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Review

Amphiboreality and Distribution of Snailfishes (Cottiformes: Liparidae) in the Arctic and the North Atlantic

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Abstract: The marine ichthyofauna of the Arctic Ocean has an ancestral origin from the Pacific Ocean and, to a lesser extent, from the Atlantic Ocean, which is explained by the amphiboreal concept, developed on groups of fish and invertebrates. Snailfishes (Liparidae) of the Arctic and the North Atlantic are analyzed in the context of this amphiboreal concept. The review is based on the data of many years of research on their taxonomy using various material of morphological differences/similarities of the taxa and patterns of species distribution against the background of biogeographic representations. For the Arctic area, 33 species of the family are known: *Liparis* (5), *Careproctus* (21), *Paraliparis* (2), *Rhodichthys* (2), and *Psednos* (3). For the Atlantic fauna, with the same number of species, their composition differs: *Liparis* (6), *Careproctus* (3), *Paraliparis* (12), *Psednos* (11), and *Eutelichthys* (1). The amphiboreal concept explains the speciation of *Liparis* and the majority of *Careproctus* as the result of trans-Arctic preglacial migrations. For other (deep-sea) species, the hypothesis of a transoceanic dispersal route is applicable; it passed from the North Pacific through the Southern Ocean and then north across the Atlantic.

Keywords: amphiboreal concept; *Careproctus*; *Liparis*; *Paraliparis*; *Psednos*; *Rhodichthys*

Citation: Chernova, N.V. Amphiboreality and Distribution of Snailfishes (Cottiformes: Liparidae) in the Arctic and the North Atlantic. *Diversity* **2022**, *14*, 1097. https://doi.org/10.3390/d14121097

Academic Editor: Bert W. Hoeksema

Received: 15 September 2022
Accepted: 6 December 2022
Published: 11 December 2022

1. Introduction

The marine fish fauna of the Arctic Ocean cannot be considered in isolation from the neighboring regions; most of the families of fishes and other animals inhabiting it are associated by their root origin to the northern parts of the adjacent Pacific or Atlantic Oceans [1–9]. Fish families of Pacific origin are Osmeridae, Stichaeidae, Lumpenidae, Pholidae, Zoarcidae, Cottidae, Psychrolutidae, Agonidae, Cyclopteridae, Liparidae, and Sebastidae [3–5]. Each of these families, richly represented in the Pacific Ocean, has a few cold-water Arctic species; they also contain some Atlantic boreal taxa, and the latter have an undoubted morphological and genetic similarity with their Pacific relatives. Families and groups of Atlantic origin are less numerous: Gadidae, Gasterosteidae, Scophthalminae (genera *Scophthalmus*, *Lepidorhombus*, *Phrynorhombus*, and *Zeugopterus*), Anarchichadidae, Petromyzonidae, and subfamily Ammodytinae (*Ammodytes*, *Gymnammodytes*, and *Hyperoplus*) [5]. As in previous cases, they include several Arctic representatives and some Pacific boreal species similar or identical to their Atlantic congeners. Thus, species of these families are subdivided into similar groups according to their range types and taxonomic rank [3,10].

First, the Pacific families have boreal–Arctic species that extend northward beyond the Bering Strait, where they are continuously distributed west- and eastward, and their Arctic populations are indistinguishable from the Pacific ones. The boundaries of their distribution in the Arctic are different, but some of them reach the Barents Sea in a western direction (*Icelus spatula*, *Triglops pingelii* in Cottidae, and *Lumpenus medius* in Stichaeidae) or Greenland in an eastern direction (*Myoxocephalus scorpioides* in Cottidae and *Eumesogrammus praecisus* in Stichaeidae). Another group consists of endemic cold-water Arctic species that are absent in the Pacific Ocean or only enter the northern coldest part of the Bering Sea, but do not enter boreal (temperate) waters further south (*Myoxocephalus quadricornis*, *Artediellus* *scaber, Gymnacanthus tricuspis* in Cottidae, and *Lycodes polaris* in Zoarcidae). The third group includes several amphiboreal taxa of Pacific origin, which in the boreal Atlantic taxonomically distinguished to the rank of species or even genera. Amphiboreal (from the Greek amphi—around, on both sides) taxa are represented in the boreal regions of the Atlantic and Pacific Oceans. In total, there are up to several dozen amphiboreal groups of fishes and invertebrates [3,6,10]. Their rank is different.

Among fishes, amphiboreal ranges (interrupted in the Arctic) are demonstrated by species: Arctic lamprey *Lethenteron camchaticum* (Petromyzontidae); capelin *Mallotus villosus* (Osmeridae); three-spined stickleback *Gasterosteus aculeatus* (Gasterosteidae); sanlance *Ammodytes hexapterus* (Ammodytidae); and Greenland halibut *Reinhardtius hippoglossoides* (Pleuronectidae). There are pairs of closely related species: oceanic herrings (*Clupea harengus* in the Atlantic and *C. pallasii* in the Pacific); cods (*Gadus morhua* and *G. microcephalus); smelts* (*Osmerus eperlanus* and *O. dentex*); halibuts (*Hippoglossus hippoglossus* and *H. stenolepis*); and wolf fishes (*Anarhichas lupus* and *A. orientalis*, Anarhichadidae). An amphiboreal distribution is found among representatives of the poachers Agonidae, sculpins Cottidae, and eelpouts Zoarcidae. Some Pacific families are represented in the Atlantic Ocean by separate genera (*Taurulus* in Cottidae, *Agonus* in Agonidae, *Cyclopterus* in Cyclopteridae, and *Ulvaria* and subgenus *Chirolophis* in Stichaeidae).

The reasons for the existence of such types of taxa and their ranges are explained by the amphiboreal concept developed for groups of fishes and invertebrates [2–4,6,10–14]. A brief overview of this hypothesis is as follows: The formation of amphiboreal taxa is associated with migrations of the North Pacific fauna through the Arctic shelf during preglacial boreal transgressions and the rupture of their ranges during the Ice Age (and the same, although on a smaller scale, is applicable to the Atlantic fauna).

Usually, two periods of different time migrations through the Bering Strait region are accepted, Pliocene (preglacial) and postglacial [2,5,6,10,11,13,15–23]. The results of Pliocene migrations through the Bering Strait, which was open at the end of the Miocene ca. 5.32 Ma [24], were well-specified amphiboreal species or even genera. The dispersal proceeded along the coasts of Siberia or through the American Arctic. The desalination-resistant species (Petromyzontidae, Osmeridae, and Pleuronectidae) probably migrated mainly along the Asian coast influenced by the flow of the great rivers. Thus, different migration routes can explain the derivation of different amphiboreal groups of species on both sides of the North Atlantic.

The Pacific–Atlantic transition of fauna prevailed, and only separate groups (Clupeidae and Gadidae) migrated in the opposite direction, from the Atlantic to the Pacific. The advantage of the Pacific–Atlantic direction is explained by the greater diversity of the more ancient Pacific fauna compared to the Atlantic, because statistically, the richer the fauna is in species, the more of them can settle through the opened strait. Another reason may lie in the prevailing direction of the currents.

During the Ice Age, the ice sheets occupied the Eurasian shelf at least four times: in the Late Saalian (>140 ka), the Early Weichselian (100–80 ka), the Middle Weichselian (60–50 ka), and the Late Weichselian (25–15 ka) periods [25]. The largest glaciers covered a huge area from the modern British Isles to Severnaya Zemlya [26]. The Bering Land Bridge existed, closing the passage from the Pacific Ocean to the Arctic [27]. The boreal fauna, which earlier occupied a vast range from the North Atlantic to the eastern Arctic, became extinct in the glaciated areas. A few elements could have been preserved in free of ice refugia; some others may have escaped from the glaciers to the bathyal depth. Cold-water fauna began to form in the cool region of the glacier-free Siberian shelf and in periglacial freshwaters. In the Atlantic, the boreal fauna retreated southward; some species could reach the Mediterranean and even the Southern Hemisphere (sandlances *Gymnammodytes*). In isolated populations, further evolutionary processes may have led to the formation of new species, including bathyal ones. The interglacial migrations may have occurred more than once, which explains the varying degree of morphological and genetic differentiation among amphiboreal taxa or populations.

Postglacial migrations were associated with the postglacial climatic optimum and boreal transgression when the Bering Strait became open (since 11 cal ka BP) [13,27–29]. This resulted in a wide distribution of shelf Pacific species into the Arctic, but since then, they have not had time to noticeably separate from the Bering Sea populations. The climate in Central Siberia has become harsher [30,31], and even the most thermophilic fishes died out there [32], and discontinuous ranges of some species have formed.

As an example, the history of the speciation of the genus *Icelus* (Cottidae) was shown [3,33]. The genus includes at least 18 species, most of which are in the Pacific Ocean. In the Pliocene, a member of the genus migrated into the Arctic and dispersed across the waters of North America to the northwestern Atlantic, where the recent species *I. bicornis* was formed. With the end of the Ice Age, this fish spread further east, occupying ice-free waters and is currently distributed along the entire Asian shelf. During this time, several related species differentiated in the North Pacific (*I. uncinalis* and *I. spatula*). Of these, during the postglacial transgression, *I. spatula* spread through the Bering Strait into the Arctic; it is currently distributed westward to the Barents Sea and eastward to Greenland. Thus, the result of preglacial migration from the Pacific Ocean is the species *I. bicornis* with the Atlantic–Arctic range. The product of postglacial migrations is the boreal–Arctic range of the Pacific species *I. spatula*, which is continuously distributed in the Sea of Okhotsk, the Bering Sea, and the Arctic.

A similar dispersal history was shown for other sculpins of the Pacific genus *Triglops* [34]. As a result of the Pliocene migrations, the boreal Atlantic species *T. murrayi* was formed in the North Atlantic. During the Ice Age, *T. nybelini* was specified as being endemic to the Arctic. In the postglacial time, the Pacific species *T. pingelii* expanded its distribution and currently has a wide boreal–Arctic range.

Another example is given by the interrupted range of the family Stichaeidae [3]. This group is most diverse in the North Pacific, where the primitive *Stichaeus* and the most derived *Stichaeopsis* and *Plagiogrammus* exist. In the western North Atlantic, there is an endemic genus *Ulvaria* (*U. subbifurcata*), whose ancestors, apparently, could have spread to the Atlantic in the preglacial time. Two species with an amphiboreal distribution, *Stichaeus punctatus* and *Eumesogrammus praecisus*, appear to have spread during the posglacial migration of the Pacific fauna.

An interesting case is represented by the anadromous Arctic lamprey *Lethenteron camtschaticum*, whose range is widely interrupted in the Laptev and East Siberian Seas, but a related, nonmigratory freshwater form *L. kessleri* (or *Lethenteron camtschaticum kessleri*) continuously settled in river basins [3,9]. The presence of these relict freshwater populations indicates that in the warm postglacial period, the range of the anadromous lamprey could also be continuous from the Far East to the White Sea, but due to subsequent climate cooling, it disappeared along the Siberian coast.

Liparids (or snailfishes) constitute a significant part of the fauna of the North Pacific; in the Arctic and the North Atlantic, at least five genera are present, but the family has not been analyzed within the framework of amphiboreality. Only the genus *Liparis* was briefly noted in this context [7]. The main aim of this review is to consider whether the amphiboreal concept is applicable to explain the modern ranges and species content of northern Liparidae. The idea was to analyze the issue in a broad way, covering all species of each genus inhabiting northern waters. This requires presenting the species composition of snailfishes living in the Arctic and the North Atlantic. Then we consider each genus from these regions and whether they contain amphiboreal species or groups. This will allow us to discuss whether the probable ways of their distribution and speciation fit into the context of the amphiboreal concept.

2. Materials and Methods

The review is based on Liparidae materials from the Arctic and adjacent areas, studied over many years of practical research in taxonomy and related disciplines (Table 1). Specimens of all four genera involved in the consideration were studied: *Liparis*, *Careproctus*, *Paraliparis*, *Rhodichthys*, and *Psednos* [35–43]. Materials of liparid species related to the theme were also researched [44–48].

Table 1. Volume of processed material of fishes of the family Liparidae, number.

Genera	Species	Specimens	Stations/Lots	Radiograms
Liparis	55	1555	525	359
Careproctus	27	549	192	142
Paraliparis	67	229	140	183
Psednos	32	42	39	45
Rhodichthys	2	7	5	5
Total:	183	2382	901	734

The subgenera and the species groups in the genus *Liparis* are given according to the review [39]. The composition of the genus *Careproctus* from the Arctic and North Atlantic is based on the published revisions [37,38], as well as on the original descriptions of eight species [36,38,40,41]. *Careproctus* of the North Pacific region was studied in connection with the problem of the systematic position of *C. gelatinosus* [37] and the redescription of the deep-sea *C. hyaleius*, the only snailfish known from the hydrothermal vents [49]. The original descriptions and reliable literary sources were used for morphologic data [50–59]. The *Careproctus* species of the Southern Ocean was analyzed when assisting Anatole Andriashev in preparing his monograph on Liparid fishes of the Southern Ocean [60]. In addition, when describing *C. paxtoni* [61], ten southern species were studied for comparison.

Methodology. To show the background, after a brief overview of the family Liparidae, the species composition for the Arctic and the North Atlantic is given. The genus *Liparis* was then analyzed for the presence of amphiboreal species or groups. The same was performed for *Careproctus* and other genera. Next, the probable ways of distribution and speciation of these taxa were discussed in the context of the amphiboreal concept.

The borders of the Arctic region are considered within the biogeographic boundaries substantiated earlier [62,63]. The area covers the Arctic shelves, the Central Arctic Basin, and the polar basins north of the Greenland–Iceland–Faroe Ridge, which delimits the neighboring (Polar and Atlantic) deep basins.

Morphological characteristics mentioned in the text. The head pore formula (e.g., 2−5−7−2) is consistent with Burke [53] and many subsequent studies of snailfishes; they are listed in order: nasal, infraorbital, preoperculo–mandibular, and suprabranchial.

The formula of the pectoral radials is given according to Andriashev [60]: Rad 4 (3 + 1) means a normal (*Liparis*-like) arrangement of four radials (three upper and one lower, separated by space); 4 (1 + 1 + 1 + 1) means that the radials are equidistant; 3 (2 + 0 + 1) means the absence of the third radial of the normal set; similarly for 3 (1 + 0 + 1 + 1), 2 (1 + 0 + 1) or 1 (0 + 0 + 1).

Designations: sg.—subgenus, *SL*—standard length, *TL*—total length; number of rays in *D*—dorsal, *A*—anal, *P*—pectoral, and *C*—caudal fins; *vert.*—number of vertebrae.

3. Results

3.1. Overview of the Family Liparidae

Snailfishes are a specialized branch of the Cottoidei [64]. In generalized species, their ventral fins are modified into a sucking disk (secondary reduced in some genera); the teeth system consists of three-lobed teeth, forming regular oblique rows; the skin has lost its scaly cover. It is a diverse family, with over 430 species from 32 genera worldwide [42,65], which are distributed in temperate and cold zones of both hemispheres and inhabit the deep water of five oceans. The vertical limits of their distribution are extremely wide because they are found in all bathymetric zones, from the littoral (*Liparis* and *Polypera*) to the abyssal plains (*Paraliparis*) and at the hadal depth of oceanic trenches up to 6–8 thousand meters

(*Pseudoliparis* and *Notoliparis*) [53,66–68]. Most snailfishes inhabit temperate areas, but they are also present in the Arctic and Antarctic, adapting to reproduce at negative temperatures. On the other hand, some south boreal species occur in waters with intensive summer heating, such as *Liparis franzi*, *L. chefuensis*, and *L. choanus* from the Yellow Sea [69] and *L. fishelsoni* from the Red Sea [70]. Many Liparid species are rare or known only from type specimens. Others are quite common and may form large aggregations; in the Sea of Okhotsk, the total biomass of snailfishes ranged from 32 to 51 thousand tons according to trawl surveys in 1997–2000 [71].

The adaptability of snailfishes is wide; along with stenohaline species, which prefer strict oceanic salinity, there are liparids that tolerate the desalination of estuaries and enter the lower streams of river (*L. liparis*). Some Arctic snailfishes (the group of *L. fabricii*) are temporarily sympagic, and their juveniles occur under the lower surface of drifting ice [72]. There are littoral species that use their sucking disk for attaching to stones and algal thalli. Other are demersal (*Liparis* and *Careproctus*) and common in shelf waters. Except for bathyal and abyssal liparids, benthopelagic and mesopelagic species exist, in which the ventral disk is reduced (for example *Nectoliparis*, *Paraliparis*, and *Psednos*) [54,60,73]. The striking diversity of liparids is the result of their evolutionary plasticity, which made possible an adaptive radiation into various habitats in different biogeographic and bathymetric zones of the World Ocean.

For the Arctic and the North Atlantic, updated data on the species composition of Liparidae are provided below.

In the Arctic area, five genera are known [35,46,74–76], and in this paper, the total number of species is 33: *Liparis* 5, *Careproctus* 21, *Paraliparis* 2, *Rhodichthys* 2, and *Psednos* 3, not including the boreal species (*L. liparis*, *L. montagui*, *Paraliparis copei*, *P. garmani*, *Psednos christinae*, and *Ps. groenlandicus*) that enter the marginal Arctic areas (Table 2). This number is incomparably less than the Pacific content of the family.

Table 2. List of Liparidae of the Arctic (including those entering marginal areas from the Atlantic).

Taxa	Range, Depth (m)	References
Genus *Liparis* Scopoli, 1777		
Subgenus *Liparis* Scopoli, 1777		
L. liparis (Linnaeus, 1766) *	SW Barents Sea (Murman), 0–78 m	[35]
L. montagui (Donovan, 1804) *	SW Barents Sea (Murman), 0–3 m	[35]
L. tunicatus Reinhardt, 1937	Circumpolar, shallow waters [35]; SW, NW, NE Greenland [77]	[35,77]
Subgenus *Careliparis* Garman, 1892		
"*L. megacephalus*" group		
L. bathyarcticus Parr, 1931 [1]	Obviously circumpolar, depth 12–510, usually 5–350 m [35]; Gulf of St. Lawrence [78]	[35,78]
Subgenus *Lycocara* Gill, 1884		
Liparis cf. *fabricii* complex [2]	Circumpolar, 12–628 (usually 40–350) m [39], near Greenland to 1460 m [77]; Gulf of St.Lawrence [78]	[39,77,78]
L. fabricii Krøyer, 1847		
L. koefoedi Parr, 1932		
L. laptevi Popov, 1933		
Genus *Careproctus* Kröyer, 1862 [3]		
Subgenus *Careproctus* Kröyer, 1862		
C. reinhardti sensu stricto (Krøyer, 1862) [3]	SW Greenland [37,79], Gulf of St. Lawrence [78]	[37,78,79]
C. longipinnis Burke, 1912	Norwegian Sea, north of Faeroe Islands, 1322 m	[37,80,81]
C. solidus Chernova, 1999	Laptev Sea, 2151–1934 m	[36,81]
C. lerikimae Orr, Kai et Nakabo, 2015	Beaufort Sea, depth 178 m	[81]
"*C. dubius*" group		
C. dubius Zugmayer, 1911	Spitsbergen, Havre Green, 150 m	[37,81]
C. derjugini Chernova, 2005	northeast of Spitsbergen, 344–363 m	[38]
C. knipowitschi Chernova, 2005	Barents Sea, 298–293 m	[38,82]
C. macrophthalmus Chernova, 2005	southwest of the Barents Sea, 260–275 m	[38,82]
C. tapirus Chernova, 2005	southwest of the Barents Sea, 170–320 m	[38]

Table 2. *Cont.*

Taxa	Range, Depth (m)	References
C. telescopus Chernova, 2005	Barents Sea, 260–307 m	[38]
C. fulvus Chernova, 2014	Kara Sea, Novaya Zemlya Trench, 190–414 m	[40]
C. rosa Chernova, 2014	southwest of the Kara Sea, 140 m	[41]
C. karaensis Chernova, 2014	Kara Sea, east of Novaya Zemlya, pelagic at 0−30 m	[41,81]
C. uter Chernova, 2014	Kara Sea, Novaya Zemlya Trench, 206 m	[41]
C. carinatus Chernova, 2014	southwest of the Kara Sea, pelagic at 0−30 m	[41]
Subgenus *Careproctula* Andriashev, 2003		
C. micropus (Günther, 1887)	Faeroe Channel, depth 540 and 608 fathoms (987–1112 m)	[37]
C. kidoi Knudsen et Møller, 2008	Baffin Bay; SW Greenland, NW Greenland, 952–1487 m	[77,83]
C. moskalevi Andriashev et Chernova, 2010	Norwegian Sea, southwest of the Bear Island, 1478–1691 m	[82,84]
C. latiosus Andriashev et Chernova, 2010	Norwegian Sea, southwest of the Bear Island, 1478–1695 m	[82,84]
C. mica Chernova, 2014	Kara Sea, Novaya Zemlya Trench, 204 m	[41,82]
C. canusocius Orr, 2020	Beaufort Sea, 488–599 m	[82]
Genus *Paraliparis* Collett, 1879		
P. bathybius (Collett, 1879)	Norwegian Basin, 1000–1847 m and pelagic at 20–1000 m; Faroe Trench, 1170 m; Central Polar Basin: northeast of Spitsbergen [35], north of the Laptev Sea, 2824–2775 m [75]; Greenland, benthopelagic, 545–1600 m [77]	[35,75,77,85–90]
P. copei copei Goode et Bean, 1896 *	SW, SE Greenland, benthopelagic, (360) 710–1460 (1902) m [77]; Gulf of St.Lawrence [78]. Elsewhere found in the North Atlantic (see Table 2)	[77,78]
P. garmani Burke, 1912 *	SW, SE Greenland, 550–987. Elsewhere found in WN Atlantic (see Table 2).	[77]
P. violaceus Chernova, 1991	Central Polar Basin, north of Severnaya Zemlya Archipelago, 2365 m	[35]
Genus *Rhodichthys* Collett, 1879		
Rh. regina Collett, 1879	Norwegian Basin, 1394–2341 m, Faroe Bank, 400–500 m; Baffin Bay, 1200–1800 m, NW Greenland, NE Greenland, benthopelagic at 1180–1480 m; Polar Basin: northeast of Spitsbergen, 1080–1090 m, north of Severnaya Zemlya, 1445 m	[35,77,91–96]
Rh. melanocephalus Andriashev et Chernova, 2010	Norwegian Basin, southwest of the Bear Island, 1470–1695 m	[84]
Genus *Psednos* Barnard 1927		
P. christinae Andriashev, 1992 (*)	SE Greenland, 843–854 m. Elsewhere found in the Mid-Atlantic Ridge (see Table 2)	[77]
P. gelatinosus Chernova, 2001	SE Greenland (63°05′54″ N), mesopelagic at 650–0 m	[46,77]
P. groenlandicus Chernova, 2001 (*)	SW Greenland (63–65° N) and SE Greenland (61°53′ N), mesopelagic at 786–1460 m. Elsewhere found in the Mid-Atlantic Ridge (see Table 2)	[46,77]
P. melanocephalus Chernova et Stein, 2002	SW Greenland, 58°15′ N, 0–3172 m and 64°03′ N, 926 m; 949–962 m	[77,97,98]
P. micruroides Chernova, 2001	SW Greenland (63°45′ N), 0–900 m and SE Greenland (63°50′18″ N), mesopelagic at 0–1333 m	[46,77,98]

* Boreal or (*) Atlantic mesopelagic species that penetrate the marginal waters of the Arctic. [1] After the revision [99], the species *L. gibbus*, that was described from the Bristol Bay of the Bering Sea, was accepted to occur circumpolarly [46,77]. Additional studies show that the Arctic specimens belong to *L. bathyarcticus*, described from Spitsbergen. [2] After the revision [99], the species *L. fabricii* Krøyer, 1847 was accepted to occur circumpolarly [46,77]. According to my studies, the Arctic specimens represent more than one species. [3] Some authors [100] regard that only one species (*C. reinhardti*) occurs all over the Arctic, which is at least strange, considering the diversity of *Careproctus* in the Pacific or the Antarctic.

In the boreal North Atlantic, the number of species is the same (33), although the composition of the genera differs: *Liparis* 6, *Careproctus* 3, *Paraliparis* 12, *Psednos* 11, and one *Eutelichthys* instead of *Rhodichthys* (Table 3).

Table 3. List of Liparidae of the North Atlantic.

Taxa	Range, Depth (m)	References
Genus *Liparis* Scopoli, 1777		
Subgenus *Neoliparis* Steindachner, 1876		
"*L. montagui*" group		
L. montagui (Donovan, 1804) *	Europe: from Portugal to Murman, intertidal and shallow waters	[35,39,90]
"*L. atlanticus*" group		
L. atlanticus (Jordan et Evermann, 1898)	WN Atlantic: Quebec, Newfoundland, Nova Scotia [99], Gulf of St. Lawrence [78]; intertidal to 90 m	[78,99]
"*L. grebnitzkii*" group		
L. inquilinus Able, 1973	WN Atlantic: from the Gulf of St. Lawrence to Cape Hatteras, 5–97 m	[101–103]
Subgenus *Liparis* Linnaeus, 1766		
L. coheni Able, 1976	WN Atlantic: Gulf of Maine, Nova Scotia, Gulf of St. Lawrence, 2–210 m	[104]
L. liparis (Linnaeus, 1766) *	Europe: from the North Sea to Murman; intertidal to 78 m	[35,39,90]
L. barbatus Ekström, 1832	Baltic Sea: Gulf of Finland, Gulf of Bothnia, shallow water, enters rivers	[35,105] (as *L.liparis barbatus*); [39] (as *L. barbatus*)
Genus *Careproctus* Kröyer, 1862		
Subgenus *Careproctula* Andriashev, 2003		
C. ranula (Goode et Bean, 1879)	WN Atlantic: Halifax Harbor, Nova Scotia, 95 m	[37,106]
"*C. merretti*" group		
C. merretti Andriashev et Chernova, 1988	EN Atlantic: Porcupine Seabight (49°37′ N, 13°49′ W), 3990–3920 m	[44]
C. aciculipunctatus Andriashev et Chernova, 1997	EN Atlantic: south of the Porcupine bank (50°13.8′ N, 14°36.1′ W), 4100 m	[45]
Genus *Paraliparis* Collett, 1879		
P. abyssorum Andriashev et Chernova, 1997	EN Atlantic: near the Porcupine Bank (49°54′ N, 13°56′ W), 3640–3715 m	[45]
P. bipolaris Andriashev, 1997	WN Atlantic: southwest of Ireland (50°12′ N, 13°40′ W), 3000–3040 m	[107]
P. calidus Cohen, 1968	WN Atlantic: Gulf of Mexico (27°25′ N, 93°40′ W), 730 m; Gulf of St. Lawrence	[78,108]
P. challengeri Andriashev, 1993	EN Atlantic: Rockall Trough (57°01′ N, 10°05′ W), Porcupine Seabight (49°46′ N, 12°31′ W), 2000–2100 m	[109]
P. copei copei Goode et Bean, 1896 *	WN Atlantic: 430–1980 m; described from the Long Island (39°12′17″ N, 72°09′30″ W), 951 m. EN Atlantic: 1125–1400 m. Elsewhere found near South Greenland (see Table 1).	[48,110], our data
P. edwardsi (Vaillant, 1888)	EN Atlantic: coast of Marocco, between Cape Spartel and Cape Blanko (33°46′ N, 9°02′ E), 1319 m	[108,111,112]
P. garmani Burke, 1912 *	WN Atlantic: from Labrador to Cape Hatteras; benthopelagic, 550–987 m. Elsewhere found near South Greenland (see Table 1).	[77,80]
P. hystrix Merrett, 1983	EN Atlantic: to the west of Britain, (49–59° N, 07–18° W), 255–1140 m [113]. WN Atlantic: (36–38° N, 70–74° W), 0–1008 m [90]	[90,113,114]

Table 3. *Cont.*

Taxa	Range, Depth (m)	References
P. liparinus (Goode, 1881)	WN Atlantic: southeast of Long Island, 891 m	[109]
P. murielae Matallanas, 1984	West of the Mediterranean Sea, 500–600 m	[115]
P. nigellus Chernova et Moller, 2008	North Atlantic: Mid-Atlantic Ridge, between the Azores and Charlie–Gibbs Fracture Zone, 1950–2107 m	[48]
P. vailanti Chernova, 2004	WN Atlantic: Laurentian Channel (46°39′ N, 58°41′ W), mesopelagic, 423 m over a depth of 1150 m	[116]
Genus *Psednos* Barnard, 1927		
P. andriashevi Chernova, 2001	EN Atlantic: west of Ireland (54°21′ N, 17°59′ W), mesopelagic at 800 m	[46]
P. barnardi Chernova, 2001	WN Atlantic: slope of New England (39°49′ N, 70°39′ W), mesopelagic at 1042–1368 m, juv at 750–1001 m	[46]
P. christinae Andriashev, 1992 (*),1	North Atlantic: Mid-Atlantic Ridge (49°48′ N, 25°55′ W), 1000–1500 m; Greenland (see Table 1)	[117]
P. delawarei Chernova et Stein, 2002	WN Atlantic: south of Cape Cod (39°48′05″ N, 70°43′28″ W), 0–1000 m	[97]
P. islandicus Chernova et Stein, 2002	EN Atlantic: 59°59.7′ N, 19°42.2′ W, 1250–1500 m	[97]
P. groenlandicus Chernova, 2001 (*)	North Atlantic: north of the Mid-Atlantic Ridge, mesopelagic, 981–2015 m over greater depth. Ellsewhere found near South Greenland (see Table 1)	[48]
P. harteli Chernova, 2001	WN Atlantic: 40°45′ N, 65°03′ W, 1008–0 m	[46]
P. mirabilis Chernova, 2001	WN Atlantic: slope of New England (39° N, 70°39′ W), 0–700 m over 1370–1700 m	[46]
P. rossi Chernova et Stein, 2004 2	WN Atlantic: Cape Hatteras (35°30.036″ N, 74°46.497″ W), 500–674 m over 900 m	[118]
P. sargassicus Chernova, 2001	Sargasso Sea (35°30′ N, 67°14′30″ W, 0–1050 m	[46]
P. spirohira Chernova et Stein, 2002	EN Atlantic: west of northern Spain (41°56.2′ N, 16°50.1′ W), 985–1010 m	[92]
Genus *Eutelichthys* Tortonese, 1959		
E. leptochirus Tortonese, 1959	EN Atlantic: southwestern part of the Mediterranean Sea and Bay of Lyon, 500–917 m	[90,112,119,120]

* Boreal or (*) mesopelagic species, which penetrate the marginal Arctic (waters of South Greenland and southwestern part of the Barents Sea). [1] The specimen from off Ireland was later described as *P. andriashevi* [46]. [2] *Psednos rossi* was separated in a new genus *Aetheliparis* Stein, 2012. Additional data are needed to decide on the validity of this genus.

3.2. Snailfishes of the Genus *Liparis*

The genus *Liparis* includes no less than 72 species, being one of the four largest genera of the family [39]. The genus is the most generalized [35,53,56,60,65]. Plesiomorphic characteristics include innumerous vertebrae (31–53), 2–4 pairs of long saber-shaped pleural ribs, two pairs of nostrils, three-lobed jaw teeth in regular rows, and presence of pseudobranchia. There is a large sucking disk (6.4–21.7% *SL* in diameter) modified from pelvic fins. The shoulder girdle of the pectoral fin possesses four notched radials and three large interradial fenestrae. The pectoral fin is notched and may include a large number of rays (up to 46). The anus and genital openings are open closer to the anal fin than to the ventral disk. In skin, green and orange pigments are present; the color is usually olive-brown, mottled, or striped. The length of most *Liparis* usually does not exceed 15–30 cm; the largest known length (*L. ochotensis*) is 74 cm [121]; the weight sometimes reaches 6 kg [122].

The species of the genus are distributed on the shelves of the Northern Hemisphere. The only species from the Southern Hemisphere, *L. antarcticus*, described from the coast of Chile, may have originated from the waters of California [123] (p. 60). The center of diversity of the genus is located in the northern part of the Pacific Ocean (81% of the species). Inside the Pacific, most of *Liparis* are found in Asian waters (83%), mainly in the Sea of Japan and Sea of Okhotsk.

The *Liparis* species is divided into five subgenera by morphological characteristics [39]; four of them (*Neoliparis*, *Liparis*, *Careliparis*, and *Lycocara*) are of interest for this review.

The subgenus *Neoliparis* is the most generalized and diverse, containing 26 species in six groups [39]. Although it is considered polyphyletic in a recent molecular study [65], I prefer to follow a taxonomic system based on morphology, until further synthetic studies are performed. Except for other characteristics, they all have a short caudal peduncle that includes up to three vertebrae. The dorsal and anal fins usually do not fuse with the caudal fin. Short gill openings are located above the base of the pectoral fin. Other species of *Liparis* lack a caudal peduncle; the dorsal and anal fins extend to the caudal fin, and the dorsal fin notch is usually absent or diminishingly small. In the boreal Atlantic, there are four species of this subgenus: *L. atlanticus*, *L. inquilinus*, and *L. coheni* inhabit the western North Atlantic; *L. montagui* occurs along the European shelf, and others live in the boreal North Pacific.

The subgenus *Liparis* is less diverse than the previous one and includes about eight species. All of them, in addition to similar counts, have teeth with lobes of the same size and short gill openings. Two species occur in the boreal Atlantic waters: *L. liparis* is found along the European shelf, and *L. barbatus* (which I consider in a rank of species) replaces the latter in the Baltic Sea. There is one species in the Arctic, *L. tunicatus*, which lives mainly in coastal areas.

The subgenus *Careliparis* includes about 30 species in five species groups [39]. Unlike other congeners, they all have large gill openings (reaching the level of 12th–19th rays of the pectoral fin) and three-lobed teeth with a noticeably larger central lobe; the body is usually deep and humpbacked. One of them, *L. bathyarcticus*, has an almost circumpolar distribution along the Arctic shelf; others live in the boreal Pacific waters.

The subgenus *Lycocara* includes at least three similar species with black-pigmented peritoneum and simple teeth (with reduced lateral lobes). They are *L. fabricii* sensu stricto (described from Bellsund, Spitsbergen), *L. koefoedi* (Green Harbor, Spitsbergen), *L. laptevi* (Laptev Sea), and some undescribed forms. They all are often considered as the *L.* cf. *fabricii* complex, which has circumpolar Arctic distribution. In the boreal waters of the Pacific Ocean, not a single congener with these characteristics is known.

3.2.1. *Liparis* of the Boreal Atlantic and the Arctic

The above shows, therefore, that only a few *Liparis* are found outside the Pacific Ocean. In the boreal Atlantic, there are six species, different from two sides of the ocean; *L. atlanticus*, *L. inquilinus*, and *L. coheni* inhabit the western North Atlantic; *L. montagui*, *L. liparis*, and *L. barbatus* are found in the eastern North Atlantic. Two of these species, *L. liparis* and *L. montagui*, may move northward within warm currents to the Murman Coast (in the western part of the Barents Sea), which is in fact the transitional area to the Arctic (in winter, the sea there is ice-free).

In the Arctic, *L. tunicatus* occurs at a shallow depth; *L. bathyarcticus* prefers deeper waters along the shelf edge. Representatives of the black-bellied complex *L.* cf. *fabricii* are found inshore and offshore, often among the ice. All of them, *L. tunicatus*, *L. bathyarcticus*, and *L.* cf. *fabricii* complex, have a circumpolar distribution and have adapted to live and reproduce in cold waters.

3.2.2. Groups of *Liparis* with Amphiboreal and Boreal–Arctic Distribution

In a frame of the amphiboreal concept, six groups of *Liparis* can be considered (Table 4).

Table 4. Groups of *Liparis* with amphiboreal and boreal–Arctic distribution.

North Atlantic	Arctic	North Pacific
Subgenus *Neoliparis* Steindachner, 1876		
"*L. montagui*" group		
* *L. montagui* Eur	–	*L. burkei* (Jordan et Thompson, 1914) Jap *L. chefuensis* Wu et Wang, 1933 Yell *L. petschiliensis* (Rendahl, 1926) Yell *L. punctulatus* (Tanaka, 1916) Jap
"*L. atlanticus*" group		
L. atlanticus WNA	–	*L. rutteri* (Gilbert et Snyder, 1898) Amer Ale *L. schantarensis* (Lindberg et Dulkeit, 1929) Okh *L. schmidti* Lindberg et Krasyukova, 1987 Jap
"*L. grebnitzkii*" group		
L. inquilinus WNA	–	*L. miostomus* Matsubara et Iwai, 1954 Hokk, Kam *L. kusnetzovi* Taranetz, 1935 Jap *L. mednius* (Soldatov, 1930) Com *L. grebnitzkii* (Schmidt, 1904) Com
Subgenus *Liparis* Scopoli, 1777		
L. coheni WNA * *L. liparis* Eur *L. barbatus* Balt	*L. tunicatus* circ	*L. brashnikovi* Soldatov, 1930 Jap, Kam *L. frenatus* (Gilbert et Burke, 1912) Jap, Hokk, Okh *L. marmoratus* Schmidt, 1950 Okh, Ber *L. bristolensis* (Burke, 1912) Ber, Al
Subgenus *Careliparis* Garman, 1892		
"*L. megacephalus*" group		
–	*L. bathyarcticus* circ	*L. meridionalis* Schmidt, 1950 Jap *L. punctatus* Schmidt, 1950 Okh *L. eos* Krasyukova, 1894 Sakh *L. rotundirostris* Krasyukova, 1894 Sakh *L. megacephalus* (Burke, 1912) eBer *L. brevicaudus* Mori, 1956 Jap *L. quasimodo* Krasyukova, 1894 Sakh *L. lindbergi* Krasyukova, 1894 Sakh
Subgenus *Lycocara* Gill, 1884		
–	*L.* cf. *fabricii* complex circ (*L. fabricii* s. str. Spits *L. koefoedi* Spits *L. laptevi* Lap)	–

* Boreal species, which penetrate the marginal waters of the Arctic (the Barents Sea). Designations of the distribution areas: Al—Alaska, Ale—Aleutian Islands, Amer—American Pacific, Balt—Baltic Sea, Beauf—Beaufort Sea, Ber—Bering Sea, circ—circumpolar distribution, Com—Commander Islands, e—eastern, Eur—Europe, Grenl—Greenland, Hokk—Hokkaido, Jap—Sea of Japan, Kam—west of the Kamchatka Peninsula, Lap—Laptev Sea, Okh—Sea of Okhotsk, Sakh—Sakhalin, Spits—Spitsbergen, St.Law—Gulf of St. Lawrence, WNA—western North Atlantic, Yell—Yellow Sea.

The "*Liparis montagui*" is the first group. The European *L. montagui* has a distinguishing characteristic; the posterior pair of nostrils is completely closed (no openings). The species with reduced posterior nostrils is absent in the Arctic, but there are four of them in the boreal Pacific: *L. punctulatus* in the Sea of Japan, *L. burkei* (sensu Kido 1988) on the Pacific side of Japan, and *L. chefuensis* and *L. petschiliensis* in the Yellow Sea (Figure 1). All five are similar to each other by other traits (including counts) and are members of the "*L. montagui*" group [39]. The distribution of this group is amphiboreal; one species occurs in the eastern North Atlantic, and four occur in the western North Pacific.

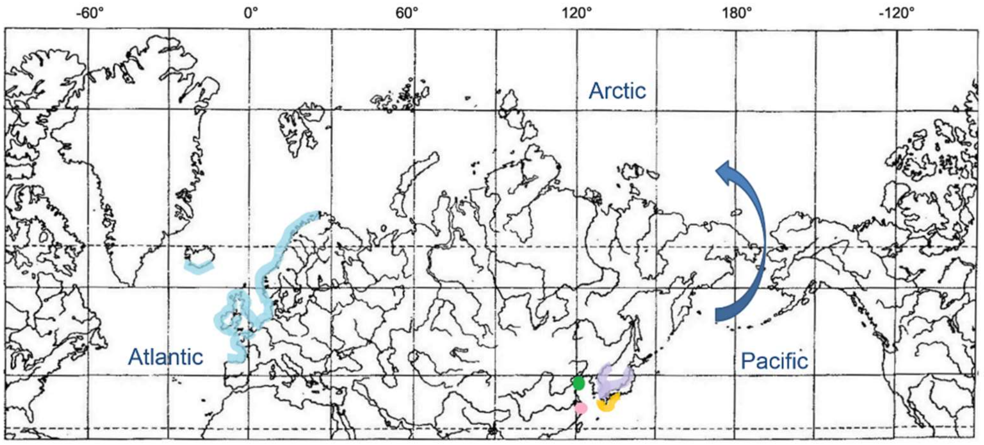


Figure 1. Distribution of "*L. montagui*" group in the Atlantic: blue line—*L. montagui*; in the Pacific: green dot—*L. petchiliensis*, pink dot—*L. chefuensis*, lilac line—*L. punctulatus*, and yellow line—*L. burkei*; arrow shows the most probable direction of the preglacial pathway.

Liparis atlanticus is characterized by a comb-like structure of the anterior part of the dorsal fin (each ray is separated). Similar species are absent in the Arctic, but there are three of them in the boreal Pacific Ocean: *L. schantarensis* (Sea of Okhotsk), *L. schmidti* (Sea of Japan), and *L. rutteri* (Aleutian Islands and American waters southward to California); they all represent the "*L. atlanticus*" group. The distribution of this group (Figure 2) is amphiboreal, with one species in the western North Atlantic and three species in the North Pacific.

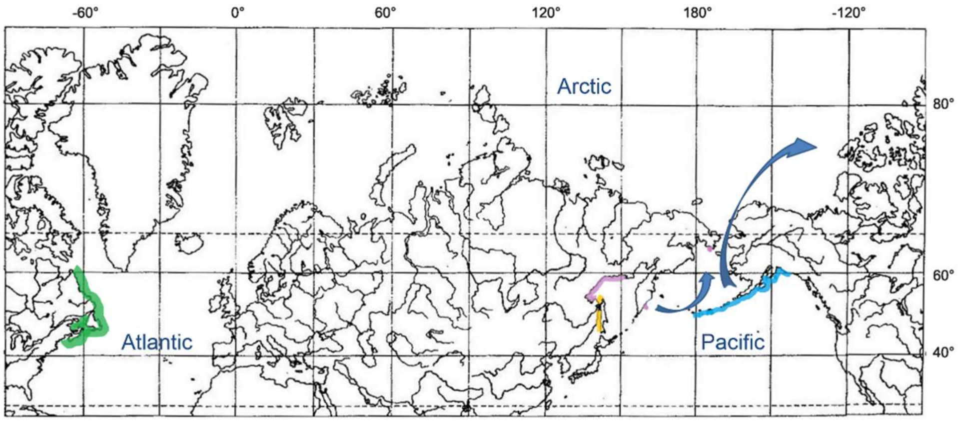


Figure 2. Distribution of "*L. atlanticus*" group in the Atlantic: green line—*L. atlanticus*; in the Pacific: lilac line—*L. shantarensis*, yellow—*L. schmidti*, and blue—*L. rutteri*; arrows show the most probable direction of the preglacial pathway.

A characteristic feature of the Atlantic snailfish *L. inquilinus* is the separated anterior lobe of the dorsal fin (with fused rays, such as in *Polypera*). Four species have the same characteristic, all from the western North Pacific: *L. grebnitzkii* (Peter the Great Bay, southeastern Kamchatka, and Bering Island), *L. mednius* (Commander Islands), *L. kusnetzovi* (Tatar Strait in the Sea of Japan), and *L. miostomus* (Hokkaido) (Figure 3). All are in the "*L. grebnitzkii*" group. The distribution of this group is amphiboreal.

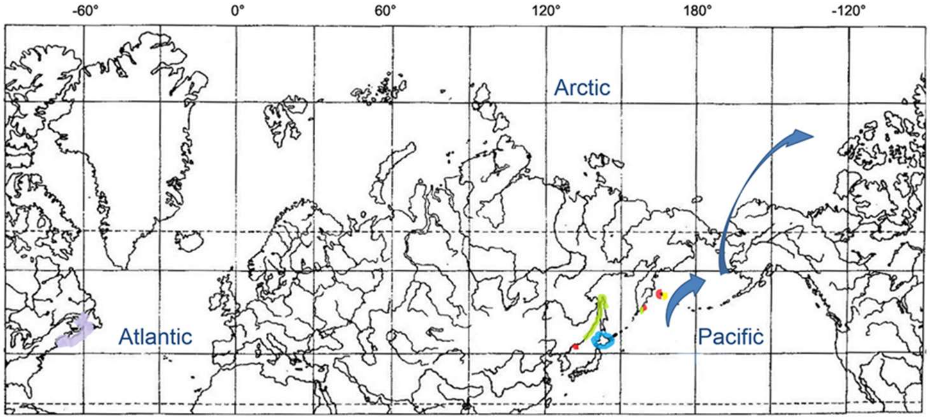


Figure 3. Distribution of "*L. grennitzkii*" group in the Atlantic: lilac line—*L. inquilinus*; in the Pacific: red dots—*L. grennitzkii*, green line—*L. kuznetsovi*, blue line—*L. miostomus*, and yellow dot—*L. mednius*; arrows show the most probable direction of the preglacial pathway.

Thus, three above-mentioned species groups ("*L. montagui*", "*L. atlanticus*", and "*L. grebnitzkii*") show examples of interrupted amphiboreal distribution, as they are absent in the Arctic and present in the boreal waters of the Atlantic and Pacific Oceans by distinct, well-defined species. All these groups have plesiomorphic characteristics and belong to the generalized subgenus *Neoliparis*.

The next group, the subgenus *Liparis*, is another example (Figure 4). Three species are present in the boreal Atlantic: *L. coheni* off the American coast, *L. liparis* along the European shelf, and *L. barbatus* in the Baltic Sea. In the Arctic, *L. tunicatus* is found, which is considered circumpolar (and the poorly studied *L. herschelinus* is described from Herschel Island at the mouth of the Mackenzie River). Four other species are known in the boreal Pacific: *L. brashnikovi* and *L. frenatus* (Sea of Japan and adjacent waters), *L. marmoratus* (Sea of Okhotsk and northern Bering Sea), and *L. bristolensis* (western Bering Sea). Thus, this group demonstrates an example of amphiboreal–Arctic distribution.

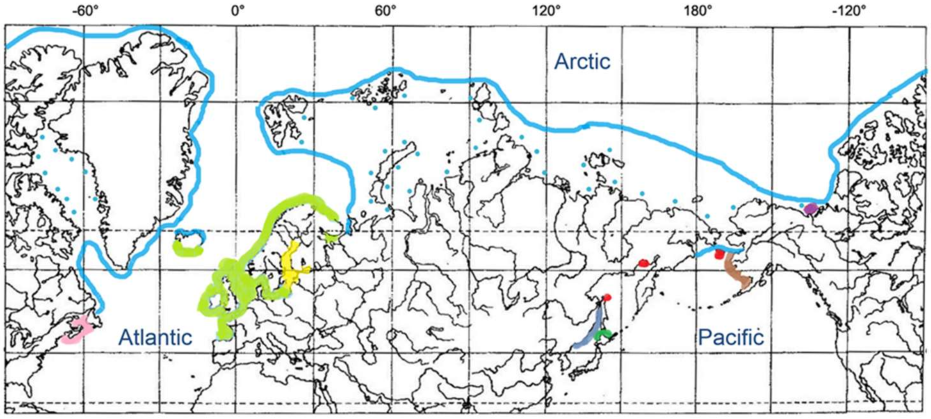


Figure 4. Distribution of the subgenus *Liparis* group in the Atlantic: lilac line—*L. coheni*, light green line—*L. liparis*, and yellow—*L. barbatus*; in the Pacific: red dots—*L. marmoratus*, dark green—*L. frenatus*, gray—*L. brashnikovi*, and brown—*L. bristolensis*; in the Arctic: blue line—*L. tunicatus* that occurs mainly in coastal zone (dots) and dark lilac—*L. hershelinus*.

The fifth group is represented by members of the subgenus *Careliparis*. The Arctic *L. bathyarcticus* is a member of the "*L. megacephalus*" group, in which the posterior pair of nostrils is reduced in size (to about half the size of the anterior pair). Eight other species, poorly studied, were described from the North Pacific: *L. eos*, *L. lindbergi*, *L. rotundirostris* and *L. quadrimodo* (all from off Sakhalin Island), *L. brevicaudus* (Sea of Japan), *L. megacephalus* (eastern Bering Sea), *L. punctatus* (Sea of Okhotsk), and *L. meridionalis* (Peter the Great Bay, Tatar Strait, and Aniva Bay). Thus, this group demonstrates an example of boreal–Arctic distribution, with most species in the North Pacific and one representative in the Arctic.

The last group is the *Liparis* cf. *fabricii* complex, which includes snailfishes with black peritoneum and simple teeth. The species with the same characteristics are not known in boreal areas. Thus, this is an example of a group that is endemic to the Arctic (and isolated enclaves of Arctic fauna, such as the harsh northern part of the Okhotsk Sea).

3.2.3. Amphiboreal Concept and Speciation of *Liparis* in the Arctic and North Atlantic

It was shown above that according to the types of ranges and the degree of taxonomic isolation, the *Liparis* species is divided into the same groups as other fish families of Pacific origin. The distribution and speciation of northern *Liparis* can be represented as follows: During preglacial migrations (the Pliocene transgression), some of the Pacific *Liparis* entered the Arctic through the Bering Strait and distributed to the Atlantic coasts of North America and Europe. Transitions, apparently, went both in the west- and eastward directions, because different species formed in the boreal waters of the West Atlantic (*L. atlanticus*, *L. coheni*, and *L. inquilinus*) and the East Atlantic (*L. montagui* and *L. liparis*). All these recent species live in the coastal shallow-water zone. This fact is consistent with the conclusion drawn for amphiboreal invertebrates: in the group of shelf species that retreated south during the Ice Age (to regions not subjected to glaciation); only littoral and sublittoral species could survive [13].

Part of the Pacific migrants could adapt to the coldness during the Ice Age, and the circumpolar *L. tunicatus* and the black-bellied complex *L.* cf. *fabricii* formed in the Arctic. They are stenotherm cold-water fishes, endemic to the Arctic. In the postglacial period, when the Bering Strait became open, they did not penetrate far south into warmer waters, such as other high Arctic species, that prefer temperatures close to zero—Arctic alligatorfish *Aspidophoroides olrikii* (Agonidae), Hamecon *Artediellus scaber* (Cottidae), Canadian eelpout *Lycodes polaris* (Zoarcidae), and Polar cod *Boreogadus saida* (Gadidae).

During the period of the postglacial climatic optimum, the ancestor of *L. bathyarcticus* was able to settle in the Arctic seas, westward at least to the Barents Sea. However, it did not have time to significantly separate from the Bering Sea group of species; *L. bathyarcticus* is still very similar to its Pacific relatives.

New data on the morphology and distribution of *Liparis* in the Arctic and adjacent waters make it possible to reconsider the idea that the Baltic *L. barbatus* is a relict of the Ice Age, preserved from the time of supposed existence of the connection between the Baltic and the White Seas [105,124]. Based on recent data, it is unlikely that the ancestral form entered the Baltic Sea from the White Sea during the Yoldian period, as this connection has been disproved [125]. More probable, it could have happened from the Atlantic, during the Littorina Sea transgression that dated from 9500 calibrated year BP [126] to 8000 cal. BP [127]. Then, due to the eustatic rise of the bottom in the area of the Belts and the establishment of the modern hydrological regime of the Baltic Sea 1000–2000 years ago [128], the continuous range of the ancestral form was interrupted, and the isolated Baltic population transformed into *L. barbatus* adapted to desalinated conditions.

The presented data show, therefore, that the history of the formation of the Arctic *Liparis* fauna does not fundamentally differ from the speciation and distribution patterns of other fish groups of Pacific origin.

In conclusion it should be noted that the phylogenetic tree of the genus *Liparis* (based on the COI analysis), which includes 25 species of this genus, shows two clades containing Arctic and Atlantic species (Figure 9 by James Orr et al. [65]). One clade includes *L. bathyarcticus*, and another (polytomic) combines seven other species (*L. liparis*, *L. inquilinus*, *L. tinicatus*, *L. atlanticus*, *L. montagui*, *L. fabricius*, and *L. bristolensis*). This can be interpreted as a correlation with two groups, migrating from the Pacific Ocean at different times (posglacial and preglacial); their further evolution proceeded independently from the Pacific congeners. However, the second clade unites rather different species (in axial skeleton and dental systems), which have morphologically similar congeners in the outer clades (*L. montagui*–*L. punctulatus*; *L. atlanticus*–*L. rutteri*). If the COI tree is followed, this means that complex morphological structures in different clades should be allowed to arise independently, which is difficult to explain. Further studies should be performed.

3.3. Snailfishes of the Arctic—Genus Careproctus

The genus *Careproctus* (sea tadpoles) includes no less than 162 species and is one of the four largest genera in the family [42] updated.

Careproctus differs from *Liparis* in the absence (reduction) of the posterior pair of nostrils and pseudobranchia and the fusion of two hypuralia in the caudal skeleton; unlike in *Liparis*, pectoral fin rays are less numerous than the anal fin rays. The origin of sea tadpoles was probably associated with the settlement of and the adaptation to the bathyal–aphotic zone; this can explain the disappearance of green and brown pigments in the skin, which makes their ground color a solid pink or orange.

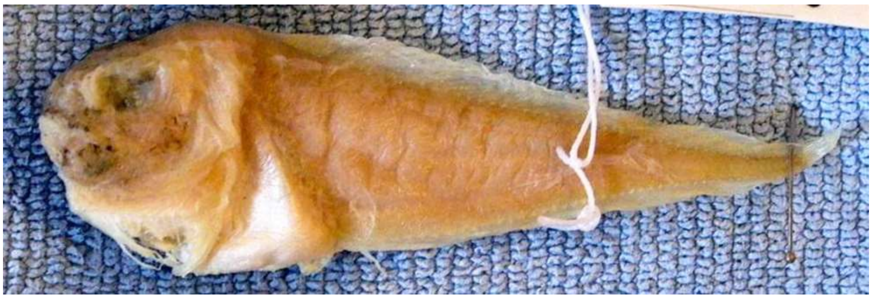
Most of the species live in the northern part of the Pacific Ocean, where at least 77 species are known [42] updated. There is no overview of the *Careproctus* for this area.

The secondary center of speciation is located in the waters of the Southern Ocean, and the revision of *Careproctus* of this fauna, performed by Anatole Andriashev, contains 44 species [60]. He subdivided the species into two subgenera, and the new sg. *Careproctula* was established (type *C. fedorovi* Andriashev et Stein 1998, the Scotia Sea). Seven southern species were included in sg. *Careproctus*, similar to the type species of the genus *C. reinhardti*, described from southwestern Greenland. They all have strong pleural ribs and notched radials 4 (3 + 1) in the pectoral girdle (=plesiomorhic *Liparis*-like features). Most sea tadpoles of the Southern Ocean (37) have been included in the sg. *Careproctula*. They do not have pleural ribs, and in the shoulder girdle, the radials are round, and the interradial fenestrae are reduced.

3.3.1. *Careproctus* of the Arctic and North Atlantic

The *Careproctus* diversity of regions is at the stage of initial description; the number of species will obviously increase, especially in the bathyal and abyssal depths of the oceans. The current list includes 21 species in the Arctic (Table 2) and 3 in the North Atlantic (Table 3). Morphologically, they can be assigned to the subgenera *Careproctus* and *Careproctula*, mentioned above [37,38] updated. There has not been an updated analysis of these species, so a brief review is necessary before looking for their relatives.

The subgenus *Careproctus* in the northern regions includes 15 taxa, all from the Arctic. Four of them are well defined: (1) *C. reinhardti* (Figure 5a) described from southwestern Greenland, the type species of the genus [37]; (2) *C. longipinnis* (Figure 5b) from the Norwegian Sea (caught at a depth of 1322 m) [37]; (3) *C. solidus* from the slope of the Laptev Sea (2151–1934 m) [36]; and (4) *C. lerikimae* from the Beaufort Sea (175–500 m) [81]. The other 11 species make up the "*C. dubius*" group: they differ from each other (Figures 6a,b and 7a) but have a set of common characters (Table 5). They all have simple teeth (simplified from the three-lobed form); the lower lobe of the pectoral fin is strongly elongated (1.3–1.5 times as long as its upper lobe) and apparently performs a tactile or taste function; the prickles on the skin are cactus-like.



(**a**)

Figure 5. *Cont.*

(**b**)

Figure 5. Arctic species of *Careproctus*: (**a**) *C. reinhardti*, Baffin Bay, ZMUC P82456; (**b**) *C. longipinnis*, Holotype ZMUC P82180, *TL* 221 mm.

(**a**)

(**b**)

Figure 6. Arctic species of *Careproctus*: (**a**) *C. fulvus*. Holotype ZIN 55421, *TL* 224 mm; (**b**) *C. rosa*. Holotype, *TL* 121 mm.

(**a**)

Figure 7. *Cont*.

(**b**)

Figure 7. Arctic species of *Careproctus*: (**a**) *Careproctus uter* (sg. *Careproctus*), Holotype; (**b**) *C. mica* (sg. *Careproctula*), Holotype, *TL* 78 mm.

Table 5. Basic characteristics of *Careproctus* from the Arctic and North Atlantic.

Subgenus *Careproctus* (pectoral radials notched, 2–3 interradial fenestra present; pleural ribs saber-like)				
Pectoral radials	4 (3 + 1)	3 (2 + 0 + 1)	3 (2 + 0 + 1)	2 (1 + 0 + 0 + 1)
Vertebrae	59–64	60	–	–
Pectoral fin rays	29–36	31	–	–
Pores 2–5–7–2	*C. reinhardti* *C. longipinnis* *C. lerikimae* "*C. dubius*"(11 species) [1]	*C. solidus*	–	–
Subgenus *Careproctula* (pectoral radials unnotched; interradial fenestra absent; pleural ribs absent or rudimentary)				
Pectoral radials	4 (3 + 1)	3 (2 + 0 + 1)	3 (2 + 0 + 1)	2 (1 + 0 + 0 + 1)
Vertebrae	60–62	57–62	64–65	69
Pectoral fin rays	26–28	22–29	27–28	22–25
Pores 2–6–7–1	*C. ranula* * *C. kidoi*	*C. micropus* *C. moskalevi* *C. latiosus* [2] *C. mica*	*C. canusocius*	*C. merretti* * *C. aciculipunctatus* *

* Atlantic species. [1] "*C. dubius*" group includes *C. carinatus*, *C. fulvus*, *C. derjugini*, *C. dubius*, *C. karaensis*, *C. knipowitschi*, *C. macrophthalmus*, *C. rosa*, *C. tapirus*, *C. telescopus*, and *C. uter*. [2] The number of pectoral radials in *C. latiosus* is variable: 4 (3 + 1) or 3 (2 + 0 + 1).

A characteristic feature of the "*C. dubius*" group is a longitudinally oval pupil, which may be associated with the low illumination of habitats in polar conditions or at a depth of the aphotic zone. In addition, in the species of the group, the anus and genital openings are shifted forward to the very edge of the pelvic sucking disk. Males have a large urogenital papilla, indicating that their fertilization process is internal. This suggests also the complexity of mating behavior. Carcinophilia (laying of eggs in the gill cavity of craboids) has not been recorded for the Arctic or Atlantic *Careproctus*, but for *C. fulvus* (from the Kara Sea), spongiophilia was described (laying of eggs in the cavity of glass sponges [40]). This suggests that in other members of this group, similar ways of caring for offspring can be present.

The subgenus *Careproctula* includes nine species, six of which occur in the Arctic areas and three in the North Atlantic. They all have round radials in the pectoral girdle, absent interradial fenestrae (or rudimentary), and absent pleural ribs (or rudimentary). The lower pectoral fin lobe is usually shorter than the upper lobe. Suprabranchial pore one, the second suprabranchial pore (=rudimentary element of the trunk lateral line) is reduced; the pore formula is 2−6−7−1. The body is elongated and low, and the maximum depth is 12–24% *SL*. The skin is usually naked and rarely with microscopic needle-like spines. Four groups can be recognized, according to the type of the shoulder girdle and the number of vertebrae (Table 5). Thus, the *Careproctula* species is heterogeneous, which makes it probable that it belongs to different phylogenetic lineages. The most generalized one is *C.* (*Careproctula*) *ranula*, having three-lobed teeth and a large disk (7.7–9.0% *SL*).

Among the Arctic species, four are deep-water fishes living at a depth of 952–1695 m: *C. kidoi* in the Baffin Bay and *C. micropus*, *C. moskalevi*, and *C. latiosus* in the northern part of the Norwegian Sea. Two others are shelf species: *C. mica* from the Kara Sea (205 m) (Figure 7b) and *C. canusocius*, which inhabits the upper slope of the Beaufort Sea (488–599 m).

Within the North Atlantic species, *C. ranula* is a boreal shallow-water fish, known from the entrance to Halifax Harbor at a depth of 95 m (WNA); *C. merretti* and *C. aciculipunctatus* are abyssal fishes that live in the Porcupine Seabight at 3990–4100 m (ENA).

3.3.2. Amphiboreal Concept and Speciation of Sea Tadpoles in the Arctic and North Atlantic

When searching for related congeners, one may view the *Careproctus* species of the Southern Ocean, the characteristics of which are uniformly described [60]. The conclusions are as follows: Arctic representatives of the sg. *Careproctus* differ from all southern species in the combination of numerous vertebrae (59–63 versus 43–59 in the majority), simple teeth (but not three-lobed), anteriorly shifted anus and genital openings, and a strongly elongated lower lobe of the pectoral fin. The head sensory system is distinguished by the absence of the postorbital pore and the presence of two suprabranchial pores (2−5−7−2). Therefore, there are no similar species in the Southern Ocean; related congeners are most likely to be found in the North Pacific.

For *C. reinhardti*, I consider *C. mederi* from the Sea of Ohkotsk to be the closest morphologically (including a large gill opening and slanted mouth), although there are significant differences between them (in the latter, the lower lobe of the pectoral fin is shorter, and the postorbital pore is present). *Careproctus longipinnis* seems to be most similar to *C. trachysoma*, known from the Sea of Japan [81].

The origin of the "*C. dubius*" group should be confidently associated with the North Pacific, as evidenced by the presence of its characteristic features in several species of the Pacific area. The lower lobe of the pectoral fin is greatly elongated in *C. colletti*, *C. cyclocephalus*, *C. gilberti*, *C. pellucidus*, *C. rastrinus*, *C. rhodomelas*, *C. spectrum*, and *C. trachysoma*. Cactus-like prickles are present in *C. acanthodes*, *C. rastrinus*, and *C. trachysoma*. The absence of the postorbital pore (formula 2−5−7−2) is known at least for *C. acanthodes*, *C. entomelas*, *C. homopterus*, *C. macrodiscus*, and *C. pellucidus*. A longitudinally oval pupil has been noted for *C. simus* and *C. spectrum* and in the holotype of *C. furcellus* [53]. Therefore, an amphiboreal concept can be discussed for Arctic species of sg. *Careproctus*, although there are not enough comparative Pacific materials for all species.

Preliminary assumptions may be as follows: During preglacial migrations, ancestral Pacific forms of sg. *Careproctus* entered the Arctic through the Bering Strait and spread toward the Atlantic. During the Ice Age, different parts of the population could move away from the glaciers to the bathyal depth, where deep-water species later formed: *C. longipinnis* in the Norwegian Sea Basin (at a depth of about 1322 m) and *C. solidus* on the northern slope of the Laptev Sea (2151–1934 m). On the shelf areas, which were repeatedly becoming free of glaciers, a species flock of the "*C. dubius*" group was produced. They are vicariant in the southwestern Barents Sea (*C. macrophthalmus* and *C. tapirus*), in the north of the Spitsbergen archipelago (*C. derjugini*), and in the depressions of the Barents Sea (*C. telescopus* and *C. knipowitschi*). In the Kara Sea, they were speciated in the southwestern area (*C. rosa*) and in the Novaya Zemlya Trench (*C. fulvus* and *C. uter*); two species have adapted to live in the pelagic zone (*C. karaensis* and *C. carinatus*).

The similarity of all these species (for example, in counts: *vert*. 59−63, *D* 53−57, *A* 47−51, *P* 29−34, and *C* 10−12) can be explained by the "bottleneck" effect, when the nomadic population in the Arctic was founded by a small number of individuals. The presence of free ecological niches and the weak pressure of competitors in the deglaciated waters can explain the variety of species. The presence of internal fertilization (and behavioral rituals associated with it) were additional factors of isolation that contributed to accelerated speciation.

Among the representatives of sg. *Careproctula*, the amphiboreal concept is most likely applied to *C. ranula*, a shallow-water fish from the boreal western North Atlantic. In preglacial times, the ancestral form probably spread from the Pacific to the Atlantic along the coast of North America, and during the Ice Age, it retreated south and formed the recent species. It is possible that other parts of the ancestral population descended from the glaciers to a bathyal depth of 952–1695 m and gave the origin to *C. kidoi* in the Baffin Basin and *C. micropus*, *C. moskalevi*, and *C. latiosus* in the Norwegian Basin. These species are rather close to each other in main characteristics (Table 4). Two *Careproctula* known from the central Arctic could have been speciated during periodical deglaciations of the Ice Age: *C. mica* in the Kara Sea (at a depth of about 205 m) and *C. canusocius* in the Beaufort Sea (488–599 m). The origin of the mentioned *Careproctula* in the Southern Ocean is less probable, because there are no similar species there.

However, in contrast to what was shown above, the speciation of the two deepest North Atlantic *Careproctula* (*C. merretti* and *C. aciculipunctatus*, 3990–4100 m) in the eastern North Atlantic was explained differently. The Bering Strait during all periods of its existence was shallow; therefore, the amphiboreal concept does not explain the origin of abyssal fishes. Their penetration into the North Atlantic was explained by another hypothesis of transoceanic dispersal (Pacific–Southern Ocean–North Atlantic), based on the materials of the worldwide ranges of Liparidae and Zoarcidae [7,60,73,129]. Among the Liparidae, this hypothesis is supposed for *Paraliparis* and, in addition, for the abyssal *C. merretti* and *C. aciculipunctatus*. This concept is beyond the scope of the present study. It is sufficient to point out that *Careproctula* like them are known from deep-sea trenches of the Southern Hemisphere; *C. vladibeckeri* and *C. atakamensis* have the same pore formula (2–6–7–1) and the presence of two opposite radials (1 + 0 + 0 + 1). The northern *C. aciculipunctatus* and *C. merretti* obviously represent a continuation of this evolutionary line, which is expressed in an increase in the metameric elements of the axial skeleton (vertebrae and fin rays) during the development of the eel-like type of locomotion in fishes at the oceanic depth [60].

The phylogeny of Liparidae based on the COI analysis includes at least 38 *Careproctus* (Figure 10 by James Orr et al. [65]). It shows two clades containing the Arctic and Atlantic species (four of them were considered in total). This can be interpreted as a correlation with two groups that migrated into the Arctic at different times. These are: (1) *C. reinhardti* and *C. lerikimae* (sg. *Careproctus*) and (2) *C. micropus* and *C kidoi* (sg. *Careproctula*). Among the outer clades, there is the Pacific species *C. trachysoma*, grouped with the first pair; the second pair is grouped with another branch of the Pacific congeners. These data are consistent with the ideas about the system and the Pacific relatives of the mentioned Arctic–Atlantic species.

3.4. Other Liparids of the Arctic and Atlantic

The genus *Paraliparis* includes no less than 117 species, twelve of which are known in the North Atlantic (Table 3) and only two in the Arctic, *P. bathybius* and *P. violaceus* (Table 2). The dispersal of *Paraliraris* into the North Atlantic and the Arctic is explained by Andriashev's hypothesis mentioned above. For the deep-sea genus *Paraliparis*, the secondary center of speciation is in Antarctica, and then, from the southwestern Atlantic, the species spread north into the depths of the North Atlantic. This route is confirmed by the morphological similarity of the northern and southern species, some of which (the *P. copei* group) demonstrate a chain of related forms [60].

The migration of the ancestor of *P. bathybius* into the Polar Basin from the Atlantic can be considered highly probable. This is supported by the discovery in the adjacent North Atlantic of a morphologically similar species *P. abyssorum* from waters south of the Faroe–Icelandic Sill [45].

Species similar to the Arctic *P. violaceus* have not yet been found. When compared with *P. bathybius*, it turns out that *P. violaceus* combines some ancestral features for the *Paraliparis* (two hypuralia, four pectoral radials, and epurale present) with characteristics of specialization (reduction in the anterior portion of the dorsal fin and the absence of the notch in the pectoral fin). This gives grounds to suggest an earlier penetration of its ancestral form into the Arctic compared to *P. bathybius*.

In the phylogeny of *Paraliparis* based on the COI analysis (Figure 11 by James Orr et al. [65]), the Arctic *P. bathybius* and the North Atlantic *P. garmani* are close to the group of South Oceanic species (*P. stehmani* and others), which is consistent with the above ideas.

Rhodichthys is the endemic genus to the Polar Basin. It was considered monotypic, but the second species, *Rh. melanocephalus*, was recently described from the Norwegian Basin southwest of Bear Island (depth of 1470–1695 m) [84]. The large oblique mouth, huge gill opening, and modified gill rakers suggest a filter feeding in these meso- and bathypelagic fishes. Until recently, there was not even an assumption about related forms. Then, the abandoned snailfish genus *Menziesichthys* was restored (based on *M. bacescui* from the Peru–Chile Trench, 1296–1317 m), and even the second species *M. alaid* was described from the area of the Kuril Islands (Sea of Okhotsk, 820 m) [130]. These fishes share some unique morphological characteristics with the *Rhodichthys*, e.g., very large gill slits reaching in front of the lower end of the pectoral fin base and gill rakers modified in a similar way, which obviously are the results of adaptations to pelagic feeding. My guess is that *Rhodichthys* may have derived from the same root as the Pacific *Menziesichthys*.

In the phylogeny of Liparidae based on the COI analysis (Figure 11 by James Orr et al. [65]), *Rh. regina* is in the South Oceanic *Paraliparis* group. However, among *Paraliparis*, there are no even remotely similar species. *Rhodichthys* differs in a unique orobranchial apparatus at the generic rank. The passway of *Rhodichthys* to the Arctic is not clear. This most likely happened before *P. bathybius* did. During the glaciations, *Rhodichthys* was probably driven to the polar depths into the meso- and bathypelagic layers, where it changed greatly, adapting to the filtering method of pelagic feeding.

Psednos includes 11 species in the North Atlantic and 3 species in the marginal Arctic. The center of origin of this genus is in Australian waters, where generalized species occur [61]. Most *Psednos* are meso- and bathypelagic fishes, found in the Atlantic, Pacific, and Indian Oceans. Many are known from several or even single specimens. Three Arctic *Psednos* (*P. gelatinosus*, *P. melanocephalus*, and *P. micruroides*) occur in the midwaters of southwest and southeast Greenland (Table 2). These areas are affected by a strong upwelling, which allows deep-sea dwellers to rise closer to the surface, and many of deep-sea Atlantic fishes are found in these marginal Arctic regions [77]. The three mentioned *Psednos* can be assigned to this fish complex (i.e., they may have an Atlantic distribution). This is all the more likely because two other species recorded in Greenland waters (*P. christinae* and *P. groenlandicus*) are also known elsewhere in the North Atlantic (on the Mid-Atlantic Ridge). Consequently, the *Psednos* of the marginal Arctic are of the Atlantic origin.

Finally, a few words on *Eutelichthys* should be added. This genus is close to *Paraliparis*, but differs in the reduction in one of the branchial rays and in the small size of adults (miniaturization). In terms of its characteristics, it is closest to the North Atlantic *P. hystryx* and *P. murieli*. Deep-sea fishes, such as *Paraliparis*, may have entered the Mediterranean from the Atlantic during the opening of the Strait of Gibraltar around 5.33 million years ago [112,131,132]. As a result of the subsequent isolation of the Mediterranean Sea from the depths of the Atlantic, the separation of the ancestral *Eutelichthys* to the generic rank could have occurred. During the same period of the Mediterranean flood, some *Liparis*, which were the ancestors of modern *L. fishelsoni* [70], may have come here from the Atlantic, but later they become extinct there, remaining only in the Red Sea as a relict form.

4. Conclusions

The data presented in the article are intended to give a broad background of complex events of transoceanic migrations of the northern representatives of Liparidae. We used the comparative methods of analyzing our materials collected over many years of Liparid studying. The conclusions are based on morphological differences/similarities of taxa, patterns of species distribution on the background of biogeographic representations, and data obtained for other groups of animals. Our results are mainly consistent with those based on multitaxon mitochondrial data that provide an overview of the dynamics of transarctic dispersal and gene flow [133]. Moreover, they expand the evidence base for further genetic research and may provide an opportunity to look at their results from a different angle.

In the study of Liparidae, a new result is an updated overview of the species composition of the Arctic. The list includes five genera, *Liparis*, *Careproctus*, *Paraliparis*, *Rhodichthys*, and *Psednos*. Of the total number of 33 species (excluding the boreal ones entering the marginal Arctic regions), the majority are representatives of the genus *Careproctus* (21). The amphiboreal concept explains the speciation of *Liparis* and the bulk of the *Careproctus* species as a result of trans-Arctic migrations. For two Arctic *Paraliparis*, the South Oceanic dispersal route can be accepted, which pass from the North Pacific through the Southern Ocean and then north across the Atlantic. The origin of the endemic *Rhodichthys* is still unclear. The *Psednos* species, found in the Arctic so far only near southern Greenland, has appeared from the Atlantic, as it is widely distributed in the meso- and bathypelagic waters of warm oceans. Thus, the liparid fauna of the Arctic, although having their ancient roots from the North Pacific, came from both neighboring oceans, mostly through the Bering Strait and, to a lesser extent, from the Atlantic. The latter route is shown for deep-sea liparids: abyssal *Careproctula* species, benthopelagic *Paraliparis*, and meso-and benthopelagic *Psednos*.

The overview of the Liparidae in the North Atlantic revealed the same number of species as in the Arctic (33), but in a different composition: fewer *Liparis* and *Careproctus*, more *Paraliparis* and *Psednos*, and *Eutelichthys* instead of *Rhodichthys*. Boreal shelf species, all *Liparis* and *C.* (*Careproctula*) *ranula*, may have speciated from the ancestors of the trans-Arctic preglacial routes; others are more likely to have South Oceanic relatives.

Further research is needed to clarify views on the formation of the snailfish fauna, on the one hand, in the field of molecular genetics, and, on the other hand, in the fields of morphology and biogeography.

Funding: This research was funded by State Assignments for the Zoological Institute of the Russian Academy of Sciences No. 122031100285-3.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data can be found in the manuscript and in the sources cited.

Acknowledgments: I thank all those who helped me during the study of museum specimens for this research, including David Stein, Horst Wilkens, Jørgen Nielsen, Peter Rask Møller, Ralf Thiel, Ingvar Byrkjedal, Guy Duhamel, Matthias Stehmann, Bo Fernholm, Irina Eidus, Hartel Karsten, Tammes Menne, Sandra Raredon, and Victoria Palm. Special gratitude goes to V. Petrov for editing the manuscript. In addition, I express my deep gratitude to the reviewers, whose comments helped me to improve the manuscript.

Conflicts of Interest: The author declares no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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