ORIGINAL PAPER

Ninel N. Panteleeva · Elena A. Frolova · Olga V. Sheiko New records of the benthic medusa *Ptychogastria polaris* Allman, 1878 (Trachylida, Hydroidea) in the Barents Sea and off the Kurile Islands (Pacific Ocean)

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Abstract This paper reports new records of the benthic trachymedusa *Ptychogastria polaris* Allman, 1878 in grab samples taken off the Kurile Islands (Pacific Ocean). Photographs showing habitats of *P. polaris* on the seabed were obtained in the southeastern Barents Sea in 1988. The new material, as well as collections of the Russian Academy of Sciences, allowed a revised morphological description. The cnidom of this species is described for the first time. The cold-water nature of the medusa is confirmed. However, its occurrence in temperate waters of the Atlantic and Pacific Oceans allows classification of the distribution area of *P. polaris* as boreal-arctic or, possibly, bipolar, according to Kramp.

Introduction

The medusa *Ptychogastria polaris* Allman, 1878 was described by Allman (1878) using a specimen caught off the East Greenland coast (Discovery Bay, Ellesmere Land: 81°44'N, 64°45'W). The later descriptions of the same species by Haeckel (1879, 1881) as *Pectillis arctica*, based on a specimen sampled off the Canadian eastern coast near Halifax (42°08'N, 63°39'W), are more complete. Later Browne (1903) made a more detailed

N.N. Panteleeva (⊠)¹ · E.A. Frolova Murmansk Marine Biological Institute, Russian Academy of Sciences, Vladimirskaya, 17, Murmansk, 183023, Russia e-mail: mmbi@online.ru; Fax: +7-4778-9100288

O.V. Sheiko

Present address: ¹Murmansk Marine Biological Institute, Kola Scientific Centre, Russian Academy of Sciences, Novaya, 50, Dalnie Zelentsy, 184631, Russia description and prepared original pictures. He suggested that the so-called "sucking cups" ("Stückchen" by Haeckel 1881) on the margin of the bell are nothing but the bases of detached tentacles. This was confirmed later by Mayer (1910), other authors and our present data (Fig. 1, Tables 1, 2). Already Browne (1903) assumed Ptychogastria polaris to be a good swimmer because of its well-developed muscles and wide velum. Later records of this species in pelagic catches from both near the sea bottom and the water surface confirmed this supposition (Kramp 1947). Since then Ptychogastria polaris has been reported off West and East Greenland, Baffin Island, Jan Mayen, northern and southeastern Iceland, in the Barents, Kara, Laptev and Bering Seas, as well as in some Norwegian fjords as far south as Bergen (Kramp 1942, 1947; Naumov 1960; Stepanjants 1989; Sirenko et al. 1996; Stübing and Piepenburg 1998). Moreover, Kramp (1957, 1961) concluded from close examination of the specimens of the Antarctic trachymedusa Ptychogastria opposita (Vanhöffen 1912) that Ptychogastria polaris and Ptychogastria opposita are in fact one species with bipolar distribution.

According to Kramp (1947, 1961), the genus *Ptychogastria* Allman 1878 encompasses three species: *Ptychogastria polaris* Allman 1878, *Ptychogastria asteroides* (Haeckel 1879), and *Ptychogastria antarctica* (Haeckel 1879). *Ptychogastria asteroides* is the smallest form, inhabiting the warm waters of the Mediterranean Sea (Kramp 1961). *Ptychogastria antarctica* is rather different from the other two species in terms of morphology and might therefore belong to another genus or even family (Kramp 1947).

Though *Ptychogastria polaris* has been described by several authors (e.g. Haeckel 1881; Browne 1903; Mayer 1910) and there is quite a wealth of figures showing morphological details and microscopic sections, drawings of the habitus of entire specimens are scarce. The routinely used picture by Haeckel (1881) is "over-schematised" and does not allow accurate identification of this species. The drawings of Bonnevie (1899), of complete live medusae sampled by G.O. Sars during the

Kamchatka Institute of Ecology, Far Eastern Department, Russian Academy of Sciences, Partizanskaya, 6, Petropavlovsk-Kamchatsky, 683000, Russia

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Norwegian North Atlantic Expedition in 1876, actually show *Ptychogastria polaris*, but were incorrectly named as "*Aequorea* sp.?". We obtained live medusae during

cruises. Another example of a habitus illustration is given by Vanhöffen (1912) for an Antarctic medusa under the probable synonym *Ptychogastria opposita*.

Fig. 1 *Ptychogastria polaris.* Lateral view of a specimen from the Pacific Ocean (*r.c.* radial canals, *cp.c.* centripetal canals, *c.c.* circular canal, *g.* gonads, *t.1* filiform tentacle, *t.2* marks of the detached presumably filiform tentacles, *t.3* tentacle with suckers (with adhesive disc), *ms.* mesenteries). Scale: 3 mm



Table 1 List of samples of *Ptychogastria polaris* from the collection of the Zoological Institute which were examined (from 1 to 10 specimens are in each sample)

Expedition	Data	Latitude (N)	Longitude (E)	Depth (m)	
RV A. Pervozvannyi	10.08.1898	69°31′	32°54′	286	
RV A. Pervozvannyi	27.05.1899	Lodeynaya Bay		13	
RV A. Pervozvannyi	13.06.1899	72°13.5′	32°10′	300	
RV A. Pervozvannyi	15.06.1899	73°25′	31°15′	350-360	
RV A. Pervozvannyi	01.07.1899	69°35′	32°26′	207-213	
RV A. Pervozvannyi	13.08.1899	74°27′	21°20′	160	
MBS? Coastal collection	20.07.1900	Kola Bay?			
RV A. Pervozvannyi	03.09.1900	75°00′	33°30′	213	
RV A. Pervozvannyi	13.05.1901	69°23′	32°55′	271	
RV A. Pervozvannyi	18.05.1901	71°00′	33°30′	220-212	
RV Ermak	22.06.1901	72°30′	35°05′	275	
RV Ermak	23.06.1901	72°51′	37°52′	240	
RV Ermak	01.08.1901	78°21′	61°18′	311	
RV A. Pervozvannyi	29.06.1901	74°30′	33°30′	250	
RV A. Pervozvannyi	30.06.1901	75°02′	33°30′	146	
RV A. Pervozvannyi	30.06.1901	75°18′	33°30′	247	
RV A. Pervozvannyi	30.06.1901	78°18′	33°10′	247	
RV A. Pervozvannyi	03.07.1901	73°40′	40°20′	276	
RV A. Pervozvannyi	07.08.1901	70°36′	53°05′	176	
RV A. Pervozvannyi	12.08.1901	71°30′	40°35′	343	
MBS, coastal collection	06.1902	Kola Bay (near Polarnyi)			
RV A. Pervozvannyi	27.07.1902	73°37.5′	52°10′	153	
RV A. Pervozvannyi	14.08.1902	75°16.5′	39°50′	204	
RV A. Pervozvannyi	25.04.1906	75°00′	33°30′	169	
RV A. Pervozvannyi	25.04.1906	74°24′	37°00′	203	
, i i i i i i i i i i i i i i i i i i i	09.08.1913	76°12′	127°40′	64	
	21.08.1913	79°16′	103°20′	101	
Plav.Mor.NiN	26.08.1923	74°02′	41°06′	260	
	25.08.1925	Black Bay (Novaya Zemlya)			
RV Lomonosov	15.09.1931	Russian Harbour (Novaya Zemlya)		30	
RV Rusakov	18.09.1931	73°42′	65°36′	120	
RV Sadko	10.07.1938	81°10′	137°16′	2500	
RV Litke	12.07.1948	76°50′	28°32′	260	
RV Litke	16.07.1948	78°19′	37°12′	152	
RV Litke	17.07.1948	79°38′	45°00′	138	
RV Litke	18.07.1948	79°36′	53°59′	237	
RV Litke	18.07.1948	79°28′	57°21'	170	
RV Litke	29.09.1948	80°30′	90°03′	174	
RV Litke	14.09.1955	82°20′	47°17′	384	

Expedition Data Latitude (N) Longitude (E) Depth (m) Number of specimens **RV** Dalnie Zelentsy 09.08.1988 69°10.8' 50°23.8' 20 3 **RV** Dalnie Zelentsy 11.08.1988 71°41.0' 43°31.0' 246 1 50°47.1' **RV** Dalnie Zelentsy 13.08.1988 74°32.0' 138 4 44°47.8' **RV** Dalnie Zelentsy 15.08.1988 71°07.8' 206 3 52°12.2′ **RV** Dalnie Zelentsy 27.06.1991 74°18.7' 265 1 **RV** Dalnie Zelentsy 18.07.1991 76°39.8' 38°39.6' 195 **RV** Dalnie Zelentsy 19.07.1991 76°35.0' 49°21.9' 270 1

Table 2 List of samples of Ptychogastria polaris from the collection of the Murmansk Marine Biological Institute (collected by authors)

Here we report new findings of *Ptychogastria polaris*, give its consistent morphological description (including the first description of the cnidom) and brief ecological diagnosis, and supply original drawings and photographs.

Materials and methods

The considered material includes: (1) collection of *Ptychogastria polaris* of the Zoological Institute of the Russian Academy of Sciences (Table 1), (2) specimens collected in the Barents Sea during cruises of the Murmansk Marine Biological Institute (Table 2), and (3) two specimens found in the Pacific Ocean (31.07.1987, Iturup Island, Fate Bay, St. 156, 200 m, sediment – silty sand, obtained by the grab corer "Ocean-50") during an expedition of RV *Tikhookeansky* (Institute of Marine Biology, Vladivostok). The last record is the first for the Kurile Islands.

In 1988 in the southeastern Barents Sea, sea-floor photographs were taken in addition to dredge and grab samples, using the underwater camera "Zelenetskaya-2". At each station, a series of 10–15 photographs were taken every 2 min from 1.5 m above the seabed. These photographs were later analysed using a stereoscope. In photographs from 2 stations, 26 specimens of *Ptychogastria polaris* were recorded. A bottom weight visible in each photograph provided a scale, which allowed estimation of the seastfloor area pictured (ranging between 1 and 2 m²) and the measurement of the bell diameters of the medusae. Using the average body weight of the animals collected from dredge samples, the biomass per square meter of the individuals visible in the photographs was calculated.

Results and discussion

Morphology

The bell of live medusae is hemispherical, sometimes slightly flattened, rather transparent; in fixed specimens, it is conical and semi-transparent. The mesogloea is moderately thick; in fixed medusae the exumbrella has 16 easily visible radiating ridges and developed, ringed circular musculature. Subtle longitudinal lines are easily discernible.

In our collections, the bell diameter is 18–24 mm (an average of 20–21 mm); the height of the bell is 11–12 mm in the specimens from the Barents Sea, and 15 and 8–9 mm respectively in the specimens from the Pacific Ocean.

The wide, dense velum with well-developed musculature extends between half and two-thirds of the bell cavity (Fig. 2). The latter is divided by mesenteries into 8 "pouches".

The mouth, of quadrangular form (Fig. 2), has a thickened muscular margin which forms four lips; the manubrium tentacles are absent.

The stomach consists of eight lobes stretched along the radial canals. These lobes are under the canals and are connected through leaf-shaped mesenteries with the subumbrella (Figs. 1, 2, 3). Eight pairs of gonads are situated above the stomach lobes and along their sides (Figs. 1, 2, 3). The gonads are elongated and sac shaped with a remarkably plicate surface. If the mouth is opened one can see eight ridges with wavy margins, which are formed by the juxtaposed walls of the stomach lobes (Fig. 2).

The circular muscles are absent in the apical part of the bell. This makes the base of the stomach clearly visible through the transparent mesogloea (from the exumbrella side). This base has the form of an eightrayed star (Fig. 4). According to Browne (1903), the eight radial canals originate from the rays of this star. The band-like radial canals gradually widen from the stomach to the circular canal and attain maximum width



Fig. 2 *Ptychogastria polaris*. Ventral view of a specimen from the Barents Sea, collected on 20.07.1900 (*m.* manubrium, *g.* gonads, *ms.* mesenteries, *v.* velum, *t.* tentacles). Scale: 3 mm



Fig. 3 *Ptychogastria polaris*. Detail of gonads (g.) and stomach pouches (*s.p.*) (*ms.* mesenteries)



Fig. 4 *Ptychogastria polaris.* Detail of the base of the stomach (*b.s.*), dorsal view (*r.c.* radial canals; *cp.c.* centripetal canals)

at the junctions with the circular canal (Fig. 1). There are also eight narrower centripetal canals steadily narrowing in the direction of the stomach. They do not reach the stomach, closing just before it (Figs. 1, 3). The wide and flattened circular canal runs along the considerably thickened margin of the bell (Fig. 1).

At the margin of the bell there are 48 clusters of marginal tentacles and, correspondingly, 48 single tentacles located between these clusters (Fig. 5a–c). Most of them are detached after fixation, and sites of their



Fig. 5 *Ptychogastria polaris.* Details of the margin of the bell of a specimen from the Pacific Ocean. **a** Lateral view; scale 2 mm; **b** ventral view; scale 2 mm; **c** schematic picture [*r.c.* radial canals, *cp.c.* centripetal canals, *c.c.* circular canal, *t.1* marks of the detached filiform tentacles, *t.2* marks of the detached tentacles with suckers (with adhesive disc)]; **d** schematic picture of the filiform tentacle; **e** schematic picture of the tentacle with suckers

detachment look like round (smaller ones) or triangular (larger ones) holes, which form a characteristic pattern. The solid (filled with endoderm cells) marginal tentacles are of two kinds: longer extensible filiform and shorter tentacles, each terminated with a cushion-like bulge (suckers with an adhesive disk).

The filiform tentacles have wide basal parts and gradually taper off (Fig. 5d). The sites of their detachment look like large triangular cells (Fig. 5, t.1). A few specimens were also found with intact filiform tentacles. They show that, of 48 filiform singular tentacles, 16 larger ones are located at the base of canals, and the rest (32) are regularly spaced between them (Fig. 5a, c, t.1).

The tentacles with suckers are grouped, have a narrow base and gradually widen towards the tips (Fig. 5e). The filiform tentacles seem to be located at the top of each cluster (Fig. 5, t.2), the tentacles with suckers being situated below (Fig. 5, t.3). The diameter of the tentacle bases and possibly their length decrease in lower rows of each cluster. The cluster includes 12–13 tentacles (samples from the Pacific Ocean), 16–18 (samples from the Barents Sea), or up to 20 according to literature data (Haeckel 1881). Thus, in total, there are 700, 900 or 1000 marginal tentacles respectively per medusa.

Table 3 Sizes of nematocysts of *Ptychogastria polaris* (μm): height (min–max) × width (min–max)

Nematocysts type	Tentacles		Manubrium	
	Barents Sea	Pacific Ocean	Barents Sea	Pacific Ocean
Stenoteles large	$10-15 \times 9-14$	13.5–15 × 12.5–13	14 × 13.5	12–15 × 10.5–13
Stenoteles small	$7 \times 5 - 6$	$7.5 - 11 \times 6 - 10$	-	_
Microbasic euryteles	6×5	$7.5 - 9 \times 4 - 5.5$	$7-8 \times 5-6$	$6-7 \times 4-5$

The number of tentacles seems dependent on the age of animals. For instance, Kramp (1947) showed that the young medusae (with the bell diameter of 8 mm) possess 16, but not 48, clusters of tentacles.

We noticed a very bright-pink coloration of the stomach when studying live specimens on board the ship during the expeditions. Brightly coloured stomach pouches and bases of the radial canals form a characteristic large scarlet eight-rayed star which is easily visible from above. The white gonads are easily discernible through the transparent pink bell. The radial, centripetal and circular canals are coloured more densely than the bell. Colour intensity is determined by the density of accumulation of scarlet pigment granules in different parts of the body. Probably these granules enter the body with certain food.

Fixed animals are either pale-rose or colourless and, after preservation with formalin, they become more opaque step by step. They look like truncated cones with a wide base. Usually, 16 ridges emerged, situated above the radial and centripetal canals and, after longer storage, shaped accessory ridges between them.

Cnidom

The cnidom of *Ptychogastria polaris* consists of two types of nematocysts: stenoteles and euryteles. The stenoteles are of typical structure (Fig. 6a–c), and there are two size groups – larger and smaller (Table 3). Discharged euryteles were not observed. However, they appear to belong to the heterotrichous microbasic euryteles. This was suggested after comparing our material (Fig. 6d) with that of Hesthagen (1971), who described in detail this type of nematocyst in *Tesserogastria musculosa*.

The nematocysts of both types are numerous in tentacles and at the margin of the manubrium. There is no perceptible difference in the nematocyst types and sizes between different types of tentacles, but distribution patterns differ remarkably between them. They are arranged more or less evenly all over the tentacles with suckers and spaced round the filiform tentacles. The sizes of nematocysts of the medusae from the Barents Sea and the Pacific Ocean are similar (Table 3).

Ecology

Medusae were photographed in 1988 on two stations in the Barents Sea (Fig. 7): 74°32'N, 50°45'E and 74°30'N, 50°24'E (135–138 m depth, temperature –1.86°C, salinity 34. 91%, sediment - clay with silty sand and small rocks). On the first station the total biomass of benthic organisms was $250.50 \pm 44.40 \text{ g/m}^2$ wet weight. Four medusae were found in the dredge sample, and 13 individuals were recorded in 9 of 15 available photographs. The population density of Ptychogastria polaris was estimated to be 0.41 \pm 0.11 specimens/m² and the biomass 0.08 ± 0.02 g/m². At the second station, the total biomass of benthic organisms averaged 226.90 \pm 34.30 g/m². Thirteen medusae were found in 9 of 11 available photographs. The population density of Ptyc*hogastria polaris* was 0.76 \pm 0.23 specimens/m² and the biomass 0.14 \pm 0.05 g/m². The medusae on the seafloor photographs were randomly distributed.

The benthic community in the study area was dominated by the echinoderms *Ophiura robusta* and *Strongylocentrotus pallidus*. Each medusa was surrounded by a bottom area free of other animals. This area was occupied by stretched thin filiform (catching?) tentacles (Figs. 7, 8). The mean diameter of the bell estimated from the photographs was 21.4 ± 0.95 mm. The shadow of the medusa seen in the photograph indicates that its bell did not lie directly on the seabed, but was slightly

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Fig. 6 Ptychogastria polaris. Details of nematocysts. a-c Stenoteles, d euryteles



Fig. 7 Ptychogastria polaris. Sea-floor photograph taken in the Barents Sea in August 1988 (74°32'N, 50°45'E, depth 137 m). Scale (black cross) 40 mm



Fig. 8 Ptychogastria polaris. Sea-floor photograph taken in the Barents Sea in August 1988 (74°30'N, 50°24'E, depth 138 m). Scale (black cross) 23 mm



Fig. 9 Distribution of *Ptychogastria polaris* in the Barents Sea; our data (collections of the Zoological Institute and MMBI)

lifted above the sediment surface by the suckered tentacles.

Most of our specimens of *Ptychogastria polaris* were collected in the Barents Sea, primarily on the open shelf with depths of more than 100 m (Fig. 9). There are only a few individuals from the Kara and the Laptev Seas (including an area north of Novosibirsk Islands). The medusae were usually found in drag samples at depths of about 100 ± 200 m, but in the Lodeynaya Bay (Barents Sea, East Murman) they were recorded on rocks at 13 m and in the Pechora Sea at 20 m. The animals generally prefer silty sand substrates.

For the first time, *Ptychogastria polaris* was found in the waters off the Kurile Islands (Pacific Ocean) within grab-corer samples.

All medusae from our collections were found in water with temperatures varying from -1.86 to $+1.8^{\circ}$ C and salinities varying between 34.52_{00}° and 34.97_{00}° . In the temperate zone, *Ptychogastria polaris* was recorded only in deep shelf waters with stable low temperatures, for



Fig. 10 Map of *Ptychogastria polaris* distribution. \bullet Literature data (Bigelow 1913; Kramp 1947; Stübing and Piepenburg 1998); \bigcirc our data (collections of the Zoological Institute and MMBI)

instance in the Pacific Ocean, off the Kurile Islands (depth of 200 m; temperature about 2°C). Present data confirm the opinion of Kramp (1947) about the coldwater nature of this species. However its records, including those from the Arctic Ocean and the temperate Atlantic and Pacific Oceans (Fig. 10), allow the classification of *Ptychogastria polaris* as a boreal-arctic form (or bipolar one, according to Kramp 1957, 1961 and Sirenko et al. 1996).

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