Invertebrate Zoology, 2013, 10(1): 143–166

Morphological evidence of depth-related speciation in deep-sea Arctic echinoderms

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ABSTRACT: Three eurybathic cosmopolitan genera of echinoderms, the holothurians *Elpidia*, the stalked crinoids *Bathycrinus* and the echinoids *Pourtalesia*, are widely distributed in the deep Arctic Ocean. The genera *Echinus* and *Gracilechinus* occur in the Arctic only in the near-Atlantic sector of the basin. In all the five genera, there is a pronounced difference in morphology between specimens occurring at different depths. It is suggested that these differences reflect the depth-related speciation that took place following three scenarios. The genera *Elpidia*, *Bathycrinus* and *Pourtalesia* penetrated the Arctic Ocean at bathyal depths and subsequently dispersed down into abyssal and upwards into upper bathyal and sublittoral. The vertical dispersion of the genera *Echinus* and *Gracilechinus* went along one direction: from the sublittoral (0–200 m) to the abyssal (>2000 m). In the genus *Elpidia* (the first scenario), new species appeared as a result of colonisation both upward and down from the bathyal. In the genera *Bathycrinus* and *Pourtalesia* (the second scenario) the radiation occurred as a result of colonization only down from the bathyal to the abyssal. In the genus *Echinus* and *Gracilechinus* (the third scenario), new species appeared along the colonization down, though not from the bathyal but from the sublittoral. Juvenile characters of shallow-water species of *Echinus* and *Gracilechinus* retain in adult deep-sea specimens. Morphological peculiarities of abyssal *Bathycrinus* and *Pourtalesia* can be related to trophic adaptations or decreasing of predators pressure in the abyssal.

KEY WORDS: morphological variability, Arctic Echinodermata, deep-sea fauna, evolution, adaptations.

Морфологические свидетельства видообразования по глубине у глубоководных арктических иглокожих

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РЕЗЮМЕ: Иглокожие трех эврибатных космополитических родов, голотурии *Elpidia*, стебельчатые морские лилии *Bathycrinus* и морские ежи *Pourtalesia,* широко распространены в глубинах Северного Ледовитого океана. Морские ежи из родов *Echinus* и *Gracilechinus* имеют ограниченное географическое распространение в Северном Ледовитом океане, встречаясь только в его приатлантическом секторе.

Представители каждого из пяти родов, обитающие на разных глубинах, заметно различаются по морфологии. Предполагается, что найденные различия указывают на видообразование, связанное с глубиной и что это видообразование происходило по трем сценариям. Роды *Elpidia*, *Bathycrinus* и *Pourtalesia* первоначально проникли в батиаль Северного Ледовитого океана и затем расселялись как вниз, так и вверх: в верхнюю батиаль-сублитораль и абиссаль. Расселение по вертикали родов *Echinus* и *Gracilechinus* было одновекторным: от сублиторали (0–200 м) до абиссали (глубже 2000 м). В роду *Elpidia* (первый сценарий) новые формы возникли в результате расселения как вверх, так и вниз. В родах *Bathycrinus* и *Pourtalesia* (второй сценарий) новые формы образовались только в результате расселения вниз: из батиали в абиссаль. В родах *Echinus* и *Gracilechinus* (третий сценарий) новые формы образовались также в результате расселения вниз, но не из батиали, а сублиторали (0–200 м). Ювенильные признаки мелководных видов сохраняются у взрослых особей глубоководных *Echinus* и *Gracilechinus*. Морфологические особенности абиссальных *Pourtalesia* и *Bathycrinus* могут быть объяснены как трофические адаптации или как реакция на снижение пресса хищников в абиссали.

КЛЮЧЕВЫЕ СЛОВА: морфологическая изменчивость, арктические Echinodermata, глубоководная фауна, эволюция, адаптации.

Introduction

The Quaternary biogeographic history of the Arctic Ocean fauna is characterized by expanding ranges for many taxa. Nesis (1983, 2001, 2003) suggested that many shallow-water taxa have survived during glaciations by dispersal into the deep. According to Gurjanova (1985) and Andriyashev (1985) most modern Arctic deep-sea species (occurring at depths >1000 m) are of recent shallow-water origin. Arctic deep-sea species have very close relatives at shallow depths, so close that some deep-sea forms are considered as sub-species (Gurjanova, 1985). To emphasize that the Arctic abyssal fauna is not closely related to the abyssal fauna of the world ocean, the term 'pseudo-abyssal' suggested by Derjugin (1915) is often used.

However, some deep-sea Arctic species do have a deep-water origin and are closely related to the abyssal fauna of the world ocean. Among such species are representatives of deep-sea Arctic echinoderm genera: the holothurians *Elpidia* and *Kolga,* the echinoid *Pourtalesia* and the stalked crinoid *Bathycrinus*. All these genera have a cosmopolitan distribution, mainly at abyssal depths (Belyaev, 1971, 1975; Gislén, 1938; Mironov, 1995a, b; Rogacheva, 2007). They probably penetrated the Arctic through the bathyal zone of the north Atlantic. Expansion of species ranges into the Arctic Basin could have resulted in depth-related speciation. This scenario is suggested by the close relationship of Arctic species occurring at different depths; also by species with depth-related morphological variability. Among examples of closely related species distributed in the Arctic in different depth zones are several isopod species of the genera *Saduria* and *Oecidiobranchus* (Kussakin, 1982), amphipods *Onisimus* (Gurjanova, 1939), caprellids *Caprella* (Vassilenko, 2004a), cumaceans *Diastylis*, *Leptostylis* and *Leucon* (Vassilenko, 2004b), opisthobranchs *Cylichnoides* (Chaban, 2004) and many other taxa.

Here we present data on five deep-sea echinoderm genera of shallow-water (*Echinus* and *Gracilechinus*) and deep-sea suggested origin (*Bathycrinus*, *Elpidia* and *Pourtalesia).* These genera demonstrate depth-related intraspecific variability or different bathymetric patterns

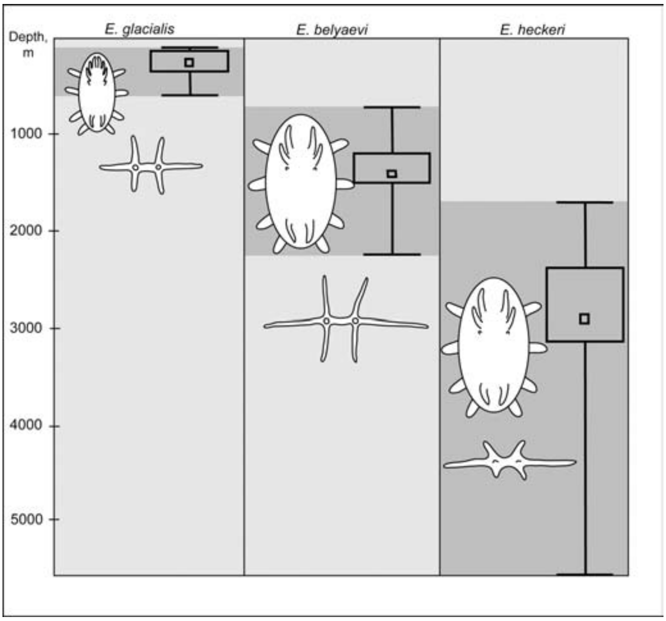

Fig. 1. Comparative morphology and bathymetric ranges of the Artic species of *Elpidia.* For each species the dorsal view, dorsal ossicles and box whiskers of vertical ranges are shown. Range of whiskers corresponds to minimum and maximum depth distribution; range of boxes is the lower and upper quartiles; midpoint displays the mean.

Рис. 1 Сравнительная морфология и вертикальное распределение арктических видов *Elpidia.* Для каждого вида приведен вид с дорзальной стороны тела, дорзальные спикулы и диаграммы вертикального распределения. Концы усов соответствуют минимальному и максимальному значению глубины; границами ящика являются первый и третий квартили; точка соответствует выборочному среднему.

among closely related species. Possible scenarios of speciation in the Arctic Ocean are discussed for each genus.

DISTRIBUTION PATTERNS OF TARGET GENERA AND ARCTIC SPECIES

The genera *Bathycrinus, Elpidia* and *Pourtalesia* are cosmopolitan. Their bathymetrical ranges extend to the hadal zone (Table 1). Representatives of these genera occur at bathyal and abyssal depths throughout the Arctic Ocean. The genus *Elpidia* is considered to have three species in the Arctic (Rogacheva, 2007), while *Bathycrinus* and *Pourtalesia* have only one each (Sirenko et al., 2010).

The only known Arctic representative of *Bathycrinus* is *B. carpenteri* Danielssen and Koren, 1877. This species is known from the deep-sea basins between Norway, the Faeroe Islands, Iceland, northeast Greenland and Svalbard, at depths from 1360 to 2815 m (Danielssen, Koren, 1877; Danielssen, 1892; Grieg, 1904; Clark, 1923; Gislén, 1938), north of the Barents Sea (Baranova, 1964; Piepenburg et al., 1996) and north of the Siberian seas, at depths from 520 to 3800 m (Djakonov, 1946; Gorbunov, 1946; Koltun, 1964; Smirnov, Smirnov, 1990, 2004).

The Arctic species of *Elpidia* are characterised by different patterns of bathymetric distribution (Fig. 1). *Elpidia heckeri* Baranova, 1989 is the deepest species, occurring from the middle bathyal to abyssal (1700–5552 m) and distributed circumpolarly. *Elpidia belyaevi* Rogacheva, 2007 is the bathyal species (610–2222 m), also with circumpolar distribution. *Elpidia glacialis* Théel, 1876 is the shallowest species

Table 1. Biogeographical features of analysed echinoderm genera.
Таблица 1. Биогеографическая характеристика исследуемых родов иглокожих.

Genus	***Bathycrinus***	***Echinus***	***Gracilechinus***	***Elpidia***	***Pourtalesia***
Number of known species	10	9	8	22	12
Number of species in the Arctic Ocean	1	1	3	3	1
Distribution range outside the Arctic Ocean	Worldwide	Pacific and Atlantic Oceans	Pacific and Atlantic Oceans	Worldwide	Worldwide
Distribution in the Arctic Ocean	Pan-Arctic	Norwegian Sea and southwest Barents Sea	Norwegian Sea and southwest Barents Sea	Pan-Arctic	Pan-Arctic
Bathymetrical range outside the Arctic Ocean (m)	(596?) 693–9345	0–2415	5–4700	650–9735	227–7340
Bathymetrical range in the Arctic Ocean (m)	460–3800	0–430	20–2198	70–5550	225–3081
Suggested origin	Deep-sea (Antarctic?)	Shallow-water North Atlantic	Shallow-water North Atlantic	Deep-sea Antarctic	Deep-sea Antarctic
Arctic species	*B. carpenteri*	*E. esculentus*	*G. acutus*, *G. alexandri*, *G. elegans*	*E. belyaevi*, *E. glacialis*, *E. heckeri*	*P. jeffreysi* (subspecies *jeffreysi*, *gibbosa* and *lata*)
Antarctic species closely related to Arctic species	*B. australis*	–	–	*E. gracilis*	*P. debilis*
Pathway to the Arctic	Through the Atlantic	From the North Atlantic	From the North Atlantic	Through the Atlantic	Through the Atlantic

occurring in the Kara and Barents Seas, eastern Greenland and possibly in the western Svalbard at depths from 73 to 610 m (Budaeva, Rogacheva, present volume). Species and bathymetric ranges overlap in *E. belyaevi* and *E. heckeri*, they were even recorded from the same station. However, the plots of bathymetric distribution of both species show that ranges of the most frequent occurrence of the two species do not coincide: *E. belyaevi* mainly occurs at depths 1100–1500 m whereas *E. heckeri* at 2300–3100 m (Rogacheva, 2007).

The echinoid species *Pourtalesia jeffreysi* Thomson, 1873 includes three subspecies. The subspecies *P. jeffreysi gibbosa* Mironov, 1995 and *P. jeffreysi lata* Mironov, 1995 are widely distributed in the Arctic but have different bathymetric ranges: from 225 to 1270 m and from 2234 to 3081 m respectively. *P. jeffreysi* is also known from depths between 1270 m (the lower depth limit of *gibbosa*) and 2234 m (the upper limit of *lata*), however there were no detail studies of specimens from these depths. The exact distribution of *P. jeffreysi jeffreysi* is unknown since this species often is confused with other north Atlantic species of *Pourtalesia*, *P. wandeli* and *P. miranda*. The only reliable record of *P. jeffreysi jeffreysi* Mironov, 1995 is from the border between the Arctic and Atlantic Oceans (Faeroe Channel, 1160 m depth) (Mironov, 1995a). Apparently *P. jeffreysi jeffreysi* is widely distributed in the central and north Atlantic.

It has been suggested that the genera *Elpidia* and *Pourtalesia* originated in the deep-sea Antarctic, and from there they invaded the Atlantic

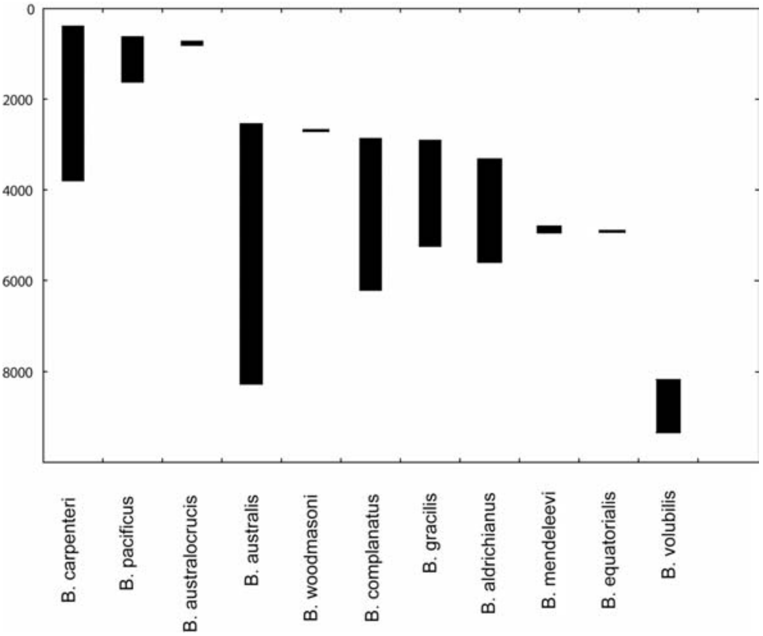

Fig. 2. Bathymetric distribution of the species of the genus *Bathycrinus*.
Рис. 2. Вертикальное распределение видов рода *Bathycrinus*.

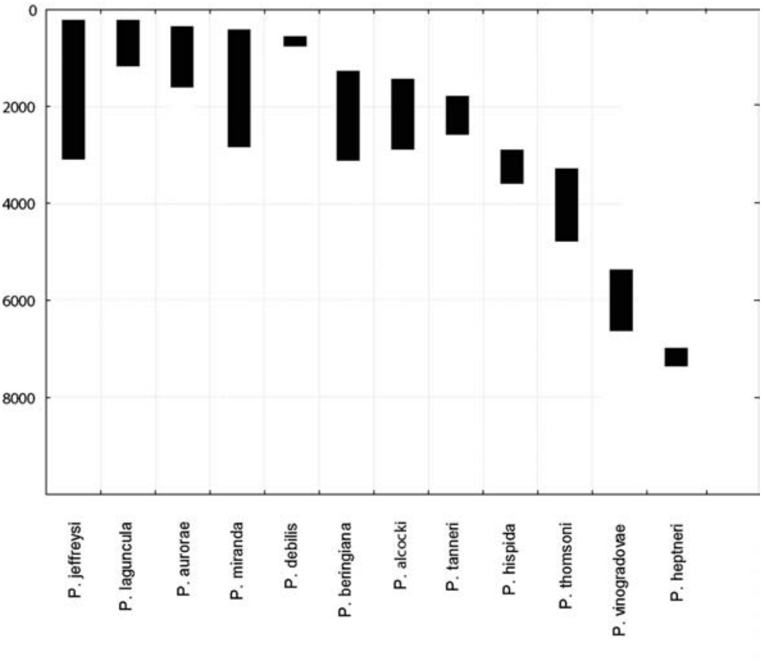

Fig. 3. Bathymetric distribution of the species of the genus *Pourtalesia*.
Рис. 3. Вертикальное распределение видов рода *Pourtalesia*.

Table 2. New samples of *P. jeffreysi* from the *Polarstern* expeditions east of Greenland and northwest of Svalbard.

Таблица 2. Новый материал по *P. jeffreysi* из экспедиций НИС *Поларштерн*, собранный к востоку от Гренландии и северо-западу от Шпицбергена.

Cruise	Station	Date	Latitude, N	Longitude, E	Depth, m	Number of specimens
ARK XIII/2	44/93a	31.07.1997	81º16.32’	13º07.36’	2234	1
ARK XIX/3c	64/463	02.08.2003	78º56.21’	04º59.18’	2606	1
ARK XXII/1c	70/177-1 (S3)	14.07.2007	78º36.26’	05º04.58’	2340	1
ARK XXIII/2	72/156-1 HG IV)	16.07.2008	79º03.39’	03º50.54’	2732	4 broken
ARK XXIII/2	72/213-2	25.07.2008	77º30.90’	14º59.09’	317	8

and subsequently the Arctic (Belyaev, 1971, 1975, 1989; Mironov, 1975, 1980, 1982; Gebruk, 1983, 1990, 1994). Some evidence exists that *Bathycrinus* also could be of the deep Antarctic origin (unpublished data).

Genera *Echinus* and *Gracilechinus* are also widely distributed. They occur in all oceans except for the Indian and Southern Ocean. The bathymetrical distribution of *Echinus* ranges from 0 to 2415 m. The genus *Gracilechinus* is known from 5 to 4700 m. The centre of species diversity of both genera is in the North Atlantic: 4 of the 9 known species of *Echinus* and 5 of 8 species of *Gracilechinus* occur in this region. In the Arctic Ocean both genera are distributed only as far as the western Barents Sea. Four species, *G. acutus* Lamarck, 1816, *G. alexandri* Danielssen and Koren, 1883, *G. elegans* Düben and Koren, 1844 and *E. esculentus* Linnaeus, 1758, are known from the Norwegian Sea. Two species, *G. acutus* and *E. esculentus*, occur both in the Norwegian and Barents Seas.

Reliable fossil records of *Echinus* and *Gracilechinus* (species close to *G. acutus* and *E. esculentus*) are known from Pliocene and Pleistocene deposits of Europe (Mortensen, 1943; Fell, Pawson, 1966). The speciation of both genera presumably took place in the North Atlantic, initially at shallow depths, followed by colonization of the deep sea. This statement is confirmed by studies of embryonic pressure tolerance, distribution patterns and depth-related trends in morphology among species of both genera considered under the genus *Echinus* (Tyler et al., 1995; Tyler, Young, 1998; Minin, 2012).

DEPTH-RELATED VARIABILITY

1. Genus *Elpidia*

The specimens examined were: 2632 *E. glacialis* from 31 stations, 1087 *E. heckeri* from 41 stations, and 368 *E. belyaevi* from 37 stations (Rogacheva, 2007, Table 1). Specimens were collected from all the major deep basins of the Arctic Ocean, including the Central Arctic, Norwegian Basin, Greenland Plain and Baffin Bay, at depths from 73 to 5552 m. All specimens were measured and the external morphology (the number and arrangement of dorsal papillae, first of all) was described. The ossicles of all three species from dorsal and ventral body walls, tentacles and tube feet were examined in approximately 200 specimens in total.

Three Arctic species are closely related (Rogacheva, 2007; Budaeva, Rogacheva, present volume) and occur at different depths (Fig. 1). The species differ mainly in ossicle morphology. There are also differences in the body shape and arrangement of papillae between *E. glacialis* and two other species (Fig. 1). The phylogenetic analysis (Rogacheva, 2007; Budaeva, Rogacheva, 2013) suggests that the Arctic was invaded by a bathyal ancestral form, close to *E. gracilis*, that later colonised abyssal and sublittoral depths. *E. belyaevi* is basal to the two other species and therefore is the closest to the ancestral form. *E. glacialis* and *E. heckeri* are more specialised forms: the former penetrating onto the continental shelf: the latter species diverging and colonising lower bathyal and abyssal depths. Several mechanisms of radiation of

Table 3. Measurements of adult *P. jeffreysi gibbosa* and *P. jeffreysi lata* (TL from 24 to 32 mm).
Таблица 3. Количественные характеристики взрослых особей *P. jeffreysi gibbosa* и *P. jeffreysi lata* (TL от 24 до 32 мм).

Character	***P. jeffreysi gibbosa***	***P. jeffreysi lata***
Maximum TL	58 mm	33 mm
Growth variability at TL from 17 to 22 mm	Conspicuous	Inconspicuous
Limits of TW/TL (mean; CV)	0.47–0.54 (0.50; 3.5)	0.49–0.60 (0.54; 6.6)
Limits of TH/TL (mean, CV)	0.48–0.51 (0.51; 4.1)	0.39–0.53 (0.46; 8.0)
Limits of GL/TL (mean, CV)	0.14–0.21 (0.18; 10.5)	0.14–0.23 (0.20; 11.1)
Limits of BL/TL (mean, CV)	0.85–0.90 (0.88; 1.8)	0.79–0.90 (0.86; 3.1)
Limits of AD/TL (mean, CV)	0.07–0.13 (0.10; 16.6)	0.10–0.18 (0.13; 18.3)
Limits of ST/TL (mean, CV)	0.60–0.66 (0.62; 2.5)	0.60–0.73 (0.64; 4.5)
RC	Usually well developed	Usually absent or weakly developed
DC	Usually well developed	Often weakly developed
Form of subanal rostrum viewed from side	Usually finger-like	Usually conical
Colour	Light to moderate violet	Dark violet

TL — length of test; TW — width of test; TH — height of test; GL — length of oral groove; BL –distance between anterior edge of test and periproct; AD — distance between anterior edge of test and posterior genital pores; ST — distance between anterior edge of test and anterior edge of sternum; DC — dorsal convexity; CV — coefficient of variation.

TL — длина панциря; TW — ширина панциря; TH — высота панциря; GL — длина орального желоба; BL — расстояние между передним краем панциря и перипроктом; AD — расстояние между передним краем панциря и генитальными порами; ST — расстояние между передним краем панциря и передним краем стернума; DC — дорзальная выпуклость; CV — коэффициент вариации.

Elpidia in the Arctic are believed to have taken place. Where they co-occur *E. glacialis*, *E. belyaevi* and *E. heckeri* show signs of parapatry adapting to overlapping depth ranges. In contrast, unusually large specimens of *E. belyaevi* in the upper bathyal of Baffin Bay are apparently an example of allopatry.

2. Genus *Pourtalesia*

Mironov (1995a) has examined 195 complete specimens of *Pourtalesia* from 20 stations. Additionally 15 specimens recently obtained from 5 stations were also examined (Table 2).

Upper bathyal subspecies *P. jeffreysi gibbosa* (<1270 m) differs from lower bathyal and abyssal *P. jeffreysi lata* (>2234 m) in having a larger, higher and longer test, a shorter oral groove, more anteriorly placed genital pores and sternal plate, a well developed hood above subanal rostrum, a lower percentage of specimens lacking labrum (29% as opposed to 61% in *lata*). The subanal rostrum in *P. jeffreysi gibbosa* is always finger-like, with a well-developed subanal fasciole (Fig. 4A, B, G, H), whereas in *P. jeffreysi lata* it is often conical with a slightly-developed subanal fasciole (Fig. 4C, D, I–L). The variability of morphological characters in the subspecies *gibbosa* and *lata* overlap, but specimens of both subspecies can be distinguished by the statistical methods (Table 3).

Morphological variability in *P. jeffreysi* is much higher than in any other species of this genus. *P. jeffreysi lata* is more variable than *P. jeffreysi gibbosa*. The test form in *P. jeffreysi lata* changes gradually from low and wide to high and narrow. We distinguished tentatively three morphological forms based on the test proportions — test width (TW) and test height (TH) in relation to test length (TL). The first form is broad and high: TW/TL >0.52 and TH/

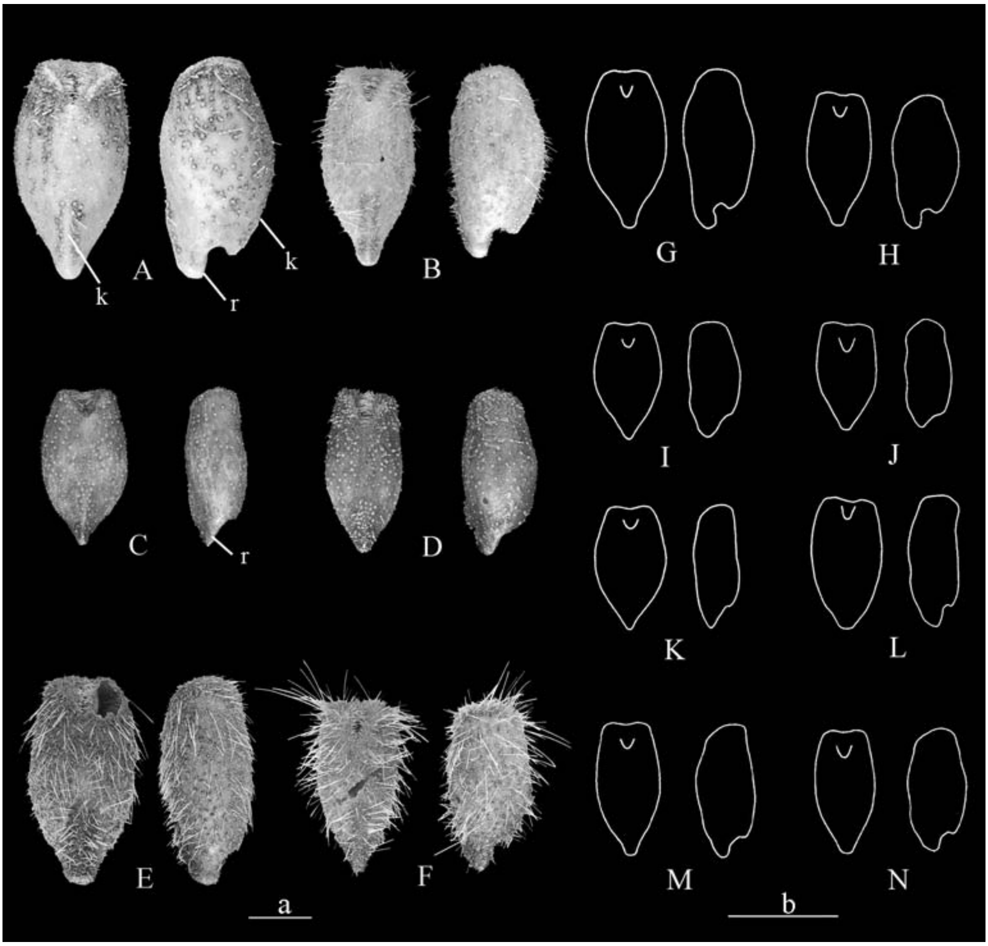

Fig. 4. Morphological variation of *Pourtalesia jeffreysi*.

A, B, G and H — *P. jeffreysi gibbosa*; C–F, I–N — *P. jeffreysi lata*: D, I, J — broad and high form, C, K, L — broad and flattened form, E, F, M, N — narrow intermediate form, transitional to *gibbosa*. G–N — after Mironov, 1995a (modified). A, B, H — *Sevastopol*, St. 1380, 67°54′N 14°18′W, 1270 m; C, D, I, K, M — *Polarstern*, cruise ARK IX/4, St. 54, 79°12′N 119°56′E; E — *Polarstern*, cruise ARK XIII/2, St. 44/93a, 81°16.32′N, 13°07.36′E, 2234 m; F — *Polarstern*, cruise ARK XIX/3c, St. 64/463, 78°56.21′N, 04°59.18′E, 2606 m; G — *Lomonosov*, St. 12, 78°03′N, 79°47′E, 426 m; J, L, N — *Litke*, St. 37, 82°39′N 33°30′E, 2899 m; k — ventral keel; r — subanal rostrum. Scale a — 10 mm (A–F); scale b — 30 mm (G–N).

Рис. 4. Морфологическая изменчивость *Pourtalesia jeffreysi*.

A, B, G и H — *P. jeffreysi gibbosa*; C–F, I–N — *P. jeffreysi lata*: D, I, J — широкая и высокая форма, C, K, L — широкая и уплощенная форма, E, F, M, N — узкая переходная к *gibbosa* форма. G–N — по: Миронов, 1995a (изменено). A, B, H — *Севастополь*, Ст. 1380, 67°54′ с.ш. 14°18′ в.д., 1270 м; C, D, I, K, M — *Поларштерн*, рейс ARK IX/4, Ст. 54, 79°12′ с.ш. 119°56′ в.д.; E — *Поларштерн*, рейс ARK XIII/2, Ст. 44/93a, 81°16,32′ с.ш., 13°07,36′ в.д., 2234 м; F — *Поларштерн*, рейс ARK XIX/3c, Ст. 64/463, 78°56.21′ с.ш., 04°59.18′ в.д., 2606 м; G — *Ломоносов*, Ст. 12, 78°03′ с.ш., 79°47′ в.д., 426 м; J, L, N — *Литке*, Ст. 37, 82°39′ с.ш. 33°30′ в.д., 2899 м; k — вентральный киль; r — субанальный рострум. Шкала: a — 10 мм (A–F); b — 30 мм (G–N).

TL >0.44 (Fig. 4D, I, J). In the second form the test is broad and flattened: TW/TL >0.52, TH/TL <0.44 (Fig. 4C, K, L). In the third form the test is narrow, transitional to *gibbosa*: TW/TL <0.52 (Fig. 4M, N) (Mironov, 1995a). These morphological forms are often found in one and the same abyssal sample but the ratio of forms (the relative number of corresponding speci-

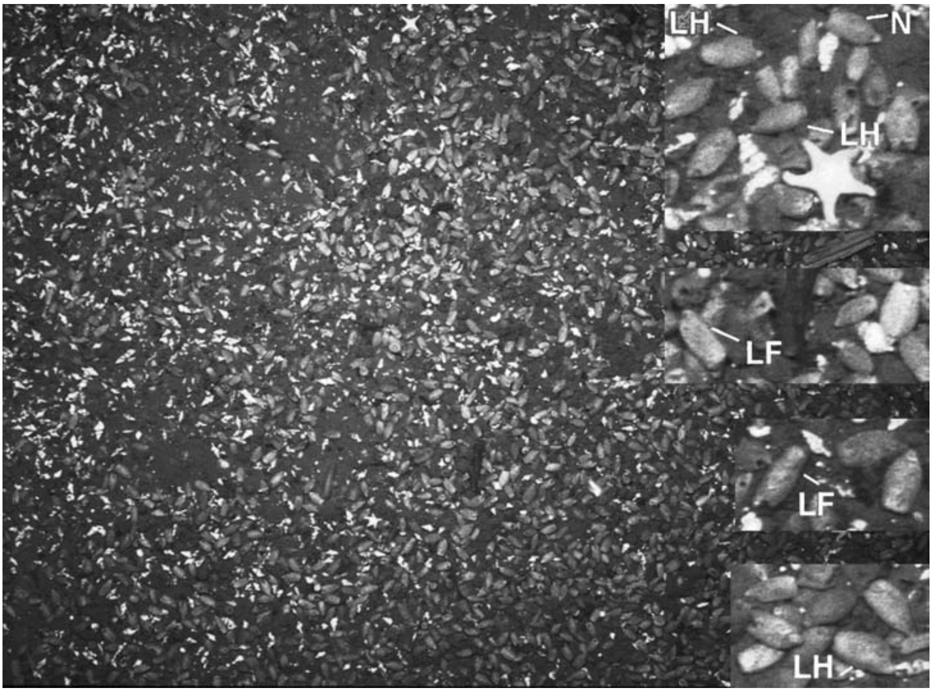

Fig. 5. Aggregation of tests of *Pourtalesia jeffreysi lata*. Locality: the Ardencaple Canyon, a channel system in the deep Western Greenland Sea, 74°N, depth ~3000 m. (Image courtesy Dr. Thomas Soltwedel). Morphological types: LH — broad-high, LF — broad-flattened and N — narrow, transitional to *gibbosa*.
Рис. 5. Скопление панцирей *Pourtalesia jeffreysi lata* в каньоне Андеркапл, западное Гренландское море, 74° с.ш., глубина ~3000 м. Фотография предоставлена Томасом Солтведелом. Морфологические типы: LH — широкий и высокий, LF — широкий и уплощенный и N — узкий, переходный к *gibbosa*.

mens) varies between samples. Apparently, these morphological forms reflect intra-specific variation. The morphology of *P. jeffreysi* occurring at depths between 1270 and 2800 m was unknown.

Both Arctic subspecies were found in the new material (Table 2). Specimens from the depth 317 m were typical representatives of *gibbosa*. Specimens from depths 2234–2732 m were *P. jeffreysi lata* corresponding to the morphological form transitional to *gibbosa*. At greater depths all the three morphological forms of the subspecies *lata* occur. An image of the seafloor showing a large aggregation of dead specimens of *P. jeffreysi lata* has been obtained from the ~3000 m deep Ardencaple Canyon, a channel system in the Western Greenland Sea at the latitude 74ºN (Fig. 5A). The three morphological types of test of the subspecies *lata* can be clearly recognised on this image: the broad-high, the broad-flattened and the narrow, transitional to *gibbosa* (Fig. 5B, C: LH, LF and N respectively).

Both Arctic subspecies were found in the new material (Table 2). Specimens from a depth of 317 m were typical representatives of *gibbosa*. Specimens from depths 2234–2732 m represented *lata*. The morphology in specimens of the subspecies *lata* corresponds to the third morphological form transitional to *gibbosa*.

Morphological differences between the subspecies of *Pourtalesia* correspond to specific adaptations to borrowing. Adaptations to burrowing in *P. jeffreysi jeffreysi* and *P. jeffreysi gibbosa* are more developed than in *P. jeffreysi lata* (Mironov, 1975, 2008). The distribution

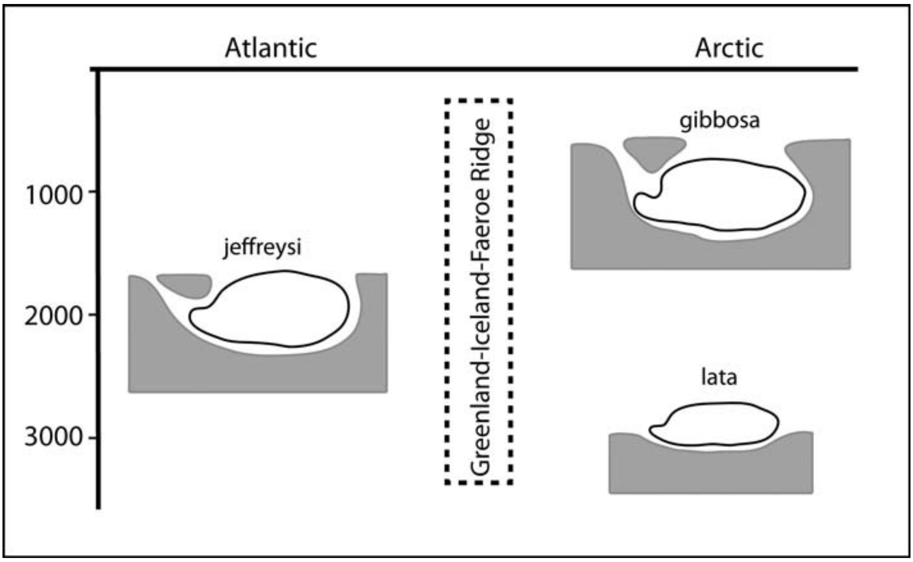

Fig. 6. Schematic illustration of burrowing ability in the subspecies of *Pourtalesia jeffreysi.* In the deepest living subspecies *lata* the burrowing ability is the least developed.

Рис. 6. Схематичное изображение способности к зарыванию у подвидов *Pourtalesia jeffreysi.* У наиболее глубоководного подвида *lata* способность к зарыванию наименее выражена.

patterns and the adaptive morphology of the subspecies suggest that *P. jeffreysi* initially dispersed from the Atlantic to the Arctic Ocean (ibid.). The ancestral form was probably bathyal with adaptations to burrowing. Colonization of the Arctic abyssal resulted in an increase of morphological variability and a reduction of adaptations to burrowing (Fig. 6).

3. Genus *Bathycrinus*

232 specimens of ethanol-preserved *Bathycrinus carpenteri*, obtained from 52 sites by 24 expeditions were examined (Table 4). The stations were located throughout the Arctic Ocean, from the Greenland-Iceland-Faeroe Ridge to the Chukchi Sea, at depths from 460 to 3800 m. Most of the specimens were fragmental; specimens from the shallowest (460–950 m) and the deepest (> 3100 m) locations were represented only by fragments of stalks.

The general morphology of *Bathycrinus carpenteri* is illustrated in Fig. 7. The following abbreviations and symbols are used: BB — basals, RR — radials, Br — brachial, IBrs1–2 — primibrachs, IIBrs — secundibrachs, Br1, Br2, Br3, … — first, second, third, … secundibrachs, P — pinnule, Ps — pinnules, Pn — pinnular, Pns — pinnulars. The sign '+' indicates a non-muscular (ligamentary) articulation between two brachials. Numbers in the brachial formulae show the numbers of consecutive Brs with muscular articulations located between two non-muscular articulations. For example, a part of arm with brachial formula 6+5 consists of 11 Brs, and a non-muscular articulation divides these ossicles into two groups, one with 6 and another with 5 Brs with 5/4 consecutive muscular articulations. The proximal brachial formulae 1+2, 3+4, 5, 6, 7 or 1+2, 3+4, 5, 6, 7, 8 are represented here as 1+2+4 and 1+2+5. Measurements of calyx and columnals are as in Fig. 1 in Mironov (2000).

Morphological variability in *Bathycrinus carpenteri* is much higher than in any other species of the genus. The variation in arm morphology is more pronounced in the proximal brachial formula and position of P1. Twenty types of brachial formula and 14 positions of P1 were found. The brachial formula 1+3+3+3+2 and positions of P1 on Br11 was the most

Table 4. Examined samples of *Bathycrinus carpenteri*.
Таблица 4. Исследованный материал по *Bathycrinus carpenteri*.

RV (year/cruise)	**Station**	**Date**	**Latitude, °N**	**Longitude°**	**Depth, m**	**Number of specimens**
Vøringen (Norwegian North Atlantic Expedition)	53	10.08.1876	65°13’	00°33’E	2814	2
M. Sars, 1900	9	26.07.1900	63º53’	06º22’W	1960	7
M. Sars, 1902	102	29.08.1902	63º13’	06º32’W	1700	4
Sadko, 1935	9	01.08.1935	~80º	~03ºE	2300	8
"	10	01.08.1935	80°02’	03°19’E	2300	3
"	12	02.08.1935	80°21’	07°03’E	660	1*
"	34	27.08.1935	81°08’	69°35’E	570	1*
"	35	28.08.1935	81°11’	66°53’E	590	1*
"	39	30.08.1935	80°44’	68°08’E	542	1*
"	59	13.09.1935	82°42’	87°03’E	2365	1*
Sadko, 1937–1938	11	17.08.1937	77°53’	117°43’E	1445	9
"	97	03.05.1937	80°30’	144°33’E	1800–2000	2*
"	98	31.05.1938	80°58’	142°50’E	1475–1510	3*
"	99	14.06.1938	81°13’	140°03’E	1630–1900	~20
"	101	24.07.1938	82°51’	137°23’E	3700–3800	2*
Drifting Ice Station SP-5	6	19.08.1950	No data	No data	1435	6
Litke	29	20.09.1955	81°18’	09°46’E	1301	4
"	32	28.10.1955	No data	No data	2036	5*
"	40	02.10.1955	82°04’	38°46’E	1017	5
"	41	06.10.1955	82º01.80’	34º58.00’E	1747	2
Ob	6	18.08.1956	78°05’7	02°25’W	2870	16
"	22	25.08.1956	81°28’5	10°01’W	2581	1*
"	45	01.09.1956	79°47’3	01°41’0W	1330	12*
Drifting Ice Station SP-22	58	05.12.1978	73°36’	159°06’W	1500-2700	2*
"	72	07.01.1979	74°30’	164°10’W	760-830	1*
"	76	13.01.1979	74°55’	167°07’W	460	1*
Håkon Mosby (1985)	85.1.11.3	11.01.1985	63º32.9’	00º07.8’E	2086	1
Akademik Mstislav Keldysh (18)	2079	20.05.1989	73°42’07	13°37’05E	1478-1540	2
" (18)	2091	24.05.1989	73°42’08	13°17’00E	1670–1691	2
" (24)	2523	27.08.1991	73°42’05	13°35’08E	1579–1589	2
" (24)	2548	01.09.1991	73°42’80	13°15’74E	1681–1695	2
" (28)	2679	22.05.1992	73°40’97	13°10’15E	1626–1685	21
" (28)	2737	31.05.1992	73°43’21	13°13’20E	1679–1693	2*
" (31)	3081	04.08.1993	73°43’25	13°16’35E	1680–1670	14
" (31)	3117	18.08.1993	73°43’25	13°17’07E	1610–1665	7
" (33)	3249	09.07.1994	73°46’90	13°09’00E	1650–1750	3
" (33)	3318	25.07.1994	73°40’03	13°23’56E	1550–1600	5
" (36)	3495	07.07.1995	73°55’19	12°52’63E	1958–1978	20*
" (36)	3555	17.07.1995	73°21’80	07°16’30E	2920–2942	10
" (36)	3572	23.07.1995	73°21’80	07°16’30E	2920–2942	1
Polarstern (ARK XI/1)	21a	02.08.1995	77°49’7	130°14’9E	1330	1
"	53	25.08.1995	81°10’8	141°47’1E	945	2*
"	60b	29.08.1995	80°16’0	150°19’5E	1580	7
"	62a	30.08.1995	80°03’2	149°46’3E	950	1*
" (ARK XV/1)	Dive 2	01.07.1999	79°04.4’	04°04.1’E	2412	1
"	Dive 4	06.07.1999	79°27.8’	02°42.3’E	2804	1
" (ARK XIX/3c)	64/441	27.07.2003	79°04.89’	04°05.77’E	2499	2*

Table 4 (contituing)
Таблица 4 (продолжение)

" (ARK XXI/1b)	68/247-1	20.08.2005	79º05.67’	03º38.68’E	3064	1
" (ARK XXIII/2)	72/247-1	16.07.2008	79º03.39’	03º50.54’E	2732	1
Healy (2005 leg2)	13	20.07.2005	75°18.75’	161°37.38’ W	2100	1
Akademik Nikolai Strakhov (25)	2434	27.09.2006	77°42.06’	07°01.65’E	1402–2410	1*
Akademik Fedorov (26)	2/413	29.07.2007	82°29.70’	64°28.05’E	1321	1

* — only fragments of stalks or stalks with basals.

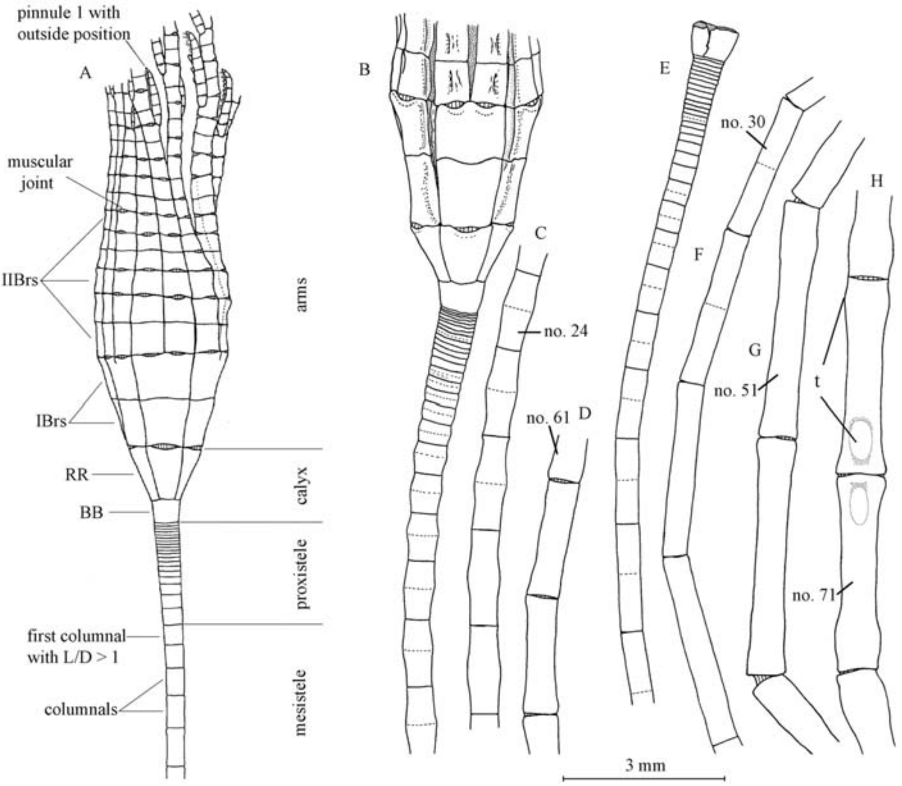

Fig. 7. *Bathycrinus carpenteri*, general morphology (A) and stalks of bathyal and abyssal specimens (B–H). Figures correspond to the number of columnals counted from the cup. B–D — *Polarstern* ARK XI/1, St. 60b, depth 1580 m; E–H — *Sadko* 1938, St. 101, depth 3700–3800 m; B, E — proxistele and upper mesistele; C, F — upper mesistele; D, G — middle part of mesistele with most elongated columnals; H — upper dististele. Abbreviations: BB — basals, RR — radials, Br — brachial, IBrs1–2 — primibrachs, IIBrs — secundibrachs, t — tubercles.

Рис. 7. *Bathycrinus carpenteri*, общая морфология (A) и стебли батиального и абиссального экземпляров (B–H).

Цифры обозначают порядковый номер членика по мере удаления от чашечки. B–D — *Поларштерн,* ARK XI/1, Ст. 60b, глубина 1580 м; E–H — *Садко,* 1938, Ст. 101, глубина 3700–3800 м; B, E — проксистель и верхняя мезистель; C, F — верхняя мезистель; D, G — средняя часть мезистели, членики которой наиболее удлиненные H — верхняя дististель. Обозначения: BB — базальные пластинки; RR — радиальные пластинки; BR — брахиаль; IBr1 — первичные брахиали; IIBrs — вторичные брахиали; t — туберкулы.

Table 5. Variability of proximal brachial formula in bathyal and abyssal specimens of *Bathycrinus carpenteri*.
Таблица 5. Изменчивость проксимально брахиальной формулы у батиальных и абиссальных экземпляров *Bathycrinus carpenteri*.

Proximal brachial	**Number of arms with the same formula**	
formula	***Polarstern*, St. 60b, 1580 m, (44 arms examined)**	***Ob*, St. 6, 2870 m (62 arms examined)**
1+3+3+3+2	24	26
1+3+3+2+3	2	10
1+3+3+3+3	5	4
1+3+3+2+2	4	4
1+3+2+2+3	0	6
1+3+2+2+2	0	5
1+3+2+3+2	0	5
1+3+3+5+2	1	1
Single cases	8 (1+5+3+3+3, 1+5+3+3+2, 1+5+3+2+2, 1+4+3+?, 1+2+3+3+3, 1+3+4+2+2, 1+3+1+3+3, 1+2+2+3+2)	1 (1+2+2+2+3)

Table 6. Variation in position of P1 in bathyal and abyssal specimens of *Bathycrinus carpenteri*.
Таблица 6. Изменчивость в расположении P1 (первой пиннулы) у батиальных и абиссальных экземпляров *Bathycrinus carpenteri*.

Position of Pinnule 1	**Number of arms with the same position of P1**	
	***Polarstern*, St. 60b, 1580 m (42 arms examined)**	***Ob'*, St. 6, 2870 m (62 arms examined)**
At Br8 outside	0	1
At Br8 inside	0	0
At Br9 outside	0	0
At Br9 inside	3	9*
At Br10 outside	2	3
At Br10 inside	2	0
At Br11 outside	25	32
At Br11 inside	0	3
At Br12 outside	0	9
At Br12 inside	4	1
At Br13 outside	1	2
At Br13 inside	1	0
At Br14 outside	4	0
At Br14 inside	0	0

* In single specimen.

common (Tables 5 and 6). No age variation of these characters is known. The surface structure of IIBrs varied in specimens from different stations from almost smooth to comb-like.

The ratio between the height and diameter of RR (H/D) varied from 0.91 to 0.57) and decreased with higher D (Table 7, Fig. 8).

The ratio between the height and diameter of the BB-ring also decreased with increasing diameter, from 0.80 to 0.63 in adult specimens (with a diameter of the upper part of stalk >0.6 mm) (Table 8). BB can be completely fused, or separated by barely seen or obvious stitches (Fig. 9). The number of short proximal columnals (with columnal length less than the diameter) increased with age. In adult specimens the number of short columnals varied from 17 to 30 (Table 8).

The form of columnals of the upper mesistele in adults varied significantly from cylindrical to barrel-shaped, with one or two thickenings in the middle part. This range of variation can occur in specimens from one station, for example St. 9 of *M. Sars* (Fig. 9). The thickening was usually crossed by a dark line, resembling a trace of the suture of fused columnals. The longest columnals always developed in the middle part of the mesistele. Its length decreased with body size (Table 8). The single adult stalk from the depth 3700–3800 m differed sharply from other stalks, collected from 460–3064 m, by having extremely elongated columnals and elevations (tubercles) at both ends of the columnal (Fig. 7G–H; Table 8). The ratio between the length and diameter of the mesistele columnals (L/D) in this specimen reached 6.9, whereas L/D in adult specimens from depths 590–2940 m was <3.42.

The only L/D value falling outside the 95% confidence ellipse is that of the deepest specimen (Fig. 10). Thus, the depth-related variation in the shape of mesistele columnals can be seen among bathyal and abyssal adult specimens. Depth variation was not observed in other morphological characters.

Extremely elongated columnals with tubercles could be a character of a new abyssal species close to *B. carpenteri*. However, material form depths exceeding 3064 m is too limited to exclude the intraspecific variability.

Table 7. Variation of radial ring form in *Bathycrinus carpenteri* from St. 60d, *Polarstern,* ARK XV/1.

Таблица 7. Изменчивость формы радиального кольца у *Bathycrinus carpenteri* со Ст. 60d, *Поларштерн,* ARK XV/1.

Diameter of RR, mm	**H/D of RR**
1.16	0.72
1.50	0.89
1.58	0.91
1.72	0.57
1.89	0.58
2.00	0.61
2.42	0.58

4. Genera *Echinus* and *Gracilechinus*

According to Mortensen (1943) the genus *Echinus* includes 17 extant species. Eight species of this genus, including *E. acutus*, *E. elegans*, *E. affinis* and *E. alexandri*, were later transferred to a separate genus, *Gracilechinus* Fell et Pawson 1966, which differs from *Echinus* by the presence of primary tubercles on each ambulacral plate (Fell, Pawson, 1966; Kroh, Mooi, 2011; Smith, Kroh 2011). Their close relationship is supported by the data of phylogenetic analysis of 657 b.p. fragment of COI gene (unpublished data). The COI tree shows *Echinus* and *Gracilechinus* as a closest pair of genera in the family Echinidae (unpublished data).

Depth-related morphological trends have been examined in all the Arctic species of both genera: one species of *Echinus*, *E. esculentus,* and three species of *Gracilechinus* — *G. acutus*, *G. elegans* and *G. alexandri*. In addition, three species from the Northeast Atlantic were examined for comparison: *E. tenuispinus* Norman, 1868, *E. melo* Lamarck, 1816 and *G. affinis* Mortensen, 1903. The samples examined included 24 *E. esculentus*, 1 *E. tenuispinus*, 11 *E. melo*, 26 *G. elegans*, 72 *G. acutus*, 25 *G. affinis* and 60 *G. alexandri*. Only one specimen, ZIN RAS Nr 1/748, originally identified by A.M. Dyakonov as *E. tenuispinus*, was not identified in this study because of the poor

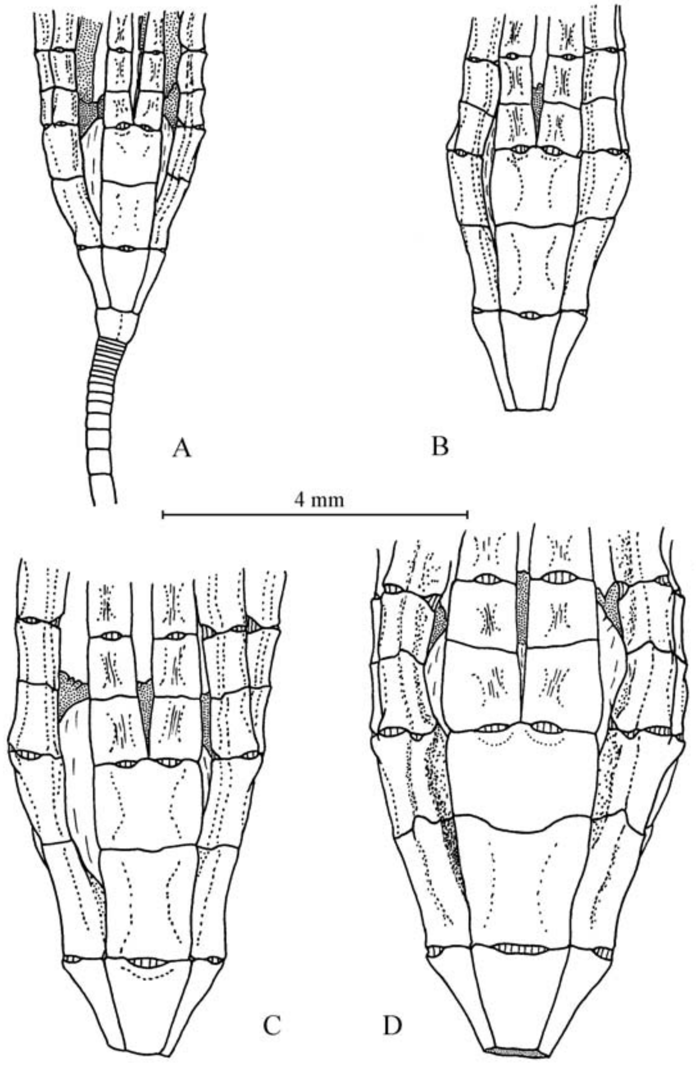

Fig. 8. Age variation of radial ring form in *Bathycrinus carpenteri* (*Polarstern* ARK XI/1, St. 60b, depth 1580 m).

A–B — juvenile specimens with high RR; C–D — adult specimens with lower RR.

Рис. 8. Возрастная изменчивость формы радиального кольца у *Bathycrinus carpenteri* (*Поларшерн,* ARK XI/1, Ст. 60b, глубина 1580 м).

A–B — ювенильные особи с высокими радиальными пластинками; C–D — взрослые особи с более низкими радиальными пластинками.

condition. Measurements of other 155 specimens are cited from Mortensen (1903, 1943).

The following nine characters were used: test diameter (TD), relative test height (RTH), relative apical complex diameter (RAp), ratio of the number of interambulacral to the number of ambulacral plates in the row (IA), the average number of secondary tubercles per coronal plate on the aboral side (STA), presence or absence of a primary tubercle on the ambulacral plates (Fig. 11), presence or absence of spines on the buccal and periproctal plates and number of

Table 8. Variation of BB and columnals in *Bathycrinus carpenteri*.
Таблица 8. Изменчивость BB (базального кольца) и члеников стебля у *Bathycrinus carpenteri*.

RV (year/cruise), Station	**Depth, m**	**H/D of BB**	**Diameter of proximal columnal, mm**	**Number of short columnals**	**Maximum L/D for columnals**
Sadko (1935), St. 35	590	0.80	0.64	17	3.07
Polarstern (ARK XI/1), St. 53	945	?	? (~0.70)	?	3.38
Polarstern (ARK XI/1) St. 62a	950	0.84	0.56	24	3.33
Polarstern (ARK XI/1), St. 60b	1580	0.67	0.68	19	3.41
"	"	0.79	0.38	14	5.70
"	"	0.69	0.68	19	3.34
M. Sars (1900), St. 9	1969	0.77	0.65	17	2.62
"	"	0.65	0.69	22	3.32
"	"	0.68	0.78	31	2.70
"	"	0.63	0.78	28	2.46
"	"	0.67	0.81	30	3.08
M. Sars (1902), St. 102	1700	0.64	1.02	28	2.40
"	"	0.68	1.01	21	2.14
Ob, St. 6	2870	0.83	0.49	17	3.58
"	"	0.74	0.60	16	2.77
"	"	0.83	0.60	17	3.31
"	"	0.75	0.64	21	2.58
"	"	0.75	0.64	17	2.78
"	"	0.77	0.65	18	3.06
"	"	0.68	0.69	19	2.72
Sadko (1938), St. 101	3700–3800	0.70	0.86	21	6.90

lateral teeth on the valves of globiferous pedicellariae. Secondary tubercles were counted on each plate in one row of ambulacral plates and one row of interambulacral plates on the aboral side. The average number of secondary tubercles per coronal plate was also calculated. The RTH, RAp, and STA are the ratios of the test height, the apical system diameter and the average number of secondary tubercles on the coronal plate on the aboral side to the test diameter.

The average value between the maximum and minimum depth of occurrence was calculated for all the studied species (Clark, 1925; Koehler, 1927; Mortensen, 1943; Gage et al., 1985; Tyler et al., 1995) except for *E. esculentus* (Table 9). Most records of *E. esculentus* were from the sublittoral, rarely from the upper bathyal depths (567 m the deepest: *Ingolf*, St. 89). One unusual record of this species at the depth of 1264 m (*Ingolf*, St. 54, 2 specimens) was not taken into account in the calculations. The three shallowest-occurring species belonged to the genus *Echinus*, the four deepest — to *Gracilechinus*. Arranging species of both genera according to the increasing average depth of occurrence revealed depth-related changes in morphology. Intraspecific depth-related morphological trends were analysed using the eurybathic species *G. acutus*: records of this species were conventionally grouped into shallow-water (<200 m depth) and deep-water (>200 m).

All nine morphological characters showed variation related to depth. With increasing depth of distribution, the maximum TD decreased, but RAp and IA increased (Fig. 12). The number of ambulacral plates lacking primary tubercle sharply decreased with increasing depth. Changes in the number of ambulacral plates and the

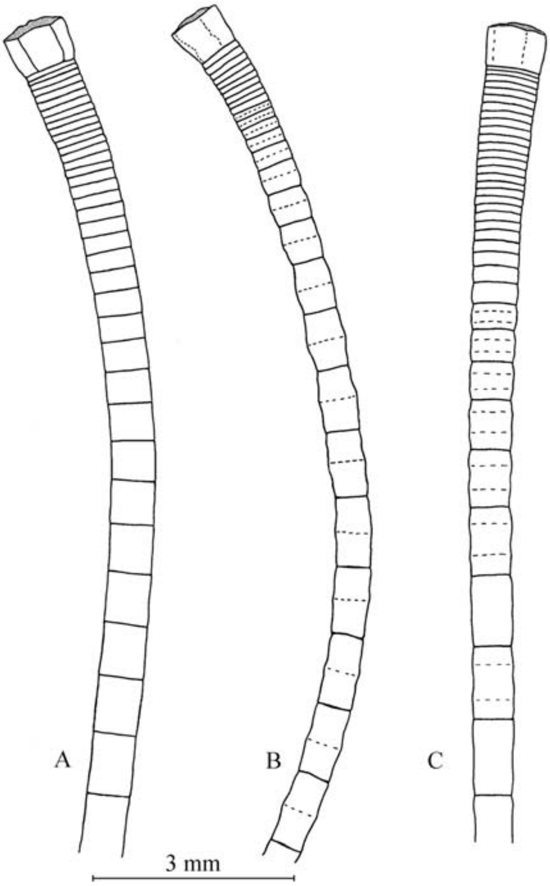

Fig. 9. Variation of the form of columnals in proxistele and upper mesistele in *Bathycrinus carpenteri* (*M. Sars* 1900, St. 9, depth 1960 m).

A — stalk with long proxistele (31 short columnals) and cylindrical columnals in upper mesistele; B — stalk with short proxistele (17 short columnals) and barrel-shaped columnals in upper mesistele; C — stalk with long proxistele (30 short columnals) and two thickenings in each mesistele columnal.

Рис. 9. Изменчивость формы члеников проксистели и верхней мезистели у *Bathycrinus carpenteri* (*M. Sars* 1900, Ст. 9, глубина 1960 м).

А — стебель с длинной мезистелью (из 31 короткого членика) и цилиндрическими члениками в верхней мезистели; B — стебель с короткой проксистелью (из 17 коротких члеников) и и боченковидными члениками в верхней мезистели; С — стебель с длинной проксистелью (из 30 коротких члеников) и с двумя утолщениями у каждого членика мезистели.

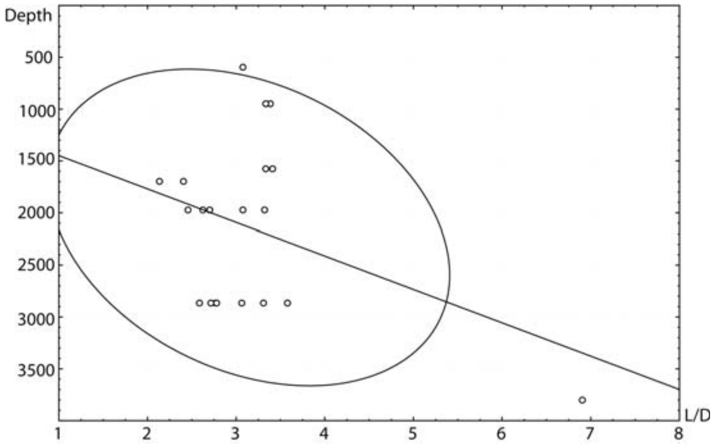

Fig. 10. Changes of L/D ratio with depth in *Bathycrinus carpenteri*.

L — length of columnal; D — maximum diameter of columnal. Regression y=1126.8+321.6*x. The ellipse shows 95% confidence interval.

Рис. 10. Изменение величины L/D с глубиной у *Bathycrinus carpenteri*.

L — длина членика стебля; D — максимальный диаметр членика стебля. Уравнение регрессии y=1126.8+321.6*x. Эллипс соответствует 95%-ному доверительному интервалу.

Table 9. Maximum test diameter in species of *Echinus* and *Gracilechinus*.
Таблица 9. Максимальный диаметр панциря у видов *Echinus* и *Gracilechinus*.

Species	Bathymetrical range	Average depth	Maximum TD (mm)
E. tenuispinus	130–200	165	71
E. esculentus	0–567 (1264)	283	200
E. melo	25–1100	563	164
G. acutus	20–1280	650	150
G. elegans	50–1710	880	97
G. affinis	770–2450	1610	51
G. alexandri	365–4700	2532	86

Species are arranged by increasing depth.
Виды представлены по возрастанию глубины обитания.

absence of primary tubercles seem to be related. Ambulacral plates with primary tubercles are larger than those without primary tubercles. With increasing numbers of ambulacral plates with primary tubercle, fewer plates fit into a row. Juveniles of shallow-water *E. esculentus* and *G. acutus* (Minin, 2012) have primary tubercle on most of their plates, IA and RAp higher than in adult specimens. Therefore, higher IA and RAp in adults of deeper-occurring species suggest retention of juvenile features.

Spines on buccal and periproctal plates tend to disappear with increasing depth. Smallest specimens of all examined species lack these spines (Minin, 2012). In shallower-occurring species (*E. tenuispinus*, *E. esculentus*, *E. melo* and *G. acutus*) buccal and periproctal spines appeared only in adult specimens. In *E. melo* and *G. acutus*, the deepest species of this group, these spines were found only in the largest and therefore oldest specimens. In deeper-living species (*G. elegans*, *G. affinis* and *G. alexandri*) buccal and periproctal spines were absent. Absence of these spines both in deeper species and young specimens of shallower species also suggests retention of juvenile features in deeper-living *Gracilechinus*.

Three other characters are also found to be depth-related. With increasing depth RTH decreased while STA and the number of lateral teeth of globiferous pedicellariae increased. These characters showed no evidence of retention of juvenile features in deep-sea species.

Similar depth-related trends in morphology were observed at the intraspecific level, in the eurybathic species *G. acutus*. The test was smaller, the RAp larger and the IA higher in deeper specimens (Fig. 12). The last two characters may indicate juvenile features in the deepest representatives of this species.

In the sequence reflecting increasing average depth of distribution, the four deepest species belong to the genus *Gracilechinus*. Distinctive trend towards retention of juvenile features in adults of deep-sea species is observed in this sequence, therefore species of the genus *Gracilechinus* retain juvenile features of shallower-occuring *Echinus*. Presence of a primary tubercule on each ambulacral plate, main diagnostic feature of *Gracilechinus*, is also a part of this trend.

The genus *Echinus* most likely has a North Atlantic shallow-water origin and this genus probably first penetrated the deep-sea in the North Atlantic (Tyler et al., 1995; Tyler, Young, 1998). The genus *Gracilechinus* appears to be originated from *Echinus* in the process of colonization of the bathyal depths (K. Minin, unpublished data).

COMPARISON OF DEPTH-RELATED SPECIATION IN DIFFERENT GENERA

The Arctic echinoderm taxa considered in this work demonstrate different scenarios of speciation with depth (Fig. 13). In the genus *Elpidia* speciation occurred with colonisation of both shallow (*E. glacialis*) and deep waters (*E. heckeri*) from the bathyal zone. The recent bathyal species suggested to be closest to the

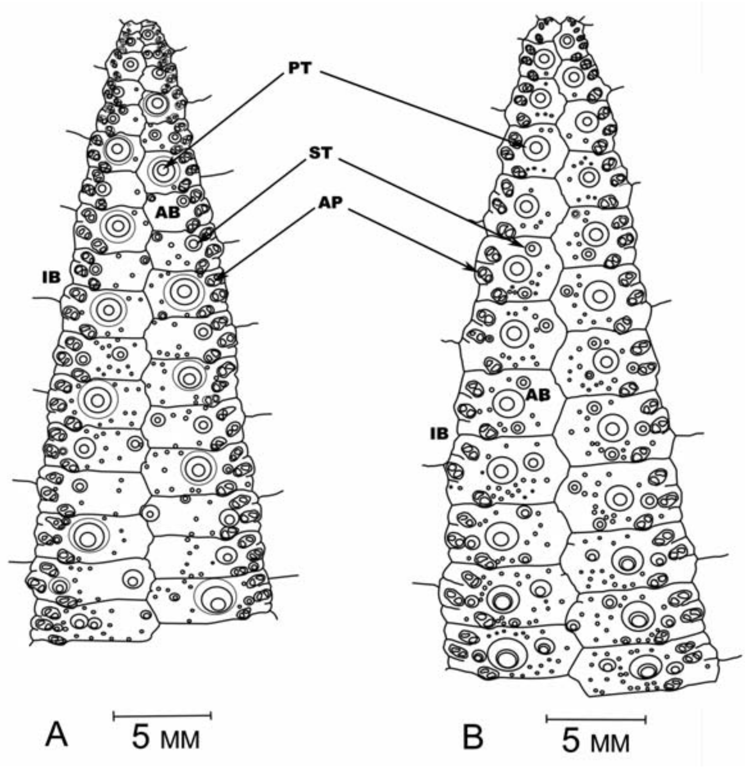

Fig. 11. Ambulacra of aboral side in *Gracilechinus*. A — *G. acutus*, B — *G. elegans*. Deeper living *G. elegans* is characterized by primary tubercle almost on every ambulacral plate. Shallower living *G. acutus* has primary tubercle only on every second or third ambulacral plate

Abbreviations: AB — ambulacral plate, IB — interambulacral plate, PT — primary tubercle, ST — secondary tubercle, AP — ambulacral pore pairs

Рис. 11. Амбулакры аборальной стороны у *Gracilechinus*. A — *G. acutus*, B — *G. elegans*. Более глубоководный вид *G. elegans* отличается наличием первичных бугорков почти на каждой амбулакральной пластинке. Представители более мелководного вида *G. acutus* имеют первичные бугорки на каждой второй или третьей амбулакральной пластинке.

Обозначения: AB — амбулакральная пластинка, IB — интерамбулакральная пластинка, PT — первичный бугорок, ST — вторичный бугорок, AP — пары амбулакральных пор

ancestral form is *E. belyaevi*. In *Pourtalesia jeffreysi* and *Bathycrinus carpenteri*, speciation was probably related only to dispersal from bathyal to deeper waters (or distribution down the slope), although colonization up-slope also took place. In *Echinus,* only one pattern of colonization was revealed, from shelf down the slope.

The speciation from bathyal to shallower waters, found in *Elpidia*, is rather an exception. The suggested pattern of speciation for *Echinus* and *Gracilechinus*, from shallow waters to the deeper, is likely more typical. At the same time, colonization of the deep sea and depth-related speciation in many genera occurred in the North Atlantic with subsequent penetration into the Arctic.

Pourtalesia jeffreysi gibbosa, *P. jeffreysi lata* and the Arctic species of *Elpidia, Echinus* and *Gracilechinus* show no clear geographic and depth isolation. Therefore the parapatric speciation of these taxa can be suggested. The only evidence of spatial isolation and an early stage of allopatric speciation is the giant form of *E. belyaevi* in the upper bathyal of Baffin Bay.

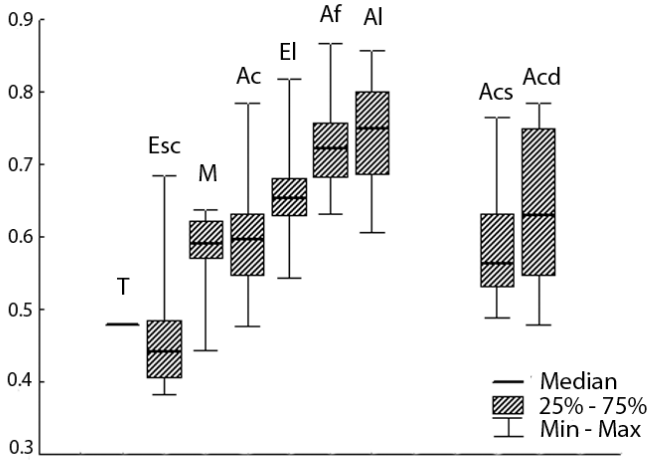

Fig. 12. Ratio of number of interambulacral plates to number of ambulacral plates in seven species of the genera *Echinus* and *Gracilechinus*. Species arranged by increasing depth.

Abbreviations: AC — *G. acutus;* AC_S — shallow-water *G. acutus*; AC_D — deep-water *G. acutus*; AF — *G. affinis*; AL — *G. alexandri*; EL — *G. elegans*; ESC — *E. esculentus*; M — *E. melo*; T — *E. tenuispinus*.

Рис. 12. Соотношение количества интерамбулакральных и амбулакральных пластинок у 7 видов родов *Echinus* и *Gracilechinus*. Виды расположены по мере увеличения глубины обитания.

Обозначения: AC — *G. acutus;* AC_S — мелководные *G. acutus*; AC_D — глубоководные *G. acutus*; AF — *G. affinis*; AL — *G. alexandri*; EL — *G. elegans*; ESC — *E. esculentus*; M — *E. melo*; T — *E. tenuispinus*.

The effect of depth on species distribution is multiple. Among the depth-related factors affecting species distribution the following have been proposed: changes in pressure of predators (Carney et al., 1983; Gage, Tyler, 1991; Sahling et al., 2003; Tarasov et al., 2005), feeding conditions and biological interactions, such as competition (Gage, 2003), sediment type (Le Danois, 1948; Oliver, 1979), topography (Vetter, Dayton, 1998), water masses (Yeh, Ohta, 2003), temperature and pressure tolerance (Somero, 1992; Young et al., 1996) and global climate change, such as glaciation (Nesis, 1983, 2001, 2003).

Tyler and Young (1998) suggested that depth speciation of *Echinus* and *Gracilechinus* in the North Atlantic may be caused by different adaptations to pressure. This hypothesis is based on experiments with embryos and larvae of *Echinus* and *Gracilechinus* showing different pressure tolerance and hence ability to disperse at different depths. Another possible mechanism of speciation is reproductive isolation. Shallow- and deep-water populations differ in the time of spawning and this can be controlled by trophic conditions (surface productivity).

In *Echinus* and *Gracilechinus*, adult specimens of deep-sea species retain juvenile features of their shallow-water congeners. It remains unclear how important these changes are for adaptation. An early stage of depth-related speciation can be suggested for the eurybathic species *G. acutus*: intraspecific variability in this species is similar to depth-related interspecific pattern in the genus *Gracilechinus*. Juvenile features or features with clear adaptation significance do not appear in the speciation of the Arctic species of *Elpidia*.

Morphological differences between the abyssal and bathyal subspecies of *Pourtalesia jeffreysi* suggest different abilities to burrowing and therefore feeding in different sediment layers. The elongated test with midline dorsal and ventral keels and finger-like subanal rostrum with well developed subanal fasciole, typical of *P. jeffreysi jeffreysi* and *P. jeffreysi gibbosa*, are more advanced adaptations to burrowing than in *P. jeffreysi lata*. The flat ventral side of test,

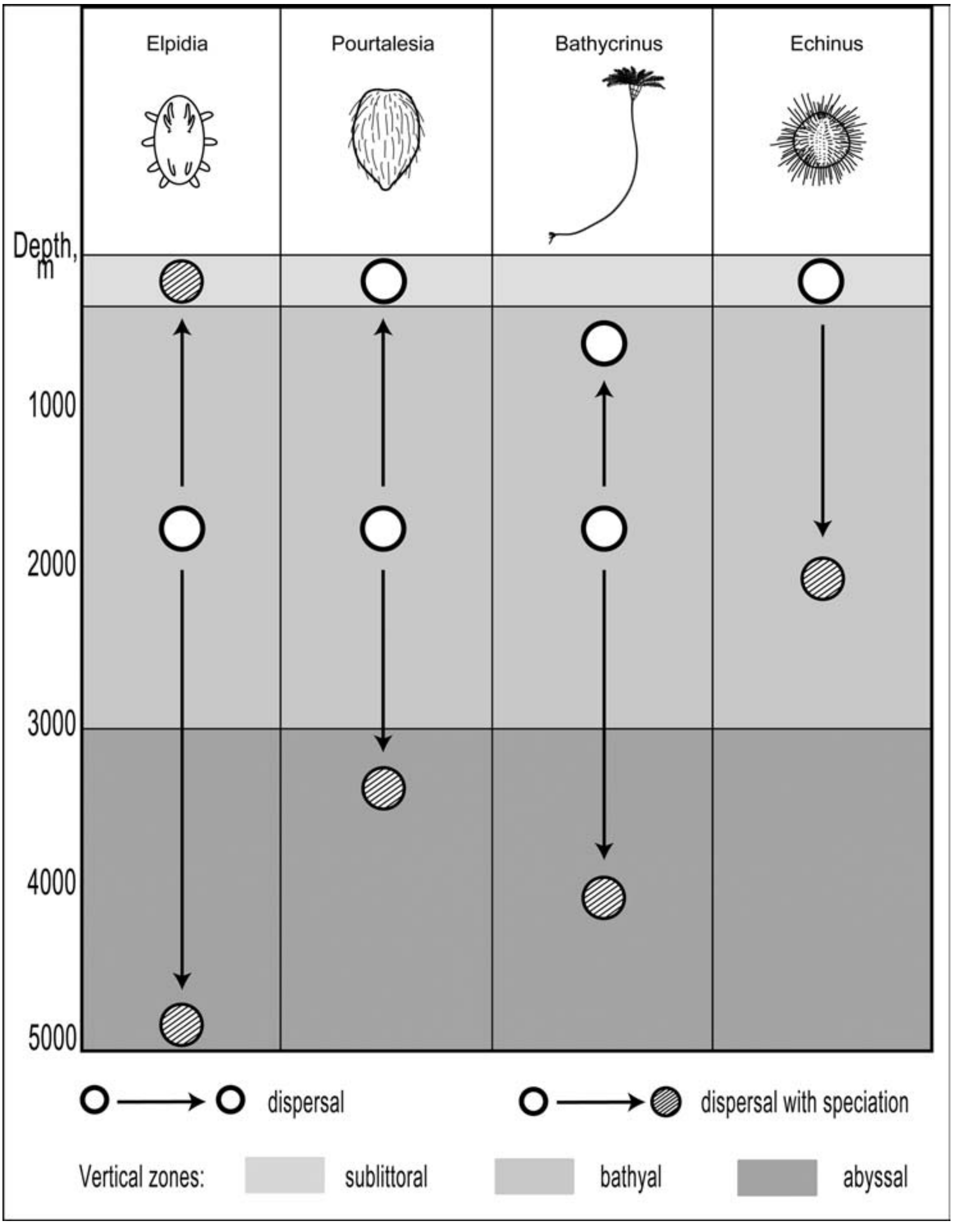

Fig. 13. Scheme of scenarios of depth-related speciation in the Arctic Ocean.
Рис. 13. Схема видообразования по глубине в Северном Ледовитом океане.

short conical rostrum and weakly developed subanal fasciole in *P. jeffreysi lata* are features typical of epifaunal echinoids (Mironov, 1975, 2008). These features may suggest that this form can switch from unselective feeding in the sediment to ingestion of only the superficial layer of sediment. The organic content in abyssal sediments is generally lower than in shallower sediments, resulting in a decline of species diversity at abyssal depths. Species richness, abundance and biomass in the central Arctic Ocean are seemingly poorer than those on the

Arctic shelf and in the abyssal of other oceans (Kröncke, 1998; Deubel, 2000; Węsławski et al., 2003; Soltwedel et al., 2009; MacDonald et al., 2010). Feeding in the sediment surface layer, most enriched in organic matter, is probably a more effective strategy under extreme oligotrophic conditions, such as in the Central Arctic. The trend towards miniaturization, pronounced in the abyssal *P. jeffreysi* and deep-sea echinids, also can result from an extremely limited food supply to the seafloor. Another possible explanation for the shift towards an epibenthic (less cryptic) mode of life is the low pressure of predators in the Arctic abyssal "benthic desert".

Unusually long stalk segments in the deepest specimen of *Bathycrinus carpenteri* can be interpreted as both juvenile and adaptive features. The relative length of stalk segments (the length–diameter ratio) always is higher in juvenile specimens of *Bathycrinus* species. At the same time long stalk segments can be an important trophic adaptation or the result of a lower predation pressure. The stalk in the deepest specimen was longer and firmer than in shallower specimens (<3000 m). In the abyssal Arctic, filtration feeding can be more effective above the substrate increasing the selective advantage of longer stalks. Fish predation on stalked crinoids in the bathyal is evident from the high number of crinoids with bitten off crown or arms, the latter partly regenerating. In the abyssal the pressure of predators is lower, therefore the stalked crinoids can be more exposed above the sediment. These are preliminary hypotheses, additional material especially from abyssal depths is required for more reliable interpretations.

Acknowledgements

We would like to thank the following colleagues who generously have loaned us specimens used in the present study: Melanie Bergmann (Alfred Wegener Institute for Polar and Marine Research, Bremerhaven), Jon Anders Kongsrud, Endre Willassen (Museum of Zoology, University of Bergen), Alexey Smirnov (Zoological Institute, St. Petersburg) and Olafur Asthorsson (Marine Institute of Iceland, BIOICE collection). We also are grateful to Thomas Soltwedel (Alfred Wegener Institute for Polar and Marine Research, Bremerhaven) for the image of aggregation of *Pourtalesia jeffreysi lata*. This work was partly supported by ArcOD, and RFBR research grants 12-05-33049, 13-04-01332 and 12-05-31525. This work is part of the project "Arctic marine fauna: data accumulated in Russia" (sub-project of the CoML "Arctic Ocean Diversity" program).

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