Colonization of the Arctic Ocean by two cosmopolitan genera of marine invertebrates

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ABSTRACT: The colonization of the Arctic Ocean by two genera of marine invertebrates widely-distributed outside the Arctic, *Paradiopatra*, a polychaete, and *Elpidia*, a holothurian*,* is described using methods of phylogenetic biogeography, including morphology-based phylogenetic reconstruction. The phylogeny of *Elpidia* was reconstructed based on a matrix of 20 morphological characters for 22 species. Maximum parsimony analysis yielded four equally parsimonious trees within the Arctic clade, comprising three species: *E. belyaevi*, *E. glacialis* and *E. heckeri*. *Elpidia gracilis* inhabiting the north Atlantic was the sister species to the Arctic clade on three of four most parsimonious tress. This suggests possible colonization of the Arctic Ocean from the North Atlantic. Comparison of pairs of species of *Paradiopatra*: *P. striata/P. pauli* and *P. yasudai/P. quadricuspis* supports the hypothesis of trans-Arctic faunal exchange. These pairs form monophyletic clades on the strict consensus tree and have representatives in the Pacific and the Arctic/North Atlantic. It is argued that dispersal of fauna most probably was directed from the north Pacific to the North Atlantic across the Arctic. Two North Atlantic species, *P. fiordica* and *P. quadricuspis*, with almost identical geographical and vertical ranges along the boundary between the North Polar Region and the Eastern Atlantic Boreal Region did not form the monophylectic clade on the phylogenetic tree and were considered as distant relatives. However the strict consensus tree had very low resolution due to high portion of homoplastic characters and relationships of the species could not be tested exhaustively.

KEY WORDS: *Paradiopatra*, *Elpidia*, phylogeny, biogeography, trans-Arctic interchange.

Колонизация Северного Ледовитого океана двумя широко распространенными родами морских беспозвоночных

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РЕЗЮМЕ: На основе реконструкции филогенетических отношений с использованием морфологических признаков и методов филогенетической биогеографии описаны

пути колонизации Северного Ледовитого океана двумя широко распространенными родами морских беспозвоночных: многощетинковыми червями *Paradiopatra* и голотуриями *Elpidia*. Филогения рода *Elpidia* была получена на основе матрицы из 20 морфологических признаков, закодированных для 22 видов. В результате анализа, проведенного методом максимальной экономии, было получено четыре равно экономных дерева. На каждом дереве присутствовала клада, объединяющая арктические виды: *E. belyaevi*, *E. glacialis* и *E. heckeri*. На трех максимально экономных деревьях вид *E. gracilis*, населяющий северную Атлантику, имел сестринское положение по отношению к арктической кладе, что позволило предположить возможный путь заселения Арктики из северной Атлантики. Сравнение пар видов из рода *Paradiopatra*: *P. striata/P. pauli* и *P. yasudai/P. quadricuspis* поддерживает гипотезу о трансарктическом обмене фаунами. Эти пары видов образуют монофилетические группировки на строгом консенсусном дереве, и каждая из них включают в себя виды, обитающие в северной Пацифике и в Арктике/северной Атлантике. Высказывается предположение о том, что вероятный путь расселения видов был направлен из северной Пацифики через Арктику в северную Атлантику. Два североатлантических вида *P. fiordica* и *P. quadricuspis* с практически полностью совпадающими ареалами и диапазонами вертикального распространения вдоль границы между Северной Полярной Областью и Восточноатлантической Бореальной Областью не показали близкородственных отношений при анализе филогении рода. Однако строгое консенсусное дерево имело низкое разрешение в виду большого количества гомопластических признаков, и поэтому анализ филогенетических отношений в роде не смог выявить все родственные связи.

1. Introduction

The Arctic Ocean has played a significant role in biotic interchange between the North Atlantic and the North Pacific since the early Pliocene (Palumbi, Kessing, 1991; Vermeij, 1991; Wares, Cunningham, 2001; Addison, Hart, 2005). The asymmetry of trans-Arctic invasion was suggested in a number of studies published during recent decades. According to Durham and MacNeil (1967), the number of species dispersed from the Pacific to the Atlantic is eight times higher than that in the opposite direction. However the analysis of the pattern of trans-Arctic species dispersion shows a strong bias in favour of species of the Pacific origin (Vermeij, 1991).

While the dominance of Pacific fauna in the trans-Arctic interchange is generally accepted, the ratio of species of Atlantic and Pacific origin in the Arctic Ocean still remains questionable.

Ekman (1935) and Gurjanova (1939) analysed endemic fauna of the high-latitude Arctic waters and suggested the role of the Pacific Ocean as donor of species greatly exceeding the role of the Atlantic Ocean. The dominance of species of the Pacific origin was also accepted by Djakonov (1945), Mironov and Dilman (2010), while Anisimova (1989) and Smirnov (1994) suggest a dominance of species of Atlantic origin. The multivariate analysis of deep-sea occurrences of polychaete species off the Eurasian and American coasts of the Arctic Ocean and the Greenland–Iceland–Norwegian Seas revealed strong Atlantic influence and absence of modern Pacific fauna (Bluhm et al., 2011). The occurrence of the Arctic-Atlantic Region in a number of schemes of biogeographical subdivision (Gontar, Denisenko, 1989; Kussakin, 1979; Petryashov, 2009) underlines the close relationships between the Arctic and the North Atlantic. However more studies of historical biogeogra-

phy of various genera are required to clarify the ratio of Atlantic and Pacific components in the modern Arctic fauna.

Three major approaches are traditionally used to reveal possible pathways of colonization of the Arctic Ocean: paleontological, morphological and molecular. Analysis of paleontological data and comprehensive molecular studies provide reliable evidence on possible schemes of trans-Arctic faunistic exchange (Palumbi, Kessing, 1991; Collins et al., 1996; Harrison, Crespi, 1999; Wares, 2001; Väinölä, 2003; Dodson et al., 2007). However the number of paleontological records in the Arctic remains limited. Molecular data for many marine taxa are rarely available because of difficulties with obtaining ethanol fixed, or frozen, material from relevant geographical areas. Morphological studies based on phylogenetic approaches may provide additional information on the colonization of the Arctic Ocean and faunistic interchange.

The main goal of the present study is to evaluate possible pathways of species dispersal in the northern hemisphere, with emphasis on colonization of the Arctic region based on studies of phylogeny in two genera of benthic invertebrates: *Paradiopatra* (Onuphidae, Polychaeta, Annelida) and *Elpidia* (Elpidiidae, Holothuroidea, Echinodermata). Both genera are widely distributed in the world ocean from subtidal to hadal depths (Belyaev, 1971; Budaeva, Fauchald, 2011), and have representatives in the Arctic, the North Pacific and the North Atlantic. A phylogeny of the genus *Paradiopatra* has been proposed by Budaeva and Fauchald (2011) and the present study was based on this. A revision of *Elpidia* was published by Belyaev (1971, 1975), who recognized several species groups based on morphological similarities, and a revision of the Arctic group of species of *Elpidia* was conducted by Rogacheva (2007).

2. Materials and Methods

Possible pathways of species dispersal in the Arctic Ocean were studied using phylogenetic biogeography. The term "phylogenetic bioge-ography" was proposed by Brundin (1966, 1972), who suggested using the phylogenetic reconstruction of a monophyletic taxon to understand its biogeographical history (Crisci et al., 2003). This method is rather descriptive and has a number of restrictions, such as the allopatric speciation and the *ad hoc* assumption about a centre of origin corresponding to geographical range of the most basal taxon in the examined monophyletic clade (Crisci et al., 2003). Nevertheless, the method allows utilization of a robust hypothesis of phylogenetic relationships within the analyzed monophyletic group of species to support suggested potential pathways of dispersal.

In the present study, we consider the Arctic Ocean to be bounded by the Greenland-Iceland-Faeroe Ridge in the Atlantic and the Bering Strait in the Pacific. The shelf areas of the Arctic, excluding the shelf of the Norwegian Sea, belong to the North Polar (or Arctic) Shelf Region (Briggs, 1974, 1995). The deep-sea areas of the Arctic, including the Norwegian and Greenland Basins, form a separate biogeographical unit of disputed rank. Biogeographical subdivision of the Arctic is discussed in more detail by Mironov (present volume).

The genus *Paradiopatra* (Onuphidae, Polychaeta) comprises 26 species including species previously assigned to the genus *Notonuphis* Kucheruk, 1987 (for details see Budaeva, Fauchald, 2011). The phylogenetic tree for the genus *Paradiopatra* was obtained from Budaeva and Fauchald (2011).

Characters for the phylogenetic analysis of *Elpidia* were obtained from unpublished original and published data. Species were examined using a compound microscope. A matrix comprising 20 morphological characters, coded over 22 terminal taxa (including 21 ingroups and one outgroup), was constructed using DELTA Editor (DEscription Language for TAxonomy, Dallwitz et al., 1999) (Table 1). All characters were treated as non-additive with equal weights. Multistate characters were treated as unordered. Polymorphic characters were included in the original matrix. Inapplicable character states were coded as '–', unknown character states as

Table 1. Character matrix used in the phylogenetic analysis of *Elpidia*.

Таблица 1. Матрица морфологических признаков, использованных для построения филогенетической реконструкции рода *Elpidia*.

Species/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Psychroplanes convexa	2	2	2	2	1	?	?	?	?	1	2	?	?	?	?	?	?	?	?	?
Elpidia kurilensis	1	1	1	3	2	2	1	1	1	1	2	2	2	2	2	2	2	3	1	1
Elpidia birsteini	1	1	1	3	2	2	1	1	1	1	2	2	2	2	?	2	2	3	1	1
Elpidia longicirrata	1	1	1	3	2	2	1	1	1	1	2	2	2	2	?	2	2	1	1	1
Elpidia hanseni	1	1	1	3	2	2	1	1	1	1	2	2	1	1	1	2	2	3	1	1
Elpidia minutissima	1	1	1	3	2	2	1	1	1	1	2	2	1	1	?	1	1	1	2	2
Elpidia chilensis	1	1	1	3	2	2	1	1	1	1	2	2	1	1	1	1	1	1	2	2
Elpidia atacama	1	1	1	3	2	2	1	1	1	1	2	1	1	1	1	2	2	1	1	2
Elpidia uschakovi	1	1	1	3	2	2	1	1	1	1	2	2	1	1	2	2	2	3	2	1
Elpidia solomonensis	1	1	1	3	2	2	1	1	1	1	2	2	1	1	2	2	2	3	1	1
Elpidia kermadecensis	1	1	1	3	2	2	1	1	1	1	2	2	1	1	2	2	2	3	1	1
Elpidia theeli	1	1	1	3	2	2	1	1	1	1	2	2	1	1	1	1	1	1	2	2
Elpidia adenensis	1	1	1	3	2	2	1	1	1	1	2	2	1	1	1	1	1	1	2	2
Elpidia antarctica	1	2	1	3	2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	2
Elpidia sundensis	1	1	1	3	2	2	1	1	1	1	1	2	1	1	2	2	2	3	2	1
Elpidia glacialis	1	1	1	3	2	1	2	2	2	2	1	2	1	1	1	1	2	2	2	1
Elpidia heckeri	1	1	1	3	2	1	1	2	2	2	1	2	2	1	2	2	2	2	1	1
Elpidia belyaevi	1	1	1	1	2	1	1	2	2	2	1	2	1	2	1	1	1	1	2	1
Elpidia gracilis	1	1	1	3	2	2	1	1	1	1	2	2	1	1	1	1	1	1	2	1
Elpidia decapoda	1	1	1	1	2	2	1	1	1	1	2	2	1	1	2	2	2	3	2	1
Elpidia ninae	1	1	1	3	2	2	1	2	1	1	2	1	1	1	2	2	2	3	2	1
Elpidia lata	1	1	1	3	2	2	1	1	1	1	2	1	1	1	2	2	2	3	2	1

'?' — character state unknown.

'?'. Maximum parsimony analysis, examination of cladogram topologies and character evolution was performed in Winclada (Nixon, 2002). The search for the most parsimonious trees was heuristic, using TBR (tree bisection and reconnection) + TBR algorithm with 1000 replicates and 100 trees held on each step. The results of parsimony analysis were summarized into strict and 50% majority rule consensus trees. The outgroup method was used for tree rooting.

The geographical ranges of all known species of *Paradiopatra* and *Elpidia* were analysed to understand the distribution patterns of both genera in the North Pacific, the North Atlantic and the Arctic. Phylogenetic reconstructions of intrageneric relationships within the genera *Elpidia* and *Paradiopatra* (Budaeva, Fauchald, 2011) were used for biogeographical implications.

3. Results

3.1. Phylogeny of *Elpidia*
3.1.1. Taxon sampling
Elpidia is one of 13 genera in the family Elpidiidae. The genus *Elpidia* comprises 21 species. *Elpidia javanica* Belyaev, 1971 is considered here as synonym of *E. sundensis* Hansen, 1956. Several species in Belyaev (1971) were designated unnamed *Elpidia* sp.1 to sp.5. *Elpidia* sp.1 is now assigned to *E. belyaevi*. Other unnamed species are known from fragments or specimens in poor condition and could not be used in the phylogenetic analysis.

The ingroup included all the 21 described species of *Elpidia*. Morphological data were obtained from the literature for the following species: *E. adenensis* Belyaev, 1971; *E. antarctica* Belyaev, 1971; *E. atakama* Belyaev, 1971; *E. birsteini* Belyaev, 1971; *E. chilensis* Belyaev, 1971; *E. decapoda* Belyaev, 1975; *E. glacialis* Théel, 1976; *E. hanseni* Belyaev, 1971; *E. kermadecensis* Hansen, 1956; *E. kurilensis* Baranova et Belyaev, 1971; *E. lata* Belyaev, 1975; *E. longicirrata* Belyaev, 1971; *E. minutissima* Belyaev, 1971; *E. ninae* Belyaev, 1975; *E. solomonensis* Hansen, 1956; *E. sundensis* Hansen, 1956; *E. theeli* Hansen, 1956 and *E. uscha-*

kovi Belyaev, 1971 (Heding, 1942; Hansen, 1956, 1975; Belyaev, 1971, 1975; Gebruk, 1993; Rogacheva, 2007).

Three species were examined during this study:

E. belyaevi Rogacheva, 2007
Material examined: BIOICE, St. 2772, 69.26º N 14.22º W, 1633 m, 3.08.1995, 13 specimens; BIOICE, St. 2773, 69.25º N 14.28º W, 1629–1630 m, 3.08.1995, 151 specimens; BIOICE, St. 2776, 68.6º N 14.67º W, 1553–1556 m, 3.08.1995, 4 specimens.

E. gracilis Belyaev, 1975
Material examined: *Discovery*, St. 9754#3, 51º8′ N 12º2′ W, 1484 m, 1978, 7 specimens; *Discovery*, St. 9753#7, 50º55′ N 12º12′ W, 1942 m, 1978, 40 specimens; *Challenger*, St. 50602#2, 51º1′ N 13º7′ W, 1980 m, 1979, 195 specimens; *Challenger*, St. 50604#1, 50º6′ N 13º53′ W, 3490–3550 m, 1979, 2 specimens; *Discovery*, St. 9756#14, 50º4′ N 13º54′ W, 3697–3680 m, 1978, 1 specimen; *Challenger*, St. 50603#1, 49º46′ N 14º2′ W, 4000 m, 1979, 2 specimens.

E. heckeri Baranova, 1989
Material examined: BIOICE, St. 3203, 64.85º N 7.86º W, 2612–2605 m, 8.07.2001, 137 specimens and fragments; BIOICE, St. 3204, 64.86º N 7.91º W, 2613–2611 m, 8.07.2001, 8 specimens.

Psychroplanes convexa (Hansen, 1975) was selected as an outgroup. Ossicles in *P. convexa* are cross-shaped, a feature also characteristic of *Elpidia antarctica*. *Psychroplanes* is considered as one of the most primitive genera of Elpidiidae (Gebruk, 1990, 1993).

3.1.2. Description of characters
(1) *Velum*
Velum represents dorsal papillae that may be partly or completely fused along their length. Velum appears in many elpidiid genera such as *Peniagone*, *Psychroplanes*, *Achlyonice*, *Kolga* and *Amperima*, and is absent in *Elpidia*, *Scotoplanes* and *Protelpidia*.

(2) *Cross-shaped ossicles*
The presence of cross-shaped ossicles is one of the main diagnostic characters of the suborder Psychropotina, including the families Psychropotidae, Elpidiidae and Pelagothuriidae. According to Hansen (1975) and Gebruk (1990) cross-shaped ossicles are more primitive than tripartite, rod-shaped and *Elpidia*-type ossicles (see below) and they derive from primary crosses, the original type of most holothurian ossicles. Only few elpidiid genera have cross-shaped

ossicles: *Rhipidothuria*, *Psychrelpidia*, *Psychroplanes* and *Peniagone*. Within *Elpidia* one species, *E. antarctica*, displays cross-shaped ossicles.

(3, 13–20) *Ossicles of the Elpidia-type*

This type of ossicles is found in all *Elpidia* species and also in *Penilpidia* and *Protelpidia*. *Elpidia*-type ossicles are rods with two pairs of horizontal arms and one pair of vertical apophyses. Vertical apophyses may be reduced in some species. The *Elpidia* species differ from each other in the shape and size of the ossicles.

(4) *Tube feet*

Tube feet in elasipodids correspond to large ambulacral appendages forming rows along ventrolateral radii. *Elpidia* has the lowest number of tube feet in the Elpidiidae, four, or rarely five, pairs. The highest number of tube feet (more than 20 pairs) ocurrs in *Psychrelpidia discrepans*.

(5) *Calcareous ring*

The calcareous ring of elpidiids consists of five radial pieces, each with two clusters of long arms radiating from a common centre. The number of arms can be constant, e.g. four in *Elpidia* and *Scotoplanes*, or varying, as in most of other genera.

(6–11) *Dorsal papillae*

Papillae in elasipodids correspond to ambulacral appendages on right and left dorsal radii. Papillae in all species of *Elpidia*, except *E. javanica*, differ in shape and arrangement. *E. javanica* lacks papillae.

(12) *Anus*

The anus in elpidiids can be dorsal, ventral or terminal. In *Elpidia* the anus is terminal/subterminal or ventral.

3.1.3. Characters and their states

1. Velum: (1) absent; (2) present.

2. Cross-shaped ossicles: (1) absent; (2) present.

3. *Elpidia*-type ossicles: (1) absent; (2) present.

4. Maximum number of tube feet, pairs: (1) 5; (2) more than 5; (3) 4.

5. Number of arms in cluster on segments of the calcareous ring: (1) 7; (2) 4.

6. Anterior and posterior groups of papillae: (1) absent; (2) present.

7. Arrangement of papillae in anterior half of body: (1) papillae placed separately and never fuse; (2) papillae placed closely and fused at the basis.

8. Comparative length of papillae in the anterior half of the dorsum: (1) papillae not decreasing gradually; (2) papillae decreasing in length towards the middle of dorsum.

9. Length of the first (anterior) and the last (posterior) pairs of papillae: (1) papillae of the first and the last pairs are different in length, or all papillae are almost of the same length; (2) papillae of the first pair are of the same length as papillae of the last pair, other papillae are shorter.

10. Relative length of anteriormost and posteriormost papillae: (1) anteriormost and posteriormost papillae differ in length, or are the same length but not the longest; (2) anteriormost and posteriormost papillae are the longest and of the same length.

11. Papillae on mid dorsum: (1) absent; (2) present.

12. Location of anus: (1) ventral; (2) terminal or subterminal.

13. Dorsal or ventral ossicles without vertical apophyses: (1) absent or occur occasionally; (2) present in > 10% of preparations.

14. Vertical apophyses: (1) ossicles with two apophyses dominate; (2) ossicles without apophyses dominate.

15. Relative length of vertical apophyses: (1) >15% of the rod length; (2) <15% of the rod length.

16. Relative diameter of rods: (1) rods enlarged between horizontal arms; (2) rods not enlarged between horizontal arms.

17. Bases of horizontal arms: (1) spaced distantly; (2) located close to each other with acute angle in some or in many ossicles.

18. Ends of rods and arms; (1) pointed, only few small spines can be present; (2) enlarged, no spines or sometimes few very small spines; (3) enlarged or bear numerous large spines.

19. Relative length of horizontal arms: (1) arms may differ in length up to 2 times; (2) arms almost of the same length.
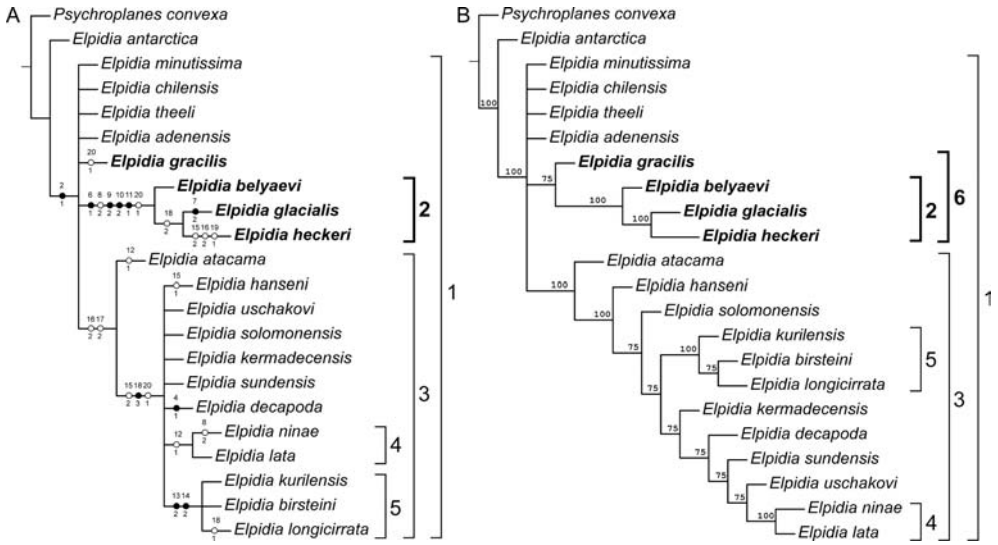
Fig. 1. Phylogenetic reconstruction of *Elpidia*.
A — strict consensus tree of four equally parsimonious trees. B — majority rule (50%) consensus tree of four equally parsimonious trees. White circles represent homoplastic synapomorphies, black circles are exclusive synapomorphies. Upper rows of numbers represent character numbers corresponding to the matrix; lower rows of numbers represent states of respective characters. Node numbers represent frequency values for each node. Numbers beside square brackets represent clades discussed in the text.

Рис. 1. Филогенетическая реконструкция отношений в роде *Elpidia*.
A — строгое консенсусное дерево, построенное на основе четырех равноэкономных деревьев. B — консенсусное дерево, построенное на основе четырех равноэкономных деревьев по методу правила большинства (50%). Белыми кружками обозначены гомопластические синапоморфии, черными кружками обозначены уникальные синапоморфии. Верхние ряды цифр на ветвях дерева A соответствуют номерам признаков в матрице, нижние ряды цифр обозначают состояния соответствующих признаков. Значения в узлах дерева B указывают на процент максимально экономных деревьев, у которых присутствует данный узел. Номера за квадратными скобками соответствуют обозначениям клад в тексте.

20. Rod diameter in the middle of largest ossicles: (1) >35 µm; (2) <35 µm.

3.1.4. Phylogenetic interrelationships

Phyloginetic analysis yielded four equally parsimonious trees with a length of 33 steps, Ci=66, Ri=81. The strict consensus tree was 37 steps in length (Ci=59, Ri=75) with *E. antarctica* as the most basal species of the genus (Fig. 1A). This species differed from the others by the presence of cross-shaped ossicles (character 2). Clade 1 contained polytomy of five species with clades 2 and 3 (Fig. 1A). Clade 2 (Fig. 1A) consisted of three species *E. belyaevi*, *E. glacialis* and *E. heckeri*. Clade 3 included several clades with species mostly occurring in deep-sea trenches. Among them species from the South Sandwich Trench (clade 4) and the North-East Pacific Trenches (clade 5) (Fig. 1A).

Our analysis was focused on clade 2 containing three Arctic species. The monophyly of this clade is supported by four exclusive synapomorphies: the presence of anterior and posterior groups of papillae (character 6), equal length of the longest anteriormost papillae (characters 8 and 9), and absence of papillae on mid-dorsum (character 11). *E. belyaevi* was the most basal species within the Arctic clade 2 (Fig. 1A). The placement of clade 2 cannot be established with confidence in the strict consensus tree because of the lack of basal resolution. The 50% majority rule consensus tree showed Arctic species combined with *E. gracilis* in a single clade as well as MPT1–3 (Figs. 1B; 2A–C).
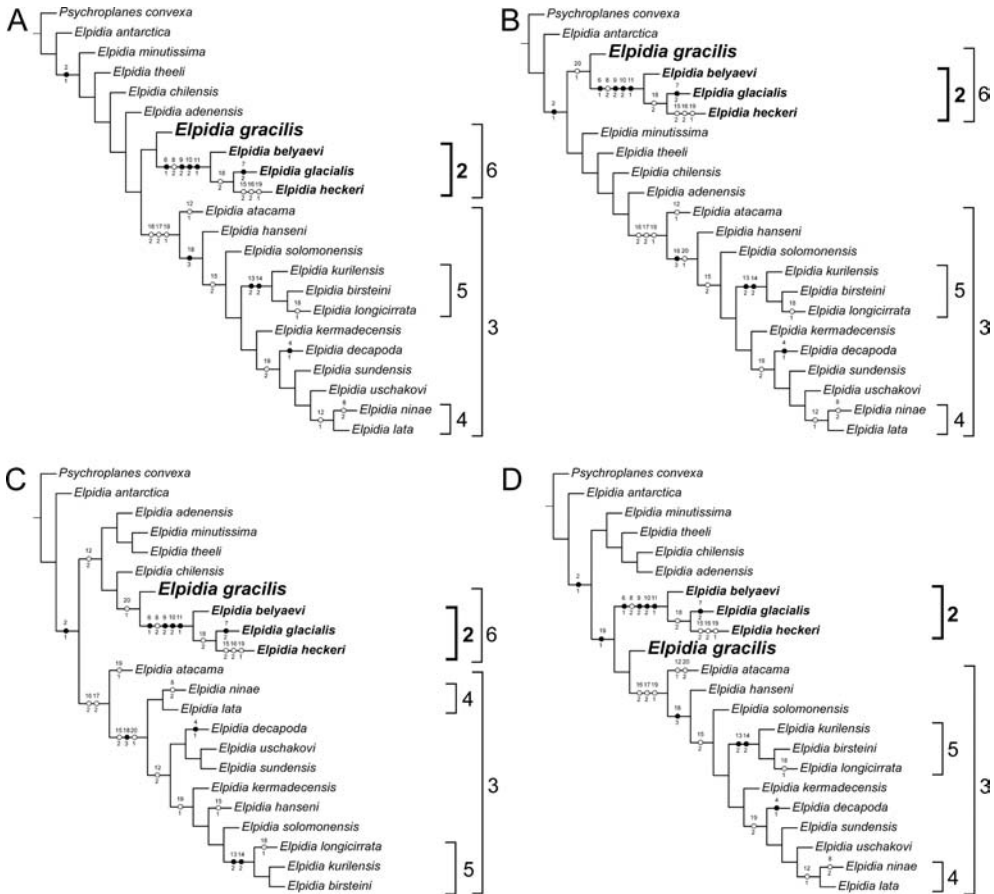
Fig. 2. Phylogenetic reconstruction of *Elpidia*. Four equally parsimonious trees (I–IV).

Рис. 2. Филогенетическая реконструкция отношений в роде *Elpidia*. Четыре максимально экономных дерева (A–D).

3.2. Phylogeny of *Paradiopatra*

Although the genus *Paradioptra* was present as a monophyleic clade on the strict consensus tree, the basal polytomy indicated very low resolution within the genus (Budaeva, Fauchald, 2011). Nevertheless two clades comprising, four species distributed in the northern hemisphere, can be recognized. *P. quadricuspis* and *P. yasudai* formed monophyletic clade 1 (Fig. 3) sharing the following characters: presence of branchiae starting from chaetigers 6–8; lateral projection of anterior parapodia from the body; two pairs of cirriform ventral cirri modifying into indistinct transverse glandular fields on the subsequent several chaetigers; and extremely long sharply pointed hoods on anterior pseudocompound chaetae. *P pauli* and *P. striata* were combined into the clade 2 (Fig. 3) based on three synapomorphies: very short lateral and median antennae; start of branchiae from chaetigers 6–8; and lateral projection of the anterior parapodia (Budaeva, Fauchald, 2011).
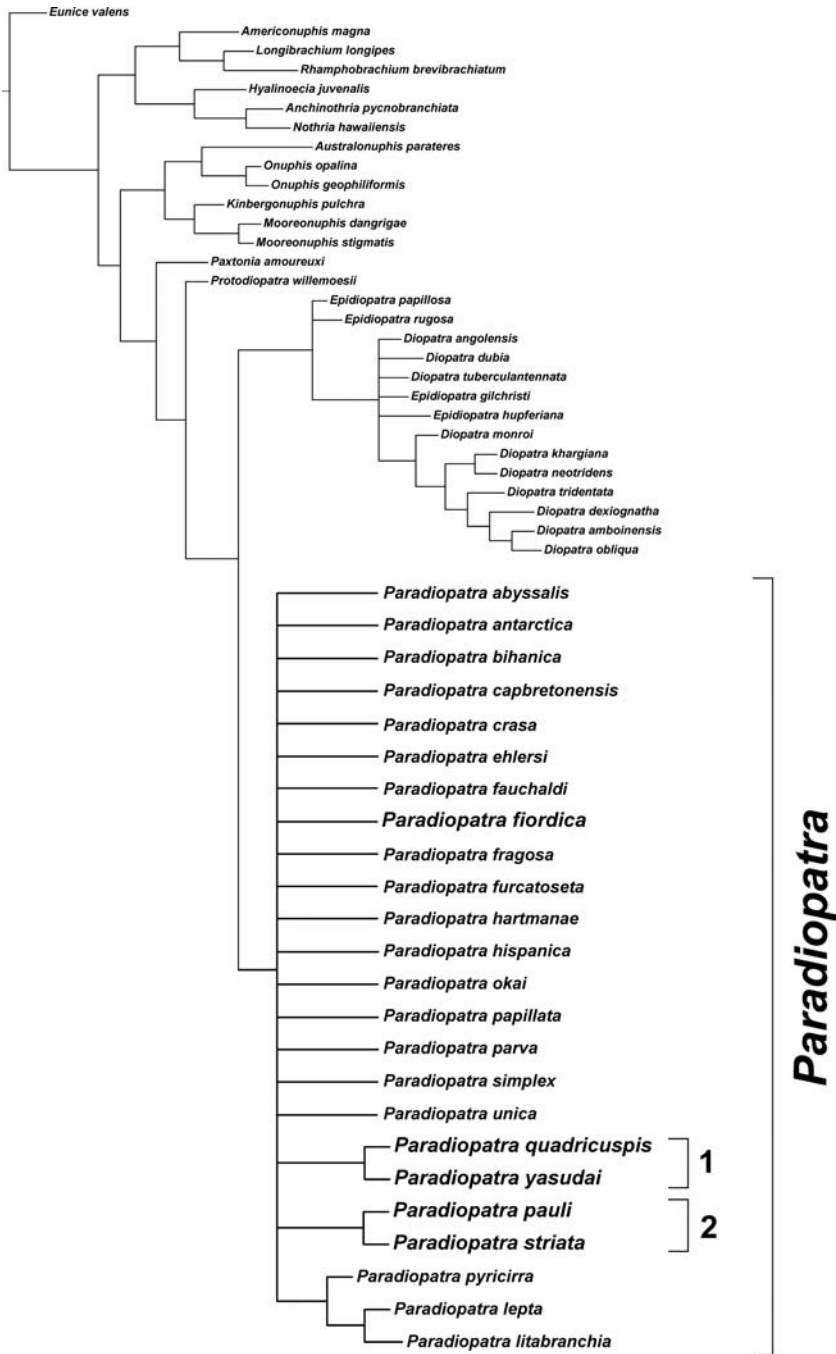
Fig. 3. Phylogenetic reconstruction of *Paradiopatra.* Strict consensus tree of 1525 equally parsimonious trees. Numbers beside square brackets represent clades used in the text (modified from Budaeva, Fauchald, 2011).

Рис. 3. Филогенетическая реконструкция отношений в роде *Paradiopatra.* Строгое консенсусное дерево, построенное на основе 1525 равноэкономных деревьев. Номера за квадратными скобками соответствуют обозначениям клад в тексте (с изменениями из Budaeva, Fauchald, 2011).

Table 2. Distribution patterns of *Elpidia* and *Paradiopatra* in the Northern Hemisphere.
Таблица 2. Распространение *Elpidia* и *Paradiopatra* в северном полушарии.

Characters	North Pacific, north of 30° N	Arctic Ocean, including the Norwegian and the Chukchi Seas	North Atlantic, north of 30° N
Elpidia			
Number of species	5	3	1
Depths, m	4100–9530	70–5550	1484–4000
Species ranges	Arctic-North Pacific — 0 Endemic — 3 Others — 2	Endemic (Arctic) — 3	Arctic-North Atlantic — 0 Endemic — 0 Others — 1
Paradiopatra			
Number of species	14	3	9
Depths, m	15–6350	68–1125	67–6350
Species ranges	Arctic-North Pacific — 0 Endemic — 10 Disjunctive Pacific-Atlantic (boreal) — 1 Others — 3	Arctic-North Atlantic (boreal) — 2 Endemic, near-Pacific (low-arctic) — 1	Arctic-North Atlantic (boreal) — 2 Endemics — 3 Disjunctive Pacific-Atlantic (boreal) — 1 Others — 3

3.3. Distribution patterns of *Paradiopatra* and *Elpidia* in the North Pacific, North Atlantic and Arctic

In the present study we focused on species inhabiting temperate and cold-water areas of the Northern Hemisphere. Species occurring in the Arctic, the North Atlantic and the North Pacific were also considered as markers of possible dispersal pathways. Distribution patterns and relationships among other species in both genera were beyond the scope of the present study and thus will not be discussed herein. The general biogeographical patterns of the genera *Elpidia* and *Paradiopatra* in the high latitudes of the Northern Hemisphere are shown in Table 2.

Species of *Elpidia* are widely distributed in the Arctic. Three species are endemic to the Arctic Ocean. The bathyal species, *E. belyaevi*, and the bathy-abyssal, *E. heckeri*, occur in the Norwegian-Greenland basin and in the Central Arctic (Fig. 4). *E. belyaevi* is also known from the Baffin Bay. The shallow-water species, *E. glacialis*, is distributed in the Kara Sea, the Barents Seas and the fjords of Greenland and Svalbard.

In contrast to *Elpidia*, species of *Paradiopatra* are narrowly distributed in the Arctic Ocean, inhabiting only near-Atlantic and near-Pacific sectors. Four *Paradiopatra* species were chosen based on their possible role in trans-Arctic fauna interchange that took place during the climate warming in the early Pliocene (Fig. 5). *P. pauli* is the single species in the genus reported exclusively from the Arctic Ocean, occurring in the northern part of the Chukchi Sea at depths 68–445 m (Annenkova, 1952; Budaeva, Fauchald, 2011). The geographical range *P. quadricuspis* is restricted to the Norwegian coast and off south-west Iceland, depth range from 154 to 780 m (Budaeva, Fauchald, 2011).

P. striata is commonly found in the Bering Sea and off Kamchatka (Budaeva, Fauchald, 2011), and reported by Imajima (1999) from Japan. This species has also been found in the north-west Atlantic off Nova Scotia (depth range from 17 to 1660 m), thus showing an amphibo-real geographical distribution. *P. yasudai* occurs in the north Pacific (in Japanese waters) at sublittoral and upper bathyal depths (from 60 to 960 m) (Imajima, 1999).
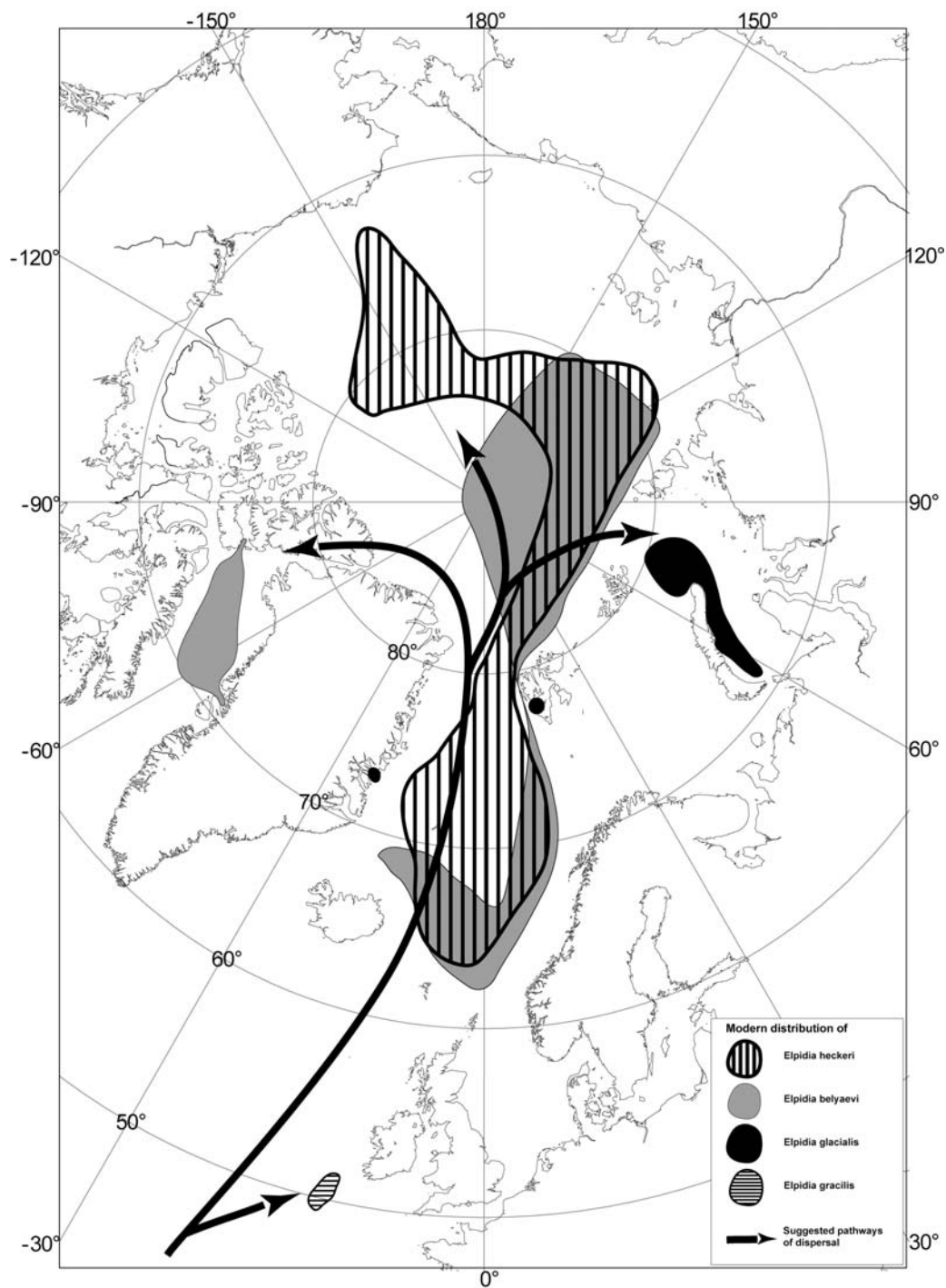
Fig. 4. Distribution of *Elpidia* in the Northern Hemisphere with suggested pathways of species dispersal.
Рис. 4. Распространение рода *Elpidia* в северном полушарии с обозначением возможных путей расселения видов.

4. Discussion

4.1. Phylogenetic biogeography of *Elpidia*

Three scenarios of colonization of the Arctic Ocean by *Elpidia* can be suggested.

1) *Elpidia* originated in the Arctic and from there dispersed around the World Ocean. This hypothesis is not supported by the phylogeny: the clade of Arctic species (clade 2) is not at the base of the tree (Figs. 1, 2).

2) *Elpidia* originated outside the Arctic and penetrated the Arctic Ocean through the North Pacific. This hypothesis also is not supported, since species in the Arctic clade 2 and the North Pacific species are not closely related. *E. hanseni* (the Kuril–Kamchatka and Izu Trenches, 8175–9735 m) is in clade 3 (Figs. 1, 2). *E. kurilensis* (the Aleutian, Kuril–Kamchatka and Japan Trenches, 6410–8100 m), *E. longicirrata* (the Kuril–Kamchatka Trench, 8035–8345 m) and *E. birsteini* (the Kuril–Kamchatka and Izu Trenches, 8060–9345 m) form a monophyletic clade 5 (Figs. 1, 2) on the strict consensus tree supported by two homologies (dorsal ossicles without vertical apophyses predominate). *E. minutissima* (the Aleutian trench and Bering Sea, 4100–5740 m) forms a polytomy with clades 2 and 3, and four other *Elpidia* species show no close relationships with the Arctic clade 2.

3) *Elpidia* originated outside the Arctic and colonised the Arctic Ocean through the North Atlantic. Monophyletic clade 2 (Figs. 1, 2) includes exclusively Arctic species and shows no close relation with other *Elpidia* species on the strict consensus tree forming a basal polytomy. On the majority rule tree (Fig. 1B) and MPT1–3 the monophyletic clade 6 (Fig. 2A–C) combines three Arctic species with the north Atlantic *E. gracilis*, supported by one homoplastic synapomorphy (presence of rods with maximum diameter >35 μm). *Elpidia gracilis* is distributed in the Antarctic and the North-East Atlantic at bathyal and abyssal depths (1484–6145 m). The depth range of *E. gracilis* in the North-East Atlantic is limited to 1484–4000 m.

We therefore suggest that *Elpidia* invaded the Arctic from the bathyal or upper abyssal of the North Atlantic.

Although none of the scenarios of Arctic colonization by *Elpidia* can be confirmed with confidence, we suggest that penetration through the North Atlantic (third scenario) is more likely. This is supported by close relationship between *E. gracilis* and the Arctic species. The North Pacific species of *Elpidia* are specialized forms, inhabiting abyssal and hadal depths. Presumably the Bering Strait serves as a barrier preventing dispersal of these species into the Arctic basin.

Belyaev (1971, 1975) discussed the biogeorahical history of the genus *Elpidia*, based on morphology of the species. He suggested that the genus originated in the Antarctic and eurybathic ancestral forms dispersed around all the oceans. These forms evolved into the recent stenobathic species mainly distributed locally at hadal depths. Four groups of species in the genus were distinguished by Belyaev. One of them, closely related to ancestral dispersal forms, is characterised by slender ossicles resembling the juvenile type. The other three groups included specialised hadal species from deep-sea trenches of the Pacific and the Antarctic, all with modified ossicles. Belyaev suggested three main pathways of dispersal from the Antarctic: along the west and the east Pacific and through the Atlantic. Colonization of the Arctic was suggested through the Atlantic (Belyaev, 1975).

Our results confirm that slender and smooth ossicles with high vertical apophyses (juvenile type, characters 14–20) are plesiomorphic, therefore this type of ossicles indeed could have been characteristic for ancestral dispersal forms. Also we can confirm close relationships between some "specialized" species according to Belyaev. However, of the three pathways suggested by Belyaev (1975), only dispersal through the Atlantic is supported by our results.

4.2. Phylogenetic biogeography of *Paradiopatra*

The low resolution of the phylogenetic reconstructions of *Paradiopatra* (Fig. 4) did not
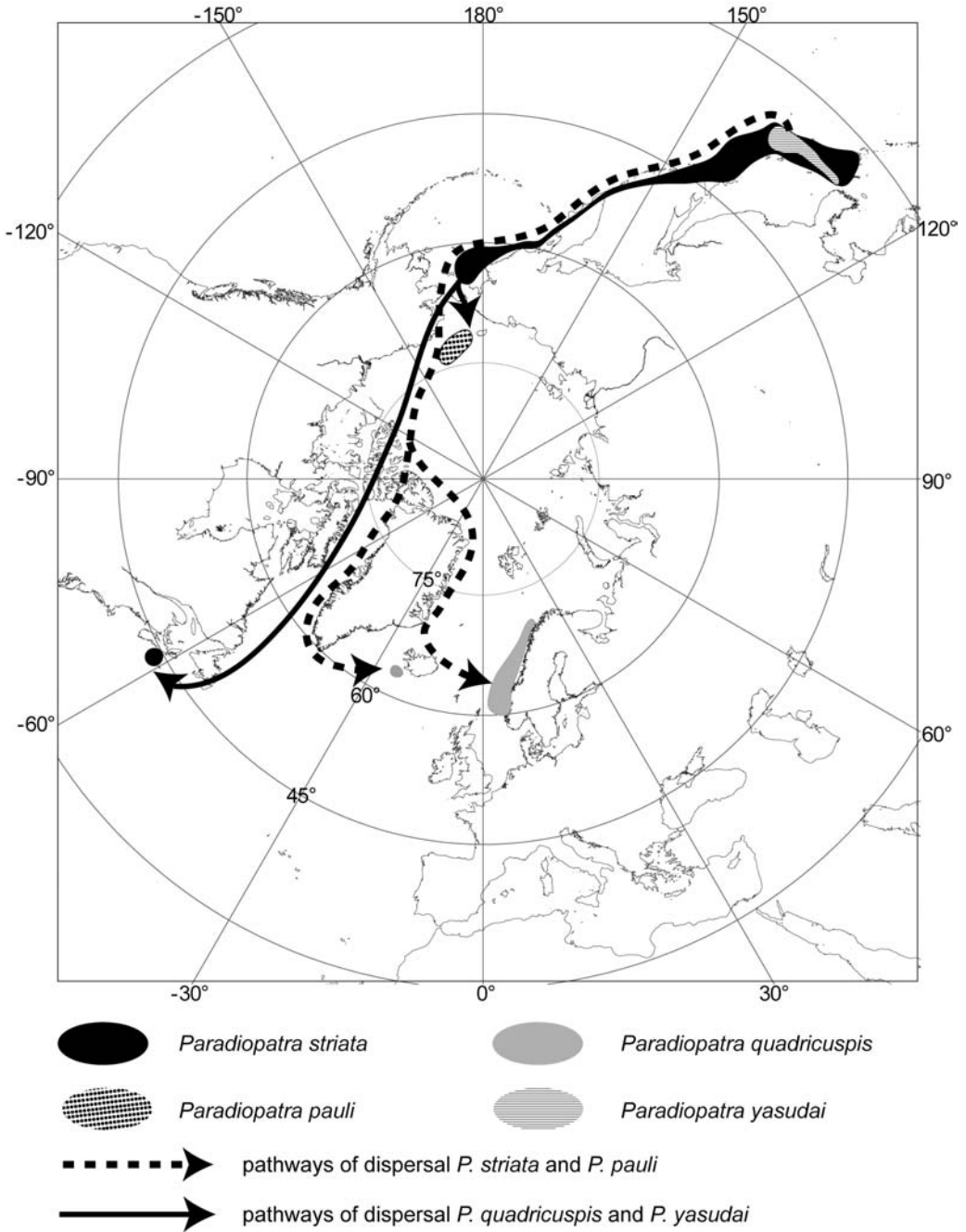
Fig. 5. Distribution of *Paradiopatra* in the Northern Hemisphere with suggested pathways of species dispersal.
Рис. 5. Распространение рода *Paradiopatra* в северном полушарии с обозначением возможных путей расселения видов.

permit identification of the most basal species in the genus, thus the centre of origin of the genus remains unknown. However, a number of well-supported clades suggest several potential dispersal pathways in the Northern Hemisphere. The species pairs *P. striata/P. pauli* and *P. yasudai/P. quadricuspis* support a hypothesis of colonization of the Arctic and the North Atlantic by Pacific fauna. Both clades comprise representatives from the North Pacific and the North Atlantic/Arctic with a large gap between their geographical ranges.

Briggs (1974, 1995, 2003, 2004) suggested that the vector of species dispersal was directed from species-rich areas to areas with a lower number of species. Following Briggs, we suggest that the more speciose fauna of the North Pacific could serve as a donor to the species poor fauna of the North Atlantic via a trans-Arctic interchange (Briggs, 2003; Mironov, 2006). The distribution of *Paradiopatra* species confirms this hypothesis. Fourteen species of *Paradiopatra* inhabit the North Pacific while only nine occur in the North Atlantic (Table 2), suggesting the Pacific origin of *P. pauli* and *P. quadricuspis* and the Atlantic representatives of *P. striata*.

Simberhoff (1986) assumed that the vector of species dispersion might be related to the actual number of individuals inhabiting donor and recipient areas. It was suggested that invasion is more likely if a source population is larger, compared to invasion from smaller populations. The population of *P. striata* in the Sea of Japan and the Bering Sea is very large and diverse (Budaeva, Fauchald, 2011; Imajima, 1999), whereas only few specimens are known from the better-studied north-west Atlantic. *P. pauli*, most closely related to the Arctic *P. striata*, occurs in the near-Pacific area, thus indicating potential faunal exchange from the North Pacific to the Arctic.

It has been proposed that migration of Pacific fauna took place along the Canadian coast rather than along that of Eurasia (Nesis, 1961; Durham, MacNeil, 1967; Gladenkov, 1978; Vermeij, 1991). The prevalence of the Canadian pathway was explained by the anticlockwise currents in the American Arctic (Canada Ba-sin), favouring migration of species from the North Pacific to the North Atlantic and preventing dispersion of the north Atlantic species in the opposite direction (Hopkins, 1967; Gladenkov, 1978; Vermeij, 1991). In addition, the extensive freshwater outflow of Siberian rivers form a low salinity barrier, preventing trans-Arctic migration of species susceptible to reduced salinity along the Eurasian coast. This hypothesis has been confirmed recently in a study of the genetic differentiation in populations of the northern capelin, revealing dispersal from the North Pacific to the North Atlantic along the Canadian Arctic (Dodson et al., 2007). Following the scheme of the Canadian pathway for shallow-water marine fauna, we suggest dispersal of *Paradiopatra* from the North Pacific to the North Atlantic along the Canadian Arctic Archipelago (Fig. 5). Penetration into the North-west Atlantic could occur along the west Greenland coast, this pathway also leading to the central north Atlantic (south of Iceland), with an alternative pathway along the east Greenland to northern Europe along the Faroe–Iceland Ridge (Fig. 5).

The geographical range of *Paradiopatra fiordica* is almost identical with that of *P. quadricuspis*, inhabiting the subtidal and upper bathyal west off Norway and south of Iceland. Both species frequently occur together in same samples (Winsnes, 1985) and usually are confused with each other in identification. However, morphologically *P. fiordica* is very distant from *P. quadricuspis*. Unlike *P. quadricuspis*, *P. fiordica* lacks branchiae; has exclusively tridentate rather than bidentate falcigers and subacicular hooks appearing from chaetiger 11–17 rather than from chaetiger 9. Although *P. fiordica* did not form a monophyletic clade with other species of *Paradiopatra* on the strict consensus tree, we speculate that being morphologically similar to *P. hispanica* and *P. papillata* (Budaeva, Fauchald, 2011), this species could have colonised the Arctic Ocean from the North Atlantic. However, this assumption is not confirmed by the phylogeny of *Paradiopatra* possibly due to a high ratio of homoplastic characters.

Acknowledgments

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