

Book Chapter

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 had an ancestral origin from the Pacific and, to a lesser extent, from the Atlantic oceans, 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 data of many years of research in taxonomy, using various material of morphological differences / similarities of 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); no *Rhodichthys* but one *Eutelichthys*. The amphiboreal concept explains the speciation of *Liparis* and majority of *Careproctus* as the result of trans-Arctic pre-glacial migrations. The hypothesis of transoceanic dispersal route, that went from the North Pacific through the Southern Ocean and then to the north across the Atlantic can be applied for the other (deep-water) species.

Keywords

Liparidae, amphiboreal concept, Arctic, *Liparis*, *Careproctus*, *Pseudnos*, *Paraliparis*, *Rhodichthys*

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, 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 these latter have an undoubted morphological and genetic similarity with their Pacific relatives. Families and groups of Atlantic origin are less numerous: Gadidae, Gasterosteidae, Scopthalthinae (genera *Scopththalmus*, *Lepidorhombus*, *Phrynorhombus*, *Zeugopterus*), Anarchichadidae, Petromyzonidae, subfamily Ammodytinae (*Ammodytes*, *Gymnammodytes*, *Hyperoplus*) [5]. As in previous case, 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, *Lumpenus medius* in Stichaeidae) or Greenland in eastern direction (*Myoxocephalus scorpioides* in Cottidae, *Eumesogrammus praecisus* in Stichaeidae).

Another group consists of endemic cold-water arctic species that are absent in the Pacific Ocean or only enter the northernmost part of the Bering Sea, but do not go further south (*Myoxocephalus quadricornis*, *Arteidiellus scaber*, *Gymnacanthus tricuspis* in Cottidae, *Lycodes polaris* in Zoarcidae).

The third group includes a number of amphiboreal taxa of Pacific origin, which in the boreal Atlantic have taxonomically separated to the rank of species or even genera. Amphiboreal (from the Greek *amphi*—around, on both sides) means living 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].

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), Greenland halibut *Reinhardtius reinhardtius* (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*, respectively); smelts (*Osmerus eperlanus* and *O. dentex*); halibuts (*Hippoglossus hippoglossus* and *H. stenolepis*), wolf-fishes (*Anarhichas lupus* and *A. orientalis*, Anarhichadidae). An amphiboreal distribution is found among representatives of 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, *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 on groups of fishes and invertebrates [2–4,6,10,12–14]. A brief overview of this hypothesis is as follows. The formation of amphiboreal taxa and their ranges is associated with migrations of the North Pacific fauna through the Arctic shelf during boreal

transgressions, and the rupture of their ranges during glacial time (and the same, although to a lesser scale, for the Atlantic fauna).

Usually two periods of different-time migrations through the Bering Strait region are accepted, Pliocene (preglacial) and postglacial [2,5,6,10,11,13,15,16—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, Pleuronectidae) probably migrated along the Asian coast influenced by the flow of the great rivers. Thus, different boreal species emerged on both sides of the Atlantic. This may explain the deriving of different amphiboreal groups of species on both sides of the Atlantic.

The Pacific-Atlantic distribution of the fauna prevailed, only a few groups (Clupeidae, Gadidae) migrated in the opposite direction, from the Atlantic to the Pacific. The advantage of the Pacific-Atlantic direction is explained by the greater species abundance of the more ancient Pacific fauna compared to the Atlantic, since 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 for 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) [25]. The largest glaciers covered a huge area from 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 occupied earlier a vast range from the North Atlantic to the eastern Arctic, have become extinct in the glaciated areas. A few elements could have been preserved in free-of-ice refugia; some other may have escape from the glaciers to 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 disperse to the Mediterranean Sea and even to the Southern hemisphere (sandlances *Gymnamodytes*). Further evolutionary processes in separated populations may have led to the formation of new species, including the bathyal ones. The interglacial migrations may have occurred more than once, which explains the varying degree of morphological and genetic differentiation between amphiboreal taxa or populations.

Postglacial migrations were associated with postglacial climatic optimum and boreal transgression, when the Bering Strait was open (since 11 cal ka BP) [13,27–29]. This led to the wide distribution of shelf Pacific species into the Arctic; they have not had time since that period to noticeably separate from the Bering Sea populations. At present, when the climate in the Siberian region has become harsher than before [30,31], the most thermophilic fishes have not survived there [32], and interrupted ranges of some species have formed.

As an example, the history of the migrations and speciation of fish of the genus *Icelus* (Cottidae) was shown [3,33]. The genus includes at least 18 species, most in the Pacific Ocean. In the Pliocene, one member of the genus migrated into the Arctic and dispersed across the waters of North America to the northwestern Atlantic, where the recent species Twohorn sculpin *I. bicornis* was formed. With the end of the ice age, this species moved further to the east, occupying free of ice waters; and currently it is distributed also along the Asian shelf. During this time, a number of related species differentiated in the North Pacific (*I. uncinialis*, *I. spatula*). Of these, during the postglacial transgression, *I. spatula* dispersed through the Bering Strait to the Arctic; it is currently distributed westward to the Barents Sea and eastward to Greenland. Thus, the result of preglacial migrations 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 in 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 Moustache sculpin *T. murrayi* was formed in the North Atlantic. During the Ice age, the Bigeye sculpin *T. nybelini* specified, it is endemic for the Arctic. The Ribbed sculpin *T. pingelii*, which currently has a wide boreal-arctic range, spread northward in the post-glacial time.

Another example gives the interrupted ranges of fishes of the family Stichaeidae [3]. This group is most diverse in the North Pacific, where the primitive (*Stichaeus*) and the most derived (*Stichaeopsis*, *Plagiogrammus*) forms exist. In the Western North Atlantic, the genus *Ulvaria* (*U. subbifurcata*) is present, endemic and morphologically generalized; its ancestors, apparently, could have spread to the Atlantic in pre-glacial times. There are also two species with an amphiboreal distribution, *Stichaeus punctatus* and *Eumesogrammus praecisus*; they apparently spread during the post-glacial migration of the Pacific fauna.

An interesting example is provided by the anadromous Arctic lamprey *Lethenteron camtschaticum*, which produced non-migratory freshwater forms in Siberian river basins [3,9]. The arctic range of the anadromous lamprey is widely interrupted in the Laptev and East-Siberian seas. Contrary, the range of the related resident lamprey *L. kessleri* (or *Lethenteron camtschaticum kessleri*) is continuous in the river basins of these seas. The presence of these relict freshwater populations indicates that in warm post-glacial 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, the anadromous form disappeared along the Siberian coast.

Liparid fishes (or snailfishes) constitute a significant part of the fauna of the North Pacific. At least five genera are present in the Arctic and the North Atlantic; but the family have not been analyzed within the framework of the amphiboreal concept. Only the genus *Liparis* was briefly noted in this context [7].

The main aim of this review is to consider if the amphiboreal concept is applicable to explaining 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 boreal Atlantic. Then one should consider each genus of the family from these regions, whether they contain amphiboreal species or groups. This will allow us to discuss whether the probable ways of distribution and speciation of representatives of these taxa fit into the context of the amphiboreal concept.

Materials and Methods

Liparidae specimens collected the Arctic and adjacent areas over many years of practical studies in taxonomy and related disciplines (Table 1). Specimens of all Arctic genera, involved in the consideration, were studied: *Liparis*, *Careproctus*, *Paraliparis*, *Rhodichthys* and *Pseudnos* [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
<i>Liparis</i>	55	1555	525	359
<i>Careproctus</i>	27	549	192	142
<i>Paraliparis</i>	67	229	140	183
<i>Pseudnos</i>	32	42	39	45
<i>Rhodichthys</i>	2	7	5	5
Total:	182	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 8 species [36,38,40,41]. *Careproctus* of the North Pacific region were studied in connection with the question 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]. *Careproctus* species of the Southern Ocean were analyzed when assisting Anatole Andriashev in preparing his monograph on Liparid fishes of the Southern Ocean [60]. In addition, when describing *C. paxtoni* [61], 10 southern species were studied for comparison.

Methodology: To show the background, after a brief overview of the family Liparidae, the species composition of snailfishes for the Arctic and the North Atlantic is given. The snailfishes of the genus *Liparis* are then analyzed for the presence of amphiboreal species or groups. The same is done for *Careproctus* and other genera. Next, the probable ways of distribution and speciation of representatives of these taxa are 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 Polar and Atlantic deep basins. The Faroe Trench, connected to the Norway Basin is included to the Arctic.

Morphological characters 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* – standart length, *TL* – total length.

Results and Discussion

Overview of the family Liparidae

Snailfishes are 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 scaly cover. It is a diverse fish family, with over 430 species from 32 genera worldwide [42,65]. Snailfishes are distributed in temperate and cold zones of the both hemispheres and inhabit the deep water of five oceans. The vertical limits of their distribution are extremely wide since they are found in all bathymetric zones, from the littoral (*Liparis*, *Polypera*) to the abyssal plains (*Paraliparis*) and at hadal depth of oceanic trenches up to 6—8 thousand meters (*Pseudoliparis*, *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 the shallow water, with the intensive summer heating: *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, some are 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].

Halopreferendum of snailfishes is wide; along with stenohaline species, which prefer strict oceanic salinity, there are liparids that tolerate 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]. Littoral species use their sucking disc for attaching to stones and algal thalli. Demersal snailfishes (*Liparis*, *Careproctus*) are common in shelf waters. Except of bathyal and abyssal liparids, benthopelagic and mesopelagic species exist, in which the ventral disk is reduced (for example *Nectoliparis*, *Paraliparis*, *Pseudoliparis*) [54,60,73]. The diversity of liparids is astounding; it is the result of their evolutionary plasticity, which have made it 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 this paper], the total number of species is 33: *Liparis* 5, *Careproctus* 21, *Paraliparis* 2, *Rhodichthys* 2 and *Pseudnos* 3, excluding boreal species (*L. liparis*, *L. montagui*, *Paraliparis copei*, *P. garmani*, *Pseudnos christinae*, *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
1. Genus <i>Liparis</i> Scopoli, 1777		
Subgenus <i>Liparis</i> Scopoli, 1777		
1.1. <i>L. liparis</i> (Linnaeus, 1766)*	SW Barents Sea (Murman), 0–78 m	[35]
1.2. <i>L. montagui</i> (Donovan, 1804)*	SW Barents Sea (Murman), 0–3 m	[35]
1.3. <i>L. tunicatus</i> Reinhardt, 1937	Circumpolar, shallow waters [35]; SW, NW, NE Greenland [77]	[35,77]
Subgenus <i>Careliparis</i> Garman, 1892		
“ <i>L. megacephalus</i> ” - group		
1.4. <i>Liparis bathyartcticus</i> Parr, 1931 ¹	Circumpolar (?), depth 12–510, usually 5–350 m [35]; Gulf of St. Lawrence [78]	[35,78]
Subgenus <i>Lycocara</i> Gill, 1884		
<i>Liparis</i> cf. <i>fabricii</i> complex ² 1.5. <i>L. fabricii</i> Krøyer, 1847 1.6. <i>L. koefoedi</i> Parr, 1932 1.7. <i>L. laptevi</i> Popov, 1933	Circumpolar, 12–628 (usually 40–350) m [39], near Greenland to 1460 m [77]; Gulf of St. Lawrence [78]	[39,77–78]

2. Genus <i>Careproctus</i> Krøyer, 1862 ³		
Subgenus <i>Careproctus</i> Krøyer, 1862		
2.1. <i>C. reinhardti</i> sensu stricto (Krøyer, 1862) ³	SW Greenland [37,79], Gulf of St. Lawrence [78]	[37,78–79]
2.2. <i>C. longipinnis</i> Burke, 1912	Norwegian Sea, north of Faeroe Islands, 1322 m	[37,80–81]
2.3. <i>C. solidus</i> Chernova, 1999	Laptev Sea, 2151–1934 m	[36,81]
2.4. <i>C. lerikimae</i> Orr, Kai et Nakabo, 2015	Beaufort Sea, depth 178 m	[81]
“ <i>C. dubius</i> ”-group		
2.5. <i>C. dubius</i> Zugmayer, 1911	Spitsbergen, Havre Green, 150 m	[37,81]
2.6. <i>C. derjugini</i> Chernova, 2005	North-east of Spitsbergen, 344–363 m	[38]
2.7. <i>C. knipowitschi</i> Chernova, 2005	Barents Sea, 298–293 m	[38,82]
2.8. <i>C. macrophthalmus</i> Chernova, 2005	South-west of the Barents Sea, 260–275 m	[38,82]
2.9. <i>C. tapirus</i> Chernova, 2005	South-west of the Barents Sea, 170–320 m	[38]
2.10. <i>C. telescopus</i> Chernova, 2005	Barents Sea, 260–307 m	[38]
2.11. <i>C. fulvus</i> Chernova, 2014	Kara Sea, Novaya Zemlya Trench, 190–414 m	[40]
2.12. <i>C. rosa</i> Chernova, 2014	South-west of the Kara Sea, 140 m	[41]
2.13. <i>C. karaensis</i> Chernova, 2014	Kara Sea, east of Novaya Zemlya, pelagic at 0–30 m	[41,81]
2.14. <i>C. uter</i> Chernova, 2014	Kara Sea, Novaya Zemlya Trench, 206 m	[41]
2.15. <i>C. carinatus</i> Chernova, 2014	South-west of the Kara Sea, pelagic at 0–30 m	[41]
Subgenus <i>Careproctula</i> Andriashev, 2003		
2.16. <i>C. micropus</i> (Günther, 1887)	Faeroe Channel, depth 540 and 608 fathoms (987–1112 m)	[37]
2.17. <i>C. kidoi</i> Knudsen et Møller, 2008	Baffin Bay; SW Greenland, NW Greenland, 952–1487 m	[77,83]
2.18. <i>C. moskalevi</i> Andriashev et Chernova, 2010	Norwegian Sea, southwest of the Bear Island, 1478–1691 m	[82,84]
2.19. <i>C. latiosus</i> Andriashev et Chernova, 2010	Norwegian Sea, southwest of the Bear Island, 1478–1695 m	[82,84]
2.20. <i>C. mica</i> Chernova,	Kara Sea, Novaya Zemlya	[41,82]

2014	Trench, 204 m	
2.21. <i>C. canusocius</i> Orr, 2020	Beaufort Sea, 488–599 m	[82]
3. Genus <i>Paraliparis</i> Collett, 1879		
3.1. <i>P. bathybius</i> (Collett, 1879)	Norwegian Basin, 1000–1847 m [86–87,90] and pelagic at 20–1000 m [35,88–89]; Faroe Trench, 1170 m [85]; Central Polar basin: north-east of Spitsbergen [35], north of the Laptev Sea, 2824–2775 m [75]; Greenland, benthopelagic, 545–1600 m [77]	[35,75,77,85–90]
3.2. <i>P. copei copei</i> 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]
3.3. <i>P. garmani</i> Burke, 1912*	SW, SE Greenland, 550–987. Elsewhere found in WN Atlantic (see Table 2).	[77]
3.4. <i>P. violaceus</i> Chernova, 1991	Central Polar basin, north of Severnaya Zemlya Archipelago, 2365 m	[35]
4. Genus <i>Rhodichthys</i> Collett, 1879		
4.1. <i>Rh. regina</i> Collett, 1879	Norwegian basin, 1394–2341 m [91–93], Faroe Bank, 400–500 m [94]; Baffin Bay, 1200–1800 m [95], NW Greenland, NE Greenland, benthopelagic at 1180–1480 m [77]; Polar basin: north-east of Spitsbergen, 1080–1090 m [35], north of Severnaya Zemlya, 1445 m [35,95]	[35,77,91–96]
4.2. <i>Rh. melanocephalus</i> Andriashev et Chernova, 2010	Norwegian basin, south-west of the Bear Island, 1470–1695 m	[84]
5. Genus <i>Pseudnos</i> Barnard 1927		
5.1. <i>P. christinae</i> Andriashev, 1992 ^(*)	SE Greenland, 843–854 m. Elsewhere found in the Mid-Atlantic Ridge (see Table 2)	[77]
5.2. <i>P. gelatinosus</i> Chernova, 2001	SE Greenland (63°05'54"N), mesopelagic at 650–0 m	[46,77]
5.3. <i>P. groenlandicus</i>	SW Greenland (63°–65° N) and	[46,77]

Chernova, 2001 ^(*)	SE Greenland (61°53'N), mesopelagic at 786–1460 m. Elsewhere found in the Mid-Atlantic Ridge (see Table 2)	
5.4. <i>P. melanocephalus</i> Chernova et Stein, 2002	SW Greenland, 58°15'N, 0-3172 m [97] and 64°03'N, 926 m; 949–962 m [77, 98]	[77, 97–98]
5.5. <i>P. micruroides</i> Chernova, 2001	SW Greenland (63°45'N), 0-900 m [46] and SE Greenland (63°50'18"N), mesopelagic at 0–1333 m [77, 98]	[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. bathyarticus*, 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. reinhardtii*) occurs all over the Arctic, which is at least strange, considering the diversity of *Careproctus* in other areas.

In the boreal North Atlantic the number of species is the same (33), although the compositions of the genera differs: *Liparis* 6, *Careproctus* 3, *Paraliparis* 12, *Pseudnos* 11; there are no *Rhodichthys* but there is one *Eutelichthys* (Table 3).

Table 3: List of Liparidae of the North Atlantic.

Taxa	Range, depth (m)	References
1. Genus <i>Liparis</i> Scopoli, 1777		
Subgenus <i>Neoliparis</i> Steindachner, 1876		
“ <i>L. montagui</i> ”-group		
1.1. <i>L. montagui</i> (Donovan, 1804)*	Europe: from Portugal to Murman, intertidal and shallow waters	[35,39,90]
“ <i>L. atlanticus</i> ”-group		
1.2. <i>L. atlanticus</i> (Jordan et Evermann, 1898)	WN Atlantic: Quebec, Newfoundland, Nova Scotia [99], Gulf of St. Lawrence [78]; intertidal to 90 m	[78,99]
“ <i>L. grebnitzkii</i> ”-group		

1.3. <i>L. inquilinus</i> Able, 1973	WN Atlantic: from the Gulf of St. Lawrence to Cape Hatteras, 5–97 m	[101–103]
Subgenus <i>Liparis</i> Linnaeus, 1766		
1.4. <i>L. coheni</i> Able, 1976	WN Atlantic: Gulf of Maine, Nova Scotia, Gulf of St. Lawrence, 2–210 m	[104]
1.5. <i>L. liparis</i> (Linnaeus, 1766)*	Europe: from the North Sea to Murman; intertidal to 78 m	[35,39,90]
1.6. <i>L. barbatus</i> Ekström, 1832	Baltic Sea: Gulf of Finland, Gulf of Bothnia; shallow water; enters rivers	[35, 105] (as <i>L. liparis barbatus</i>); [39] (as <i>L. barbatus</i>)
2. Genus <i>Careproctus</i> Kröyer, 1862		
Subgenus <i>Careproctula</i> Andriashev, 2003		
2.1. <i>C. ranula</i> (Goode et Bean, 1879)	WN Atlantic: Halifax Harbor, Nova Scotia, 95 m	[37,106]
“ <i>C. merretti</i> ” -group		
2.2. <i>C. merretti</i> Andriashev et Chernova, 1988	EN Atlantic: Porcupine Seabight (49°37'N, 13°49'W), 3990–3920 m	[44]
2.3. <i>C. aciculipunctatus</i> Andriashev et Chernova 1997	EN Atlantic: south of the Porcupine bank (50°13.8'N, 14°36.1'W), 4100 m	[45]
3. Genus <i>Paraliparis</i> Collett, 1879		
3.1. <i>P. abyssorum</i> Andriashev et Chernova, 1997	EN Atlantic: near the Porcupine Bank (49°54'N, 13°56'W), 3640–3715 m	[45]
3.2. <i>P. bipolaris</i> Andriashev, 1997	WN Atlantic: south-west of Ireland (50°12'N, 13°40'W), 3000–3040 m	[107]
3.3. <i>P. calidus</i> Cohen, 1968	WN Atlantic: Gulf of Mexico (27°25'N, 93°40'W), 730 m; Gulf of St. Lawrence	[78,108]
3.4. <i>P. challengerii</i> Andriashev, 1993	EN Atlantic: Rockall Trough (57°01'N, 10°05'W), Porcupine Seabight (49°46'N, 12°31'W), 2000–2100 m	[109]
3.5. <i>P. copei copei</i> 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	[48,110], our data

	Greenland (see Table 1).	
3.6. <i>P. edwardsi</i> (Vaillant, 1888)	EN Atlantic: coast of Morocco, between Cape Spartel and Cape Blanco (33°46' N, 9°02' E), 1319 m	[108,111–112]
3.7. <i>P. garmani</i> Burke, 1912*	WN Atlantic: from Labrador to Cape Hatteras; benthopelagic, 550–987 m. Elsewhere found near South Greenland (see Table 1).	[77,80]
3.8. <i>P. hystrix</i> 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]
3.9. <i>P. liparinus</i> (Goode, 1881)	WN Atlantic: southeast of Long Island, 891 m	[109]
3.10. <i>P. murielae</i> Matallanas, 1984	West of the Mediterranean Sea, 500–600 m	[115]
3.11. <i>P. nigellus</i> Chernova et Moller, 2008	North Atlantic: Mid-Atlantic Ridge, between the Azores and Charlie-Gibbs Fracture Zone, 1950–2107 m	[48]
3.12. <i>P. vailanti</i> Chernova, 2004	WN Atlantic: Laurentian Channel (46°39'N, 58°41'W), mesopelagic, 423 m over a depth of 1150 m	[116]
5. Genus <i>Pseudnos</i> Barnard, 1927		
5.1. <i>P. andriashevi</i> Chernova, 2001	EN Atlantic: west of Ireland (54°21' N, 17°59' W), mesopelagic at 800 m	[46]
5.2. <i>P. barnardi</i> 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]
5.3. <i>P. christinae</i> Andriashev, 1992 ^(*) 1	North Atlantic: Mid-Atlantic Ridge (49°48'N, 25°55'W), 1000–1500 m; Greenland (see Table 1)	[117]
5.4. <i>P. delawarei</i> Chernova et Stein, 2002	WN Atlantic: south of Vape Cod (39°48'05"N, 70°43'28"W), 0–1000 m	[97]
5.5. <i>P. islandicus</i> Chernova et Stein, 2002	EN Atlantic: 59°59.7'N, 19°42.2'W, 1250–1500 m	[97]
5.6. <i>P. groenlandicus</i> Chernova, 2001 ^(*)	North Atlantic: north of the Mid-Atlantic Ridge, mesopelagic, 981–2015 m over greater depth. Ellsewhere found near South	[48]

	Greenland (see Table 1)	
5.7. <i>P. harteli</i> Chernova, 2001	WN Atlantic: 40°45'N, 65°03'W, 1008-0 m	[46]
5.8. <i>P. mirabilis</i> Chernova, 2001	WN Atlantic: slope of New England (39°N, 70°39' W), 0– 700 m over 1370–1700 m	[46]
5.9. <i>P. rossi</i> Chernova et Stein, 2004 ²	WN Atlantic: Cape Hatteras (35°30.036 N, 74°46.497"W), 500–674 m over 900 m	[118]
5.10. <i>P. sargassicus</i> Chernova, 2001	Sargasso Sea (35°30'N, 67°14'30"W, 0–1050 m	[46]
5.11. <i>P. spirohira</i> Chernova et Stein, 2002	EN Atlantic: west of northern Spain (41°56.2'N, 16°50.1'W), 985–1010 m	[92]
6. Genus <i>Eutelichthys</i> Tortonese, 1959		
6.1. <i>E. leptochirus</i> Tortonese, 1959	EN Atlantic: south-western part of the Mediterranean Sea and Bay of Lyon, 500–917 m	[90,112,11 9–120]

* 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 *Pseudnos rossi* was separated in a new genus *Aetheliparis* Stein, 2012. Additional data is needed to decide on the validity of this genus.

Snailfishes of the Genus *Liparis*

The genus *Liparis* includes not less than 72 species, being one of the four largest genera of the family [39]. The genus is considered to be the most generalized [35,53,56, 60,65]. Plesiomorphic characters includes innumerable 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 4 notched radials and 3 large interradiial fenestrae. The pectoral fin is notched and may include a large number of rays (up to 46). The anus and genital opening 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]; weight sometimes reaching 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 [124] (p. 60). The center of diversity of the genus is located in the northern part of the Pacific Ocean, where most of the species occur (81% of the genus content). Inside the Pacific, most of *Liparis* are found in Asian waters (83%), mainly in the Sea of Japan and Sea of Okhotsk.

By morphological characters, *Liparis* species are divided into 5 subgenera [39]; four of them (*Neoliparis*, *Liparis*, *Careliparis*, *Lycocara*) are of interest for this review.

Subgenus *Neoliparis* is most generalized and diverse. It contains 26 species in six groups of similar species [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 done. Except of other characters, they all have a short caudal peduncle that includes up to 3 vertebrae. The dorsal and anal fins usually 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 on the caudal fin, and dorsal-fin notch is usually absent or diminishingly small. In the boreal Atlantic, there are 4 species of this subgenus; *L. atlanticus*, *L. inquilinus* and *L. coheni* inhabit the Western North Atlantic; *L. montagui* occurs along the European shelf, others live in the boreal North Pacific.

Subgenus *Liparis* is less diverse than the previous subgenus and includes about eight species. All of them, except of similar counts, have teeth with lobes of the same size and short gill opening. Two of them live 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 found in the Arctic, *L. tunicatus*, which lives mainly in coastal and freshened areas.

Subgenus *Careliparis* includes about 30 species in 5 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 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.

Subgenus *Lycocara* includes at least 3 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 are often considered as *L. cf. fabricii* complex, which has circumpolar Arctic distribution. In the boreal Pacific Ocean, not a single congener with these characters is known.

***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 6 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 northwards 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 shallow depth; *L. bathyarcticus* prefers deeper waters along the shelf edge. Representatives of the black-belly 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 along the Arctic shelf. They all adapted to live and breed in cold waters (to -2.0°C).

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		
“ <i>L. montagui</i> ”-group		
* <i>L. montagui</i> (Donovan, 1804) Eur	–	<i>L. burkei</i> (Jordan et Thompson, 1914) Jap <i>L. chejuensis</i> Wu et Wang, 1933 Yell <i>L. petschiliensis</i> (Rendahl, 1926) Yell <i>L. punctulatus</i> (Tanaka, 1916) Jap
“ <i>L. atlanticus</i> ”-group		
<i>L. atlanticus</i> (Jordan et Evermann, 1898) WNA	–	<i>L. rutteri</i> (Gilbert et Snyder, 1898) Amer Ale <i>L. schantarensis</i> (Lindberg et Dulkeit, 1929) Okh <i>L. schmidti</i> Lindberg et Krasnyukova, 1987 Jap
“ <i>L. grebnitzkii</i> ”-group		
<i>L. inquilinus</i> Able, 1973 WNA	–	<i>L. miostomus</i> Matsubara et Iwai, 1954 Hokk, Kam <i>L. kusnetzovi</i> Taranetz, 1935 Jap <i>L. mednius</i> (Soldatov, 1930) Com <i>L. grebnitzkii</i> (Schmidt, 1904) Com
Subgenus Liparis Scopoli, 1777		
<i>L. coheni</i> Able, 1976 WNA		<i>L. brashnikovi</i> Soldatov, 1930 Jap, Kam
* <i>L. liparis</i> (Linnaeus, 1766) Eur	<i>Liparis tunicatus</i> Reinhardt, 1837 circ	<i>L. frenatus</i> (Gilbert et Burke, 1912) Jap, Hokk, Okh
<i>L. barbatus</i> Ekström, 1832 Balt		<i>L. marmoratus</i> Schmidt, 1950 Okh, Ber
		<i>L. bristolensis</i> (Burke, 1912) Ber, Al

Subgenus <i>Careliparis</i> Garman, 1892		
<i>“L. megacephalus”</i> - group		
–	<i>Liparis bathyartcticus</i> Parr, 1931 circ	<i>L. meridionalis</i> Schmidt, 1950 Jap
		<i>L. punctatus</i> Schmidt, 1950 Okh
		<i>L. eos</i> Krasnyukova, 1894 Sakh
		<i>L. rotundirostris</i> Krasnyukova, 1894 Sakh
		<i>L. megacephalus</i> (Burke, 1912) eBer
		<i>L. brevicaudus</i> Mori, 1956 Jap
		<i>L. quasimodo</i> Krasnyukova, 1894 Sakh
		<i>L. lindbergi</i> Krasnyukova, 1894 Sakh
Subgenus <i>Lycocara</i> Gill, 1884		
–	<i>Liparis</i> cf. <i>fabricii</i> complex circ (<i>L. fabricii</i> Krøyer, 1847 Spits <i>L. koefoedi</i> Parr, 1932 Spits <i>L. laptevi</i> Popov, 1933 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.

“Liparis montagui”-group. The European *L. montagui* has a distinguishing character: the posterior pair of nostrils is completely closed (no openings). The species with reduced posterior nostrils are 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, *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, four occur in the Western North Pacific.

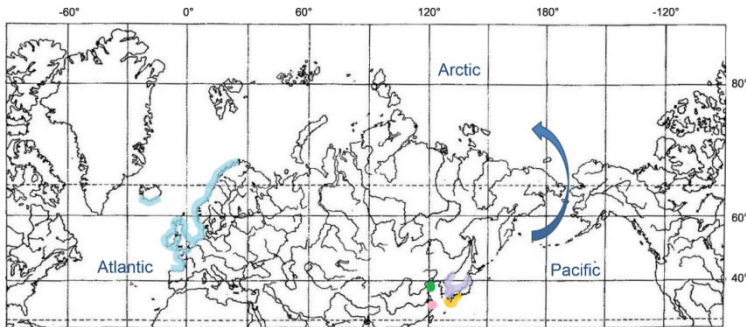


Figure 1: Distribution of “*L. montagui*”-group, in the Atlantic: blue color – *L. montagui*; in the Pacific: green color – *L. petchiliensis*, pink – *L. chefuensis*, lilac – *L. punctulatus*, yellow – *L. burkei*; arrow shows the most probable direction of the preglacial pathway.

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 southwards to California); all represent the “*L. atlanticus*”-group (Figure 2). The distribution of this group is amphiboreal, with one species in the Western North Atlantic and three species in the North Pacific.

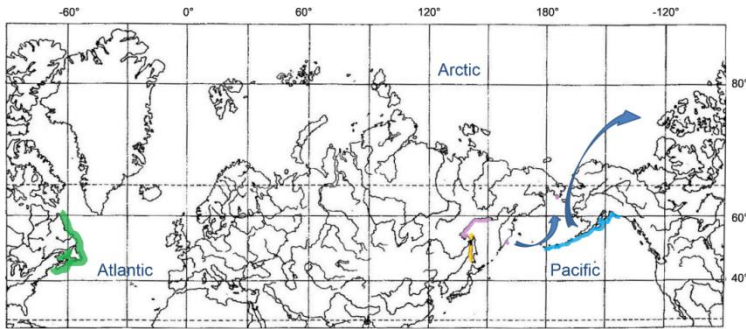


Figure 2: Distribution of “*L. atlanticus*”-group, in the Atlantic: green color – *L. atlanticus*; in the Pacific: lilac color – *L. shantarensis*, yellow – *L. schmidtii*, blue – *L. rutteri*; arrow shows the most probable direction of the preglacial pathway.

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

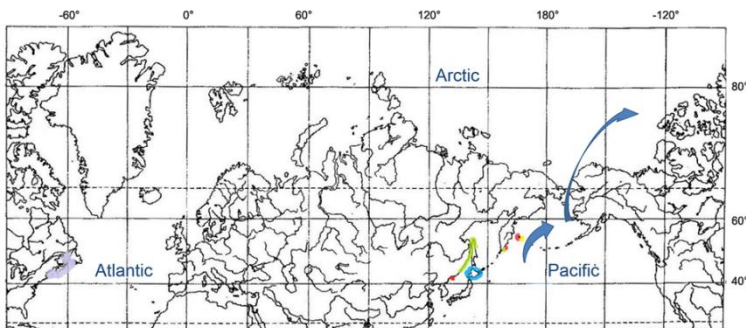


Figure 3: Distribution of “*L. grebnitzkii*”- group, in the Atlantic: lilac color – *L. inquilinus*; in the Pacific: red – *L. grebnitzkii*, green – *L. kusnetzovi*, blue – *L. miostomus*, yellow – *L. mednius*; arrow shows the most probable direction of the preglacial pathway.

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 characters and belong to the generalized subgenus *Neoliparis*.

The next group, the subgenus *Liparis*, gives 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. There is *L. tunicatus* in the Arctic circumpolarly (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. brashnikovii* 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.

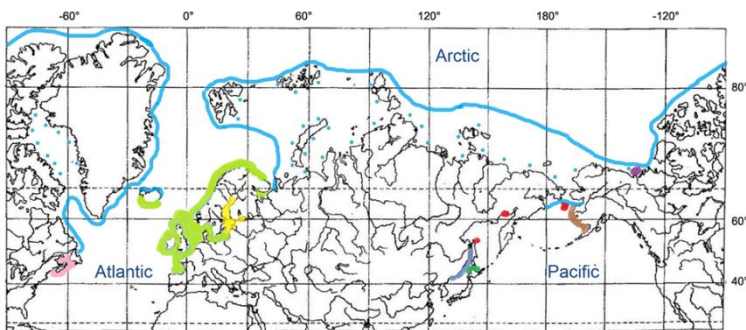


Figure 4: Distribution of “*L. liparis*”- group, in the Atlantic: lilac color – *L. coheni*, light green – *L. liparis*, yellow – *L. barbatus*; in the Pacific: red – *L. marmoratus*, dark green – *L. frenatus*, gray – *L. brashnikovii*, brown – *L. bristolensis*; in the Arctic: blue – *L. tunicatus*, occurs mainly in coastal zone (dots), dark lilac – *L. herschelinus*.

The fifth group is represented by members of the subgenus *Careliparis*. The Arctic *L. bathyarticus* is the 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 the majority of species in the North Pacific and one representative in the Arctic.

The last group is represented by *Liparis* cf. *fabricii* complex, which includes snailfishes with black peritoneum and simple teeth. The species with the same characters are not known in boreal areas. Thus, this is an example of a group, endemic for the Arctic, belonging to the genus of the Pacific origin.

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, *Liparis* species are 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 pre-glacial 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, since 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 made for amphiboreal invertebrates: in the group of shelf species that have been 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 coldness during the Ice age and in the Arctic the circumpolar *L. tunicatus* and the black-bellied complex *L. cf. fabricii* formed under conditions of glacial cooling and salt pulsations. They are stenotherm cold-

water fishes, endemic for the Arctic. In the postglacial period, when the Bering Strait became open, they did not penetrate far south into warmer waters, like 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 post-glacial climatic optimum, the ancestor of *L. bathyarticus* was able to settle in the Arctic seas, westward at least to the Barents Sea. Ecologically, the species is confined to a relatively warm (low positive) water mass, which occupies an intermediate layer along the continental slope of the Arctic. However, it did not have time to significantly separate from the Bering Sea group of species, which are currently very similar to each other.

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 Sea [105,124]. Based on recent data, it is unlikely that the ancestral form entered the Baltic from the White Sea during the Yoldian period, as this connection has been disproved [125]. More probable, it could happen 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 (fig. 9 by James Orr et co-authors [65]). One clade includes *L. bathyartcticus*, another (polytomic) combines seven other species (*L. liparis*, *L. inquilinus*, *L. tinicatus*, *L. atlanticus*, *L. montagui*, *L. fabricius*, *L. bristolensis*). This can be interpreted as a correlation with two groups, migrating from the Pacific Ocean at different times (postglacial and preglacial); their further evolution proceeded independently in other geographic regions. However, the second clade unites rather different species (in axial skeleton, dental system), which have morphologically similar congeners in outer clades (*L. montagui* – *L. punctulatus*; *L. atlanticus* – *L. rutteri*). If the COI tree is followed, this means that independent occurrence of complex morphological structures in different clades should be accepted, which can hardly be explained. Further studies should be done.

Snailfishes of the Arctic – Genus *Careproctus*

The genus *Careproctus* (Sea tadpoles) includes not less than 162 species, being one of the four largest genera in the family [42, updated].

Careproctus differs from *Liparis* in absence (reduction) of the posterior pair of nostrils and pseudobranchia, 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 settlement and 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, made by Anatole Andriashev, contains 44 species [60]. The species were subdivided by him in two subgenera; the sg. *Careproctula* (type *C. fedorovi* Andriashev et Stein 1998, the

Scotia Sea) was established, except of the nominative one. Seven southern species were included in the sg. *Careproctus*, being similar to the type of the genus *C. reinhardti* described from the south-western Greenland. They all have strong pleural ribs and 4(3+1) notched radials in the pectoral girdle (which are plesiomorphic *Liparis*-like features). Most of Sea tadpoles of the Southern Ocean (37) have been included in the sg. *Careproctula*. They are characterized by the reduction of the pleural ribs, and in the shoulder girdle, the reduction of the interradiial fenestrae (radials are round); in many of them, the number of radials is reduced.

***Careproctus* of the Arctic and North Atlantic**

The *Careproctus* fauna of the Arctic and North Atlantic is at the stage of initial description; their number will obviously be replenished in this vast region, especially in the bathyal and abyssal depths of the ocean. The current list of species includes 21 taxa in the Arctic (Table 2) and 3 ones in the North Atlantic (Table 3). Morphologically they can be assigned to subgenera, mentioned above: *Careproctus* and *Careproctula* [37,38, updated]. An updated analysis of these species has not been carried out, so a brief review is necessary before looking for their relatives.

Subgenus *Careproctus* in 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 of the genus *Careproctus* [37], 2) *C. longipinnis* (Figure 5b) from the Norwegian Sea (caught at a depth 1322 m) [37]; 3) *C. solidus* from the slope of the Laptev Sea (2151—1934 m) [36] and 4) Dusty snailfish *C. lerikimae* from the Beaufort Sea (175—500 m) [81]. The other 11 species are combined in the "*C. dubius*"-group, since they, differing from each other (Figure 6a, b; Figure 7a), share a complex of common characters (Table 5). They all have simple teeth (secondarily simplified from three-lobed ones); the lower lobe of the pectoral fin is greatly elongated (1.3–1.5 times as long as its upper lobe) and obviously has tactile or taste functions; prickles on the skin are cactus-like.

Table 5: Basic characters of species of the genus *Careproctus* from the Arctic and North Atlantic.

Subgenus <i>Careproctus</i> (radials notched, 2-3 fenestra present; pleural ribs saber-like)				
Pectoral radials	4(3+1)	3(2+0+1)	3(2+0+1) ³	2 (1+0+0+1) ³
Vertebrae	59–64	60		
Pectoral-fin rays	29–36	31		
Pores 2–5–7–2	<i>C. reinhardti</i>	<i>C. solidus</i>		
	<i>C. longipinnis</i>			
	<i>C. lerikimae</i>			
	“ <i>C. dubius</i> ”(11 species) ¹			
Subgenus <i>Careproctula</i> (radials round, unnotched; fenestra absent, pleural ribs absent or weak 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	<i>C. ranula</i> *	<i>C. micropus</i>	<i>C. canusocius</i>	<i>C. merretti</i> *
	<i>C. kidoi</i>	<i>C. moskalevi</i>		<i>C. aciculipunctatus</i> *
		<i>C. latiosus</i> ²		
		<i>C. mica</i>		

* Atlantic species.

¹ Composition of the “*C. dubius*”-group – *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).

³ There are no species with such characters in the subgenus *Careproctus*.



(a)



(b)

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

A peculiar characteristic of the "*C. dubius*"-group is a longitudinally-oval pupil, which may be associated with the low illumination of habitats in a polar conditions or at a depth of aphotic zone. In addition, in the species of the group the anus and genital opening are shifted forward, to the very edge of the ventral disc. 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.



(a)



(b)

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

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, no interradiation fenestrae (if rarely present, then small, rudimentary); pleural ribs reduced (absent or rudimentary). The lower pectoral-fin lobe is shorter than the upper one (except for *C. merretti* and *C. aciculipunctatus* with the lower lobe 1.2 times longer). Suprabranchial pore one, the second suprabranchial pore (= rudimentary element of the trunk lateral line) is reduced; pore formula 2-6-7-1. Body elongated and low, maximum depth 12-24% SL. Skin usually naked, rarely with microscopic needle-like spines. Among these nine, four groups can be recognized, according to the type of the shoulder girdle and the number of

vertebrae (Table 5). The most generalized is *C. (Careproctula) ranula*, having three-lobed teeth and large disk (7.7—9.0 % *SL*). Thus, *Careproctula* species are heterogeneous, which makes it probable that they belong to different phylogenetic lineages.

Among the Arctic species, four are deep-water fishes living at a depth 952–1695 m: *C. kidoi* in the Baffin Bay, *C. micropus*, *C. moskalevi* and *C. latiosus* in the northern part of the Norwegian Sea. Two of them 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; *C. merretti* and *C. aciculipunctatus* are abyssal fishes that live in the Porcupine Seabight at 3990—4100 m.



(a)



(b)

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

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 characters of which are uniformly described [60]. The conclusions are as follows. Arctic representatives of the sg. *Careproctus* differ from all southern species in combination of numerous vertebrae (59–63), simple (not three-lobed) teeth, an anteriorly shifted anus and genital opening, 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 (the lower lobe of the pectoral fin is shorter, the postorbital pore present in the latter). *Careproctus longipinnis* seems to be most similar to *C. trachysoma*, known from Sea of Japan [81].

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 (and their absence in southern species). 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*, *C. spectrum* and in the holotype of *C. furcellus* [80]. Therefore, for Arctic species of sg. *Careproctus*, an amphiboreal concept can be discussed, although there are not enough comparative materials from the Pacific fauna for all species.

Preliminary assumptions may be as follows. During pre-glacial migrations, an ancestral Pacific forms of sg. *Careproctus* entered the Arctic through the Bering Strait and spread towards the Atlantic. During the Ice age, different parts of the population could move away from the glaciers to bathyal depth, where deep-water species later formed: *C. longipinnis* in the Norwegian Sea basin (about 1322 m) and *C. solidus* on the northern slope of the Laptev Sea (2151–1934 m). On the shelf areas, which were repeatedly getting free of glaciers, a species flock of the “*C. dubius*”-group was produced, vicariant in different areas: 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, *C* 10–12) can be explained by the “bottleneck” effect, when a new population, that has penetrated into the Arctic, was founded by a small number of individuals. The variety of species can be explained by the presence of free ecological niches and the weak pressure of competitors in the deglaciated aquatories. The accelerated speciation was facilitated apparently by obvious presence of internal fertilization in “*C. dubius*”-species and related behavior rituals that worked as additional factors of isolation.

Among the representatives of sg. *Careproctula*, the amphiboreal concept is most likely applied to *C. ranula*, a shallow-water fish from the boreal WN Atlantic. In pre-glacial time, the ancestral form probably spread to the Atlantic along the coast of North America, and during the Ice age retreated south and formed the recent species. It is possible that other parts of the ancestral populations descended from the action of glaciers to bathyal depth (952–1695 m) and gave the origin to *C. kidoi* in Baffin basin and *C. micropus*, *C. moskalevi* and *C. latiosus* in the Norwegian basins. These species are rather close each other in main characters (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 about 205 m) and *C. canusocius* in the Beaufort Sea (488–599 m). This assumption is preliminary, since for confirmation, it is necessary to find related species in the fauna of the Pacific Ocean. The origin of the mentioned *Careproctula* in the Southern Ocean is less probable, since there are no similar species there.

However, in contrast to what was shown above, the penetration of the two deepest North Atlantic *Careproctula* (*C. merretti* and *C. aciculipunctatus*, 3990—4100 m) into the North Atlantic was explained differently. The Bering Strait was shallow during the periods of its existence; therefore, the amphiboreal route does not explain the origin of abyssal fishes. Their penetration into the North Atlantic was explained by the hypothesis of transoceanic dispersal, based on the materials of the worldwide ranges of fishes of the families Liparidae and Zoarcidae [7,60,73,129]. Among the Liparidae, this hypothesis was mainly based on *Paraliparis*, but, in addition, this path has been supposed for the abyssal North Atlantic *C. merretti* and *C. aciculipunctatus*. This concept is beyond the scope of present study and is not discussed in details. 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). It was shown, that the northern *C. aciculipunctatus* and *C. merretti* represent a continuation of this evolutionary line of *Careproctula*, which is expressed in an increase of the metameric elements of the axial skeleton during the development of the eel-like type of locomotion of fishes at oceanic depth [60].

The phylogeny of the *Careproctus* based on the COI analysis, which includes at least 38 species of this genus, shows two clades containing the Arctic and Atlantic species (a total of four of them have been studied) (fig. 10 by James Orr et co-authors [65]). This can be interpreted as a correlation with two groups that migrated into the Arctic and Atlantic at different times. These are: 1) *C. reinhardti* and *C. lerikimae* (subgenus *Careproctus*); among related Pacific species there is *C.*

trachysoma; 2) *C. micropus* and *C. kidoi* (subgenus *Careproctula*), which are grouped with the Pacific species of the genus. These data are consistent with the ideas about the Pacific origin of mentioned Arctic-Atlantic species. Northern abyssal species of the genus of South-ocean origin have not been genetically studied.

Other Liparids of the Arctic and Atlantic

The genus *Paraliparis* includes not 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 *Paraliparis* into the North Atlantic and the Arctic is explained by the Andriashev's hypothesis mentioned above. For deep-sea *Paraliparis*, the center of their secondary speciation is located in the Antarctic region, and from the southwestern Atlantic they penetrated north, to the depths of the North Atlantic. This route is confirmed by morphologic similarity of the northern and southern species, some of which demonstrate a chain of related forms [60].

The arriving of ancestor of *P. bathybius* in the Polar Basin from the Atlantic Ocean can be considered very probable. This is supported by the discovery of a morphologically similar species in the adjacent North Atlantic: *P. abyssorum* from waters south of the Faroe–Icelandic underwater threshold [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* group (two hypuralia, 4 pectoral radials, epurale present) with characters of specialization (reduction of the anterior portion of the dorsal fin, complete reduction of notch rays in the pectoral fin). This gives grounds to suggest an earlier penetration of its ancestral form into the Arctic Basin compared to *P. bathybius*.

In the phylogeny of *Paraliparis* based on COI analysis (fig. 11 by James Orr et co-authors [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 of the Polar basin, considered monotypic, but the second species, *Rh. melanocephalus* has recently been described from the Norwegian basin south-west of the Bear Island (depth 1470–1695 m) [84]. The large oblique mouth, huge gill opening, and modified gill rakers suggest a filter feeding in these meso-bathypelagic fishes. Until recently, there was not even an assumption about forms close to it. 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 characters with the *Rhodichthys*, e.g. very large gill slits reaching in front of lower end of pectoral-fin base, gill rakers modified by similar way, which obviously are results of adaptations to pelagic feeding. My guess is that *Rhodichthys* may have derived from the same root as Pacific *Menziesichthys*. In the phylogeny of Liparidae based on COI analysis (fig. 11 by James Orr et co-authors [65]), *Rh. regina* is found among the south-oceanic *Paraliparis*. But among *Paraliparis*, there are no even remotely similar species. *Rhodichthys* differs in a unique orobranchial apparatus at the generic rank. The way of *Rhodichthys* distribution into the Arctic is unclear; most likely this happened before *P. bathybius* did. During the glaciations, *Rhodichthys* was probably driven to the polar depths into the mesobathypelagic layers, where it changed greatly, adapting to the filtering method of pelagic feeding.

Psednos encounters 11 species in the North Atlantic and 3 in marginal Arctic area. The center of origin of this genus is associated with the waters of the Australian continent, where the most generalized species are found [61]. Most species are meso- and bathypelagic, known 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 mesopelagic waters of South-West and South-East Greenland (Table 2). These are the areas of strong upwelling that allows deep-sea inhabitants to pass up closer to

surface, and many of deep-sea Atlantic fishes are found in these marginal Arctic regions [77]. Three *Pseudnos* can be related to this fish complex. This is all the more likely since two other species recorded in Greenland waters, *P. christinae* and *P. groenlandicus*, are also known in the northern part of the Mid-Atlantic Ridge. Consequently, the *Pseudnos* 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 of one of the branchial rays and in the small size of adults (miniaturization). In terms of its characters, it is closest to the North Atlantic *Paraliparis hystrix* 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, 131–133]. 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 from the Atlantic, but later become extinct there, remaining only in the Red Sea as a relict form.

Conclusion

The data presented in the article aim to provide a wide background of the complex events of trans-Arctic migrations (and briefly of the southern trans-oceanic route) of the northern fish fauna on an example of the family Liparidae. We used the comparative methods of analyzing our materials collected over many years of Liparid studies. The conclusions are based on morphological differences /similarities of taxa, patterns of distribution of species on the background of biogeographic representations and data obtained for other groups of animals. Our results do not contradict much with studies based on multi-taxon mitochondrial data that provide an overview of the dynamics of inter-oceanic trans-Arctic dispersal and gene flow [134]. Moreover, they broaden 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, the new result is updated overview of the species composition in the Arctic. The list includes 5 genera, *Liparis*, *Careproctus*, *Paraliparis*, *Rhodichthys* and *Psednos*. Of the total number of 33 species (excluding boreal ones entering the marginal Arctic regions), the majority (21) are representatives of the genus *Careproctus*. The amphiboreal concept explains the speciation of *Liparis* and the bulk of the *Careproctus* species as a result of trans-Arctic migrations; in addition. For two Arctic *Paraliparis*, the transoceanic dispersal route can be accepted that was shown earlier for this genus, which dispersed from the North Pacific through the Southern Ocean and then north across the Atlantic. The origin of the endemic *Rhodichthys* is still unclear. *Psednos* species, found in the Arctic so far only in the waters of Greenland, have appeared from the Atlantic, as they are widespread in the meso- and bathypelagic layer of warm oceans. Thus, the liparid fauna of the Arctic, although having its ancient roots from the North Pacific, came from both neighboring oceans, in majority through the Bering Strait and to a lesser extent from the Atlantic. The latter route was shown for deep-sea liparids: part of sg. *Careproctula* species, benthopelagic *Paraliparis* and meso-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*; *Eutelichthys* instead of *Rhodichthys*. Boreal shelf species, all *Liparis* and *C. (Careproctula) ranula*, may have speciated from the ancestors of the trans-Arctic routes; others are more likely to have South-oceanic relatives.

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

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