The migration of cold-water species from the Black Sea basin to the Mediterranean apparently occurred much later and on a limited scale. In particular, the mollusk *Ecrobia maritima*, typical of the Black Sea [112], and individuals of brown trout carrying the mitochondrial DNA haplotypes typical of the Black Sea basin [76] are quite rare in the Mediterranean basin.

The Balkan Peninsula, which is rich in cold water bodies, including the karstic ones, proved to be the most favorable habitat for the cold-water invaders in the Mediterranean [19]. Some cold-tolerant taxa occur only in the Balkan Peninsula (the nine-spined sticklebacks and the lamprey *Eudontomyzon hellenicus*); furthermore, the most ancient haplotypes of some aquatic taxa widespread in the Mediterranean region (the noble salmon and three-spined sticklebacks) are found in this area [49,64,76,135].

The Balkan Lake Ohrid harbors an especially large number of cold-water species [19]. Current studies of the Lake Ohrid biota have confirmed the high degree of endemism and the antiquity of its fauna; it has been found that some of its elements are older than the lake itself, the bottom sediments of which began to form about 1.36 Mya (see [171] for review). In particular, representatives of the genus *Gammarus* Fabricius, 1775 (Amphipoda) appeared on the Balkan Peninsula even before the emergence of Lake Ohrid [172]. This is evidenced by the fact that different phylogenetic lineages of *Gammarus* descending from a common ancestor are widespread throughout the Balkan Peninsula, but only one of them is represented in Lake Ohrid, which served as an Ice Age refugium for many species [173].

The cool mountain streams of the Mediterranean region and the upper Euphrates basin, in which unique species of freshwater mollusks of the family Unionidae have survived, also play an important role in the preservation of the relict fauna. This family is represented here by relict genera exhibiting direct genetic relationships with the Eastern Asian fauna [99,101,105].

The dispersal of animals from the Paratethys was mainly directed westward. However, a representative of a typical Ponto-Caspian genus of bivalve mollusks, *Monodacna* Eichwald, 1838, has recently been found in the Neopleistocene sediments of Transbaikalia [174]. This genus has not been recorded from the earlier strata in the region. The earliest known representative of *Monodacna* lived in the Pliocene in the southwest of modern Anatolia [175], and this suggests dispersal of some taxa from the Paratethys in the northeastern direction (Figure 1, arrow 5). At the same time, it is obvious that further study is required to fully understand the ways and mechanisms of *Monodacna* migration to southeastern Siberia.

#### 4.3. Dispersal of Cold-Water Species from the Ponto-Caspian and Mediterranean to Northern Europe and North America

Although the Paratethys lost its direct connection with the Atlantic and Arctic oceans in the Upper Miocene [17], aquatic animals may have sometimes migrated from the Paratethys to the basins of these oceans as a result of rare events of watershed interception caused by geological processes, primarily of orogenic nature (Figure 1, arrow 4). Apparently, this is how the carriers of one of the haplotypes characteristic of the Black Sea brown trout invaded the Rhine basin, the upper reaches of which were then part of a vast water system, now narrowed to the Danube basin [76]. Probably, the European pearl mussel migrated to the Rhine basin from the area of the present-day Black Sea basin together with the brown trout. The same route of dispersal is most likely for the gastropod *Ecrobia polysarca*, which lived on the Atlantic coast of modern France in the Neogene, and for one of the phylogenetic lineages of the three-spined stickleback, which transferred the ancestor of the trematode *Magnibursatus caudofilamentosa* to Northern Europe from the Black Sea basin. As noted above, this parasite has been found in three-spined stickleback living off the coasts of Denmark [65] and Northern Germany [176].

At the same time, the connection of the Paratethys with the Atlantic through the Mediterranean Sea and the Strait of Gibraltar was preserved even when the direct connection with the Atlantic Ocean had already been interrupted [17]. Recent genetic data show that some forms that migrated from the Paratethys to the Mediterranean Sea spread later to the Atlantic and reached the Arctic regions of Europe, migrating northward along the coast. Moreover, having passed through the Strait of Gibraltar, representatives of these forms crossed the ocean and reached North America, after which they dispersed along its eastern coast up to the Arctic regions (Figure 1, arrow 3).

Analysis of the median-joining network of the COI mitochondrial gene has revealed that the modern populations of the brown trout from Morocco are most closely related to the common ancestor of the northern European brown trout (subspecies *Salmo trutta trutta*), the Atlantic salmon, and two endemic species of this genus, one of which, *S. ohridanus* Steindachner, 1892, inhabits Lake Ohrid and another, *S. obtusirostris* (Heckel, 1851), occurs only in the Adriatic basin rivers [76].

As noted above, representatives of three genera of seals (Phocidae) migrated along with the noble salmon across the Strait of Gibraltar to the Atlantic and then to the Arctic. Isopod crustaceans of the genus *Jaera* Leach, 1814 [177] were also among the species that migrated from the Mediterranean, inhabited the Atlantic, and reached the Arctic Ocean.

Analysis of the median-joining network of the *Cyt b* gene has demonstrated that the so-called transatlantic lineage of haplotypes of the three-spined stickleback very early separated from the ancestral haplotype of European populations. Representatives of this lineage (along with those of the so-called European lineage) spread across Europe and crossed the Atlantic Ocean [64].

There are grounds to believe that the Mediterranean was also the initial point of dispersal of the gastropod species *Ecrobia ventrosa* across Western and Northern Europe and that it spread along the same route as the noble salmon did (see Section 3.7). Most probably, *Ecrobia* mollusks in North America are also of the Mediterranean origin, their ancestors having migrated there following the path of the ancestors of the Atlantic salmon. This conclusion is based on the fact that *E. maritima*, a species close to the North American species *E. truncata*, lives in the Adriatic Sea [112], in the same region as *Salmo obtusirostris*.

Interestingly, the Adriatic Sea fauna includes some representatives of a typical marine fauna that also occur off the coast of Scandinavia (the nemertean species *Callinera buergeri* Bergendal, 1900) or in the White Sea (the hemichordate *Saccoglossus mereschkowskii* (Wagner, 1885)) [178]. It seems that the Adriatic is now the only part of the Mediterranean where cold-tolerant species can find suitable environmental conditions.

#### 4.4. Evolutionary and Ecological Characteristics of Fresh- and Brackish-Water Cold-Tolerant Species of Southern Europe

Due to the abundance and good preservation of aquatic mollusk shells in the Paratethys fossil record, the evolution of this group has been studied particularly well. It has been used as an example to show that the evolutionary processes in the Paratethys basin were intense and rapid owing to frequent changes in the paleoenvironment (sea-level fluctuations, connections and isolation of water bodies, fluctuations of salinity, etc.). As a result of a series of habitat transformations in the Paratethys basin, mass extinctions periodically occurred, but the extinct species and genera of mollusks were quickly replaced by descendants of the surviving taxa, which occupied the vacated niches. At the same time, the descendants sometimes acquired completely new adaptations that were not characteristic of the ancestral taxa: “Partly vacant ecological niches were occupied with newly emerging species in groups that did not previously contain the corresponding life forms (supralimital specialization)” [179] (p. 412).

Apparently, similar processes also occurred during the evolution of other cold-water aquatic organisms discussed here. For example, there is practically no doubt that precisely the Paratethys was the place of origin of the burbot, the only species of the cod family that switched to the freshwater environment. There is reason to believe that this happened in one of the isolated (or semi-isolated) parts of the Paratethys due to its gradual desalination.

Another example is lymnaeid snails of the genus *Radix* Montfort, 1810, which is represented in the modern fauna only by freshwater forms. Nevertheless, the fossil record shows that mollusks morphologically similar to the extant members of this genus gave rise, in the course of their evolution in the Paratethys, to some forms capable of surviving at a high salinity [155]. These forms are currently regarded as a separate subfamily (or even family), Valencienniinae Kramberger-Gorjanovic, 1923 [180,181]. It is possible that the adaptability of the ancestors of the extant *Radix* species to high salinity has allowed them not only to populate the Paratethys, but also to repeatedly colonize mineralized hydrothermal springs and brackish lakes after that [110,156,182–184].

Due to repeated changes in salinity and temperature in individual semi-isolated parts of the Paratethys, many modern aquatic organisms of the Paratethys origin are characterized by high eurythermy and euryhalinity and have retained a high evolutionary potential. An exception is freshwater pearl mussels (Margaritiferidae), which disperse mainly at the stage of parasitic larvae and can serve as a good example of phylogenetically immobilized organisms [185].

Like other species of unstable habitats [186], the hydrobionts considered in this paper exhibit a high phenotypic plasticity, whereas their molecular evolution, in contrast, has been slowed down to date. The noble salmons living in Southern Europe [74,76] is a striking example of such organisms. The most ancient haplotype of the brown trout has been preserved in populations separated by thousands of kilometers, in the basins of the Aral, Caspian, and Mediterranean seas.

However, although the molecular evolution of the noble salmons and other Southern European species living under unstable conditions has been slowed down, some of them (e.g., the three-spined stickleback and noble salmons), having colonized new, northern habitats, gave rise to several rapidly evolving lineages. In particular, a new species, the Atlantic salmon, has originated from the northern populations of the brown trout.

Apparently, the long stay under unstable abiotic environmental conditions accounts for the high adaptive potential of a number of aquatic organisms that still inhabit the Ponto-Caspian basin (the largest remnant of the Paratethys). These adaptive capacities determine the possibility of their dispersal far beyond their native ranges, and this process not only continues, but has considerably accelerated due to human activities, especially the construction of canals and the development of navigation. In recent decades, several Ponto-Caspian species have invaded central Europe [187], Northern Russia [24], and even the Great Lakes of North America [188].

Thus, the large-scale westward migration of aquatic organisms from eastern Eurasia, the intensity of which decreased millions of years ago after the disappearance of the network of water bodies in Middle and Central Asia, has resumed recently.

## 5. Conclusions

Cold-water fauna spread from Asia to the area of modern Europe not only through Siberia; apparently, the Southern Asian route of westward migration via the Paratethys played a much greater role. Some planarians and unionids probably spread via this route, which ran through modern Central and Middle Asia, in the Late Mesozoic to Early Cenozoic; during the Oligocene, this was the route of dispersal of schizothoracine fish, the ancestors of some genera of nemacheiline loaches, freshwater pearl mussels, some salmonid and stickleback species, and numerous thermophilic aquatic organisms.

A well-grounded hypothesis on the dispersal of aquatic organisms through the aquatic systems of Middle and Central Asia that have disappeared since then largely explains the emergence of disjunct (European–Far Eastern) ranges of many groups of freshwater hydrobionts.

The Paratethys and its basin were the places of intense evolution of cold-water migrants from the Pacific Ocean coast and taxa originating in Central Asia mountains, and adaptation of some marine groups to fresh water. As a consequence, the genera *Salmo*, *Caspiomyzon*, *Potomida*, *Microcondylaea*, *Leguminaia*, *Unio*, *Ecrobia*, and, probably, *Lota*, arose.

The most intense migration of cold-tolerant forms from the Paratethys into the Mediterranean took place in the Miocene from the area of the present-day Caspian Sea through the Araks Strait.

The Ponto-Caspian and Mediterranean basins were the starting points of the dispersal of some cold-tolerant and euryhaline aquatic organisms (including the noble salmon, three-spined stickleback and its parasite *Magnibursatus caudofilamentosa*, European pearl mussel, seals, gastropods of the genus *Ecrobia*, and isopods of the genus *Jaera*) that reached the Atlantic and gained a foothold in Northern Europe and North America.

Many cold-tolerant species of the Ponto-Caspian and Mediterranean basins have repeatedly shifted from one environment to another in the course of their evolution; therefore, they have acquired high levels of eurythermy and euryhalinity and, hence, retained a high evolutionary potential. Although their molecular evolution is slow, they gave rise to a number of rapidly evolving forms; in particular, the Atlantic salmon has evolved from the brown trout still inhabiting the region of origin.

The Ponto-Caspian region still remains an important reservoir of species colonizing fresh- and brackish-water systems of Europe and even North America; some Ponto-Caspian migrants have managed to spread far beyond their native range in the past decades.

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