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ORIGINAL ARTICLE

Medusae of the genus *Rhabdoon* (Hydrozoa: Anthomedusae: Tubularioidea) in the Arctic Ocean

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Abstract

One hundred and three specimens of juvenile and mature one-tentacle, relatively small-sized hydromedusae of unclear systematic position were found in the zooplankton collections from the Arctic Ocean. Examination of the mature specimens led to the conclusion that their morphology fits with the last diagnoses of the genus *Rhabdoon* (Anthomedusae) and that they belong to the species named here as *R. reesi*. The study of the morphology and cnidome composition of immature medusae suggested them to be young stages of the same species. The comparative study of these juvenile forms with *Yakovia polinae*, the medusae described previously from the Arctic as a new genus and new species, suggested *Y. polinae* to be a junior synonym of *R. reesi.* The distribution of *R. reesi* in the Arctic Ocean is mapped according to recent and historical records.

Key words: *Arctic ocean, one-tentacle medusae, cnidophores, genus Rhabdoon*

Introduction

In the zooplankton collections obtained recently in the Arctic Ocean in several expeditions of RV *Polarstern* (1993–1998) and one expedition of the USCGC *Healy* (2005) we found specimens of relatively small-sized (0.5–2 mm) one-tentacle Anthomedusae clearly distinct from another one-tentacle medusa *Paragotoea bathybia* Kramp, 1942 (Pages & Bouillon 1997; Brinckmann-Voss & Arai 1998) previously registered in this area as *Paragotoea elegans* (Margulis 1989; Kosobokova & Hirche 2000). A single tentacle of this newly found medusa was carrying a conspicuous terminal knob of cnidophores laden with nematocysts. Similar one-tentacle Anthomedusae, identified by Shirley (1966) as *Hybocodon* sp. and later referred as *Pararhysomedusa reesi* by Shirley & Leung (1970) were initially recorded in the Central Arctic in the plankton collections of the drifting stations ARLIS I and ARLIS II. Shirley & Leung (1970) included *P. reesi* in their guide as a new species belonging to a new (unknown until now) genus *Pararhysomedusa.* The authors presented some important characters of the species morphology, size range and a schematic drawing of an adult specimen (Shirley & Leung, 1970). In the list of references they cited a paper by Shirley accepted by the *Journal of the Fisheries Research Board of Canada*, which judging from its title (Medusae, Siphonophores, and Ctenophores of the Central Arctic with the description of a new genus and species of Anthomedusae) would have had to present a description of this new species. To our knowledge, this paper was not published at that time. Somewhat later, Margulis (1989) found similar but much smaller one-tentacle medusae in the collections of the Soviet drifting station Severniy Polus-23 (North Pole-23). The author considered this medusa as a new genus and new species, and named it *Yakovia polinae* (Margulis, 1989). Great similarity between the latter two species on the one hand, and our specimens on the other, along with the unclear systematic status of *P. reesi* encouraged us to review the published information on this one-tentacle Anthomedusae from the Arctic Ocean and other regions.

Material and methods

Zooplankton samples used in the present study were collected during four Arctic cruises (ARK) of the RV *Polarstern* (1993, 1995, 1996, 1998) and the Ocean

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Exploration cruise (OE-2005) of the USCGC *Healy*. In September 1993 (ARK IX/4) and July–September 1995 (ARK XI/1) zooplankton was collected along nine transects from the shelves of the Kara and Laptev seas over the continental slope into the adjacent deep Nansen and Amundsen basins and at a transect across the Lomonosov Ridge at 82°N. In August 1996 (ARK XII) and August 1998 (ARK XIV) sampling was carried out in the deep Amundsen and Makarov basins. In June–July 2005 samples were taken in the Canada Basin. The location of stations relevant to the present paper are shown in Figure 1 and Table I.

During ARK IX/4, XI/1, XII and OE cruises, zooplankton was collected vertically with a multinet (Hydrobios, Kiel, 0.25 m^2 mouth opening, 150 μm mesh size). During ARK XIV, a larger model of multinet with a 0.36 m^2 mouth opening and 150 μm mesh size was used. Five depth strata were sampled from the bottom or 1500 m to the surface during ARK IX/4. In all other expeditions, the entire water column or the upper 3000 m were sampled in two successive vertical hauls from the bottom and 300 m to the surface. Sampling intervals were bottom (3000 m)–2000–1000–750(500)–300–0 m for the deep casts and 300–200–100–50–25–0 m for the shallow casts. At some stations (ARK cruises), additional qualitative sampling was carried out with bongo nets (0.28 m^2 mouth opening, 300 and 500 μm mesh size) from the bottom or 1500 m to the surface. Samples were preserved in 4% borax-buffered formaldehyde.

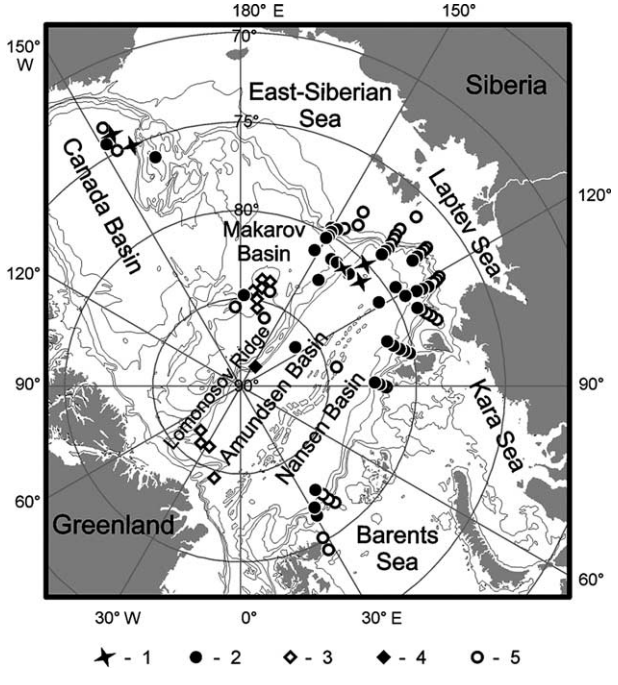

Figure 1. *Rhabdoon reesi* distribution in the Arctic Ocean. Black stars: locations where adult *Rhabdoon reesi* were found during the present study; black circles: findings of juvenile specimens; white circles: no *Rhabdoon reesi* found; white rectangles: findings according to Shirley & Leung (1970); black rectangle: findings according to Margulis (1989).

In total we examined five adult and 98 immature one-tentacle anthomedusae specimens from the listed collections, presumably belonging to the same genus and species. One adult and three juvenile specimens were observed alive. Mature (ZIN RAS 10589 and 10590) and juvenile specimens (ZIN RAS 10591, 10592, 10593) are deposited in the collections of the Zoological Institute of the Russian Academy of Sciences (St Petersburg, Russia). In addition, the holotype (N 1/10062) and 10 paratypes (NN2/10063–11/10089) of *Y. polinae* (Margulis, 1989) specimens were re-examined from the collections of the Zoological Institute (St Petersburg, Russia). A juvenile specimen paratype (N ROMIZ B3632) is deposited in the collection of the Royal Ontario Museum (Toronto, Canada).

Results and discussion

The morphological features of adult mature one-tentacle medusae from our collections match well with the characters of *P. reesi* described by Shirley & Leung (1970). The authors listed the following important morphological characters of the adult medusae: one marginal tentacle, an absence of gastric tentacles, and "gonads on stomach only, not sausage form" (Shirley & Leung 1970: 5). An approximate medusa drawing (figure 6) showed one marginal tentacle with a terminal "pompon" and the absence of marginal bulbs (except for one). Medusae size was also present in the table on p. 17. Further investigation had shown that a more detailed original description of the species could be found in Shirley (1966) under the name *Hybocodon* sp. Later, this initial identification was reconsidered, and the same medusa appeared in Shirley & Leung (1970) as a new species and a new genus *P. reesi*. Unfortunately, the description by Shirley (1966) cannot be regarded as a published one, according to the International Code of Zoological Nomenclature, 4th edn (Section 8.1; 9). At the same time, both the morphological characters in the identification key and Shirley & Leung (1970): figure 6) are sufficient for reliable identification of the species and make the name available⋆. On this basis, we believe that their description should be accepted as the first description of the species *P. reesi* Shirley et Leung, 1970.

The medusae were collected at five stations in the Arctic Ocean (Figure 1). No information is available about deposition of the types. As the adult specimens from our collections fit well to the description by Shirley & Leung (1970), we initially considered

Table I. Findings of *Rhabdoon reesi* in the Arctic Ocean during the present study.

Cruise, station no.	Date	Latitude, N	Longitude, E	Bottom depth (m)	Maximum depth of haul (m)
ARK IX/4					
14	13.08.93	81°27′	34°35’	2719	1500
16	15.08.93	82°12′	30°53’	2465	1500
19	18.08.93	82°45′	40°15’	2994	1500
32	02.09.93	78°43′	132°21′	2975	1500
35	04.09.93	78°23′	133°04′	2062	1500
38	05.09.93	78°10′	133°25′	982	980
47	08.09.93	77°11′	126°16′	995	990
50	10.09.93	77°44′	125°46′	1990	1500
53	12.09.93	79°15′	122°53′	3244	1500
54	13.09.93	79°11′	119°54′	3071	1500
56	14.09.93	78°40′	118°34′	2618	1500
58	15.09.93	78°00′	118°44′	1930	1500
60	16.09.93	77°34′	118°26′	1181	1000
70	21.09.93	78°45′	112°42′	1141	1140
ARK XI/1					
7	26.07.95	79°27′	148°07′	223	200
25	07.08.95	81°06′	105°24′	2642	2500
27	08.08.95	81°14′	106°45′	3133	3000
31	11.08.95	80°46′	103°23′	1484	1435
32	11.08.95	80°39′	103°03′	621	500
33	12.08.95	80°26′	102°00′	266	245
40	15.08.95	78°32′	133°50′	1738	1700
42	16.08.95	78°42′	134°42′	2149	2000
45	18.08.95	80°00′	134°56′	3426	3200
47	20.08.95	80°00′	134°56′	3907	3500
49	22.08.95	80°55′	132°00′	2708	2600
51a	23.08.95	81°03′	136°32′	1830	1750
52	24.08.95	81°07′	138°47′	1292	1200
55	25.08.95	81°10′	140°06′	1693	1600
57	27.08.95	81°11′	143°24′	2643	2500
60	28.08.95	80°17′	150°18′	1642	1500
62	29.08.95	80°05′	149°51′	1072	1000
64	30.08.95	79°53′	149°49′	580	500
65	30.08.95	79°30′	148°14′	232	225
75	04.09.95	80°56′	122°40′	3566	3566
91	10.09.95	82°04′	91°02′	1079	1000
92	10.09.95	82°02′	90°56′	525	525
ARK XII					
55	09.08.96	86°10′	125°49′	4384	3500
76	17.08.96	82°32′	143°34′	1958	1900
ARK XIV					
38	16.07.98	85°08′	172°25′	1518	1450
OE-05 West					
6	08.07.05	73°59′	153°40′	3850	3000
7	09.07.05	74°18′	152°12′	3841	3000
9	14.07.05	75°10′	155°54′	3854	3000
11	16.07.05	75°54′	159°35′	1615	1570

them to belong to *P. reesi*. However, there was another very small (<1 mm) one-tentacle medusa found in the Arctic Ocean by Margulis (1989), which was very similar to *P. reesi* (Shirley & Leung 1970). It also had a single marginal tentacle carrying a terminal knob of cnidophores laden with nematocysts, only one marginal bulb at the tentacle base, a bottle-shaped manubrium, no mouth lips, vacuolated cells on the upper part of the manubrium, and four radial canals (Margulis 1989). According to Margulis (1989), its umbrella was of somewhat different shape, being triangular in most cases, and had a pointed apex. In more rare cases, its top was rather smooth and flattened (Figure 2A–D). In contrast to *P. reesi*, the manubrium stretched outside the umbrella margin very noticeably (Figure 2C–E). These differences in the umbrella and manubrium shape may explain at least partially why Margulis

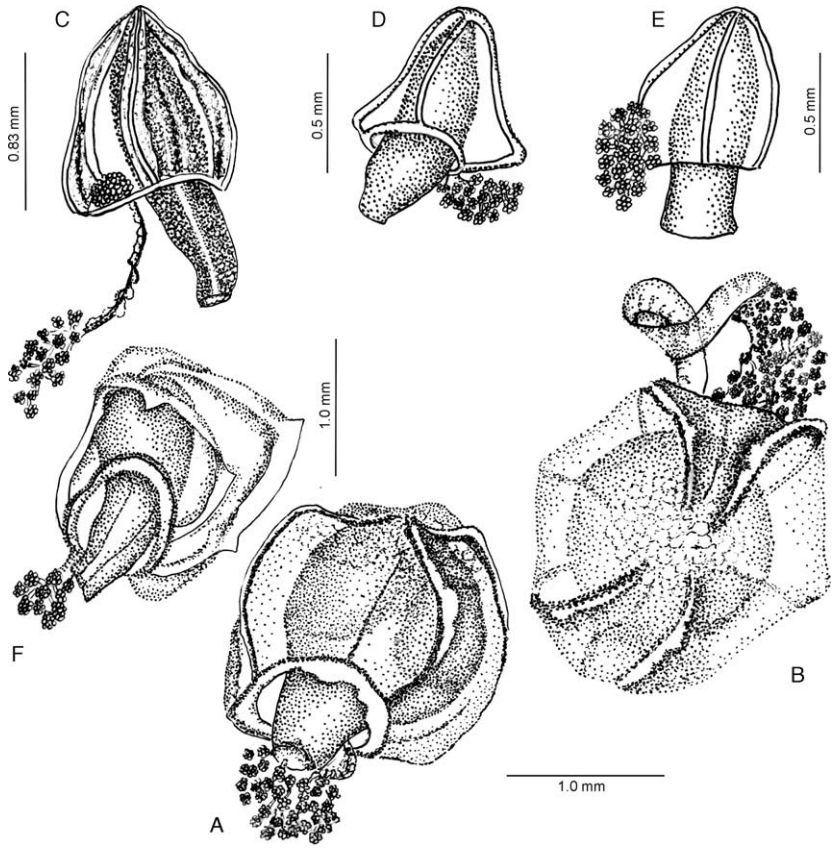

Figure 2. *Rhabdoon reesi* (Shirley et Leung 1970). (A) Side view of an adult specimen. (B) Adult specimen from the top of the umbrella. (C–F) Immature specimens. (C) Holotype specimen of *Yakovia polinae* Margulis (ZIN RAS, no. 1/10062, collected by drifting station NP-22, 16 April 1978, 88°N 142°E, 200–0 m). (D) Paratype specimen of *Yakovia polinae* Margulis (ZIN RAS, no. 2/10063, same location). (E) Juvenile specimen (ZIN RAS, no. 10592, collected during the ARK XI/1 expedition of R/V *Polarstern*, station 36-045, 18 August 1995, 80°N 134°56'E). (F) An older immature specimen (no. 10593 from the same location).

(1989) considered this medusa as a new genus and a new species *Y. polinae* Margulis, 1989. Noteworthy is that Margulis (1989): 126) also mentioned the great similarity between *P. reesi* and her new species. Our comparative examination of adult and juvenile forms from our collections (Figure 2E, F, 3A, D) and Margulis' holotype and paratype specimens (Figure 2C, D) brought us to the conclusion that they all belong to the same species. Specifically, the tentacle morphology is very close in all specimens studied. As we will show below, the cnidome of our juvenile and Margulis' specimens includes the same types of nematocyst as in our mature specimens, with just a slight difference in the desmonemes' size and capsule shape. Moreover, re-examination of the holotype of *Y. polinae* showed the absence of gonads, despite Margulis' (1989) description of the beginning of their development as a circular thickening on the manubrium in this particular specimen. This, subsequently, suggested that *Y. polinae* are young immature specimens of *P. reesi* and cast additional doubts about the validity of the species *Y. polinae*.

During a further comparison of our adult specimens with anthomedusae described earlier we found that the Arctic specimens are morphologically very close to *Rhabdoon singulare* Keferstein & Ehlers, 1861. The latter species was initially described from the Mediterranean Sea, later found again and described as *Rhysomedusa pomponina* (Vannucci & Soares Moreira 1966; Brinckmann-Voss 1970; Goy 1972; Hamond 1974) and then reattributed by Brinckmann-Voss (1987), Goy (1991), Pages et al. (1992), Benovic & Lucic (1996) and Medel & Lopez-Gonzalez (1996) back to *R. singulare*. Similarity between our specimens and *R. singulare* cast doubts about the validity of the genus *Pararhysomedusa* erected by Shirley & Leung (1970) not as a new genus, but together with a new species *P. reesi.* Below we list the most important features common for both *R. singulare* and our specimens:

(1) Very small size: the umbrella height is less than a few (1–5) mm.
(2) The umbrella shape is oval or conical.
(3) There is a single marginal tentacle with a terminal thickening: "pompon".
(4) The terminal thickening of the tentacle consists of cnidophores laden with nematocysts.

(5) The tentacle is approximately half the umbrella height in the adult specimens; the young specimens have shorter tentacles; often they are contracted in such a manner that the "pompon" lies close to the umbrella margin or even draws into the subumbrella.
(6) Marginal bulbs are either absent or only one is present, corresponding to the marginal tentacle.
(7) Four radial canals correspond to four longitudinal mesogleal ribs on the exumbrella surface.
(8) Several meridional rows of nematocyst accumulations are located between radial canals on the exumbrella surface.
(9) Discrete nematocysts are scattered on the exumbrella surface; as a rule, they do not form groups.
(10) The manubrium occupies the most part of the subumbrella cavity or extends slightly beyond the umbrella margin in the adult specimens. In the immature specimens, the manubrium significantly extends beyond the umbrella margin.
(11) A gonad forms a circular thickening on the middle portion of the manubrium.
(12) Tentacles or lips are not present on the manubrium mouth.
(13) Vacuolated cells are present in the mesoglea, especially above the manubrium on the top of the umbrella, along the mesogleal ribs, and around the mouth.

Conceptually, the listed features characterize the genus *Rhabdoon*. Based on them, we attribute our species to the genus *Rhabdoon*, and keeping the species name given by Shirley & Leung (1970), to the species *R. reesi* (Shirley et Leung, 1970). Subsequently, we consider *Y. polinae* as a juvenile stage of *R. reesi* and *Y. polinae* as its younger synonym.

Because a definition of the genus *Rhabdoon* was not published originally (Keferstein & Ehlers 1861), and only a short diagnosis was published later (Bouillon 1985; Bouillon & Boero 2000; Bouillon et al. 2004), we suggest a more detailed definition below based on the examination of our specimens from the Arctic Ocean and literature data.

Genus *Rhabdoon* Keferstein et Ehlers, 1861

Rhabdoon: Keferstein & Ehlers 1861: 86; Bouillon 1985: 112; Brinckmann-Voss 1987: 135; Bouillon & Boero 2000: 150; Bouillon et al. 2004: 108.

Rhysomedusa: Vanucci & Soares Moreira 1966: 2; Brinckmann-Voss 1970: 32.

Pararhysomedusa: Shirley & Leung 1970: 5.

Yakovia: Margulis 1989: 126.

Adult medusae are bell-shaped, with a round-flattened top. Juvenile medusae have a more conical shape. A single marginal tentacle is a characteristic. The tentacle of formalin-preserved specimens has a short and thin stalk and a terminal round "pompon" consisting of cnidophores laden with nematocysts. The top of the subumbrella cavity does not reach the top of the bell. The bottle-shaped manubrium has an oval mouth without marginal lips or tentacles. The outer narrow part of the manubrium reaches the margin of the subumbrella or leans out slightly. The manubrium of the juvenile medusa leans out of the subumbrella cavity remarkably. Gonads are located around the middle portion of the manubrium. Four radial canals are located along the mesogleal ribs of the exumbrella. Six to 12 longitudinal furrows of the nematocyst accumulations are present on the exumbrella surface, diffuse nematocysts are scattered between them. The wide velum bends into the subumbrella cavity. Marginal bulbs are absent, only one of them, corresponding to the single tentacle, may be developed.

The cnidome (Figure 4) includes three types of nematocyst only: stenoteles, desmonemes and microbasic heteronemes. Such a depleted cnidome is typical for a number of genera of the superfamily Tubularioidea. Noteworthy is that it is more impoverished than in the representatives of the family Tubulariidae (Bouillon 1985; Bouillon et al. 2004).

Type species *Rhabdoon singulare* Keferstein et Ehlers 1861

Two species, *Rhabdoon singulare* Keferstein et Ehlers 1861 (=*Rhysomedusa pomponina* Vannucci et Soares Moreira 1966) and *Rhabdoon reesi* (=*Pararhysomedusa reesi* Shirley et Leung 1970) are included in this genus. The first species was collected in subtropical areas: Mediterranean Sea (Vanucci & Soares Moreira 1966; Brinckmann-Voss 1970; Goy 1972, 1991), Adriatic Sea (Benovic & Lucic 1996); Iberian Peninsula and Balearic Islands (Medel & Lopez-Gonzales 1996); South-Eastern Atlantic – Benguela Current (Pages et al. 1992) and in temperate waters of the South Ocean – Bass Strait (Hamond 1974). The second one was found at bathy- and mesopelagic depths of the Arctic Ocean (Figure 1, Table I).

As a detailed description of *R. reesi* was not published previously, we present it below for both adult and juvenile specimens collected in the Arctic Ocean.

***Rhabdoon reesi* (Shirley et Leung 1970)** (Figures 1 and 2A–F, 3A–D, 4, 5A–D)
Pararhysomedusa reesi Shirley and Leung 1970: 5, 10, 16, 17.
Yakovia polinae Margulis 1989: 126, 127, Figure 1

Adult medusae are small. Their bell height varies from 1.0 to 5.0 mm, whereas the maximum diameter reaches 3.25 mm. The umbrella is usually campanulate, with a flattened top (Figure 2A, B, 6). "[The] umbrellar margin is slightly oblique sloping downwards from the tentacular side" (Shirley 1966). Nematocysts form four to six meridional furrows on the exumbrella and are also scattered on its surface without order. Four radial canals correspond to the exumbrella longitudinal mesogleal ribs. One of the canals, corresponding to the single marginal tentacle, is shorter than the others. "Three of the marginal bulbs are rudimentary; one bearing the tentacle is well-developed" (Shirley 1966). A single tentacle terminates with a large spherical construction consisting of cnidophores laden with nematocysts (Figure 5A, B). The flask-shaped manubrium with a simple round opening is situated on a tubular neck. It extends slightly beyond the velar opening. The umbrella walls and their mesogleal ribs contain vacuolated cells.

The cnidome includes three types of nematocyst (measured in μm) (Figure 4A, B): stenoteles (largest 17.5–24.0 × 14.0–16.0; medium 12.0–15.0 × 9.0–10.5; smallest 9.9–10.0 × 9.2–10.0); desmonemes (9.0–11.0 × 5.2–7.0) and microbasic heteronemes (13.0–15.0 × 4.8–5.5). Stenoteles are dominant capsules in cnidophores, in longitudinal nematocyst furrows on the exumbrella, and around the manubrium mouth. Capsules of heteronemes and desmonemes are more rare. We did not find discharged capsules in the preserved specimens.

The small immature specimens have an almost triangular umbrella with a pointed apex of the bell; height 0.5–1.5 mm, diameter 0.5–1.0 mm. In the description of *Hybocodon* sp., Shirley (1966) also noted that the apical part of the umbrella of small immature specimens, in contrast to adult medusae, has a "triangular" or "conical" apex. The manubrium is elongated and bottle-shaped. The narrow terminal part of the manubrium extends beyond the velar opening, sometimes more than half of its length. Only one marginal bulb corresponding to the marginal tentacle is present. In preserved specimens, a single marginal tentacle of the smallest medusae has a short stalk that terminates in "a pompon" of the same construction as in adult specimens described above. In more advanced juveniles, the tentacle elongates, and cnidophores sometimes do not form "a pompon" but are distributed along the terminal portion of the tentacle (Figure 2C). The exumbrella of advanced specimens has longitudinal ribs corresponding to the four radial canals (Figure 2F). Longitudinal rows of nematocysts are absent; nematocysts are distributed on the exumbrella without any order. Gonads are not developed.

The cnidome of juvenile specimens includes the same types of nematocysts as in adult specimens (in μm) (Figure 4C, D): stenoteles (largest 15.0–17.5 × 12.5–15.0; medium 9.8–12.5 × 7.5–10.5; smallest 9.5–10.0 × 9.5–10.0), desmonemes (7.5–9.0 × 4.5–5.2), microbasic mastigophores (11.0–14.5 × 4.0–5.5).

Both the adult and juvenile specimens had the same milky-yellowish live colour, which almost did not change after preservation.

Although the obvious differences in the bell shape between the mature and juvenile specimens are present, they could be well regarded as age variability. According to our observations, the younger (=smaller) a specimen is, the more triangular top of the bell it has (Figure 3). The bell top becomes more flattened and rounded with age, as well as the bell height increases and covers the larger portion of the manubrium. The major differences between the mature and smaller immature specimens are, consequently, the absence of longitudinal rows of nematocysts, smaller desmoneme size, and the different shape of the desmoneme capsulae (Figure 4D). The similar case with desmoneme size regarded as age variability was noted for the other close species of Tubularioidea (Svoboda et al. in press). Therefore, we believe that the differences between

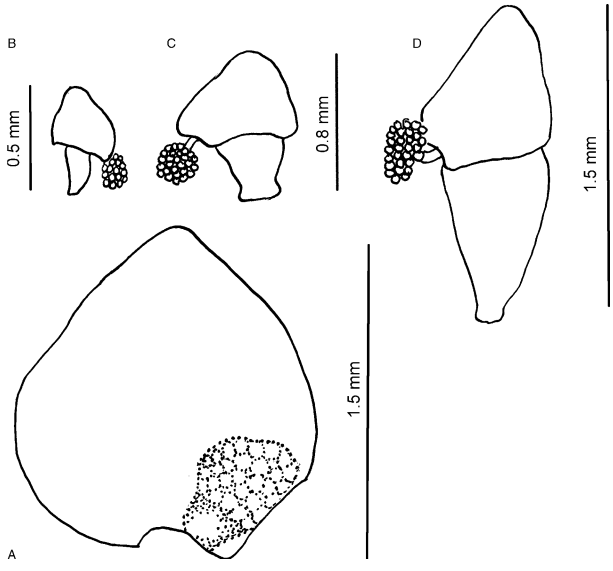

Figure 3. Ontogenetic differences of the umbrella shape in *Rhabdoon reesi.* (A) Adult medusa. (B–D) Immature juveniles.

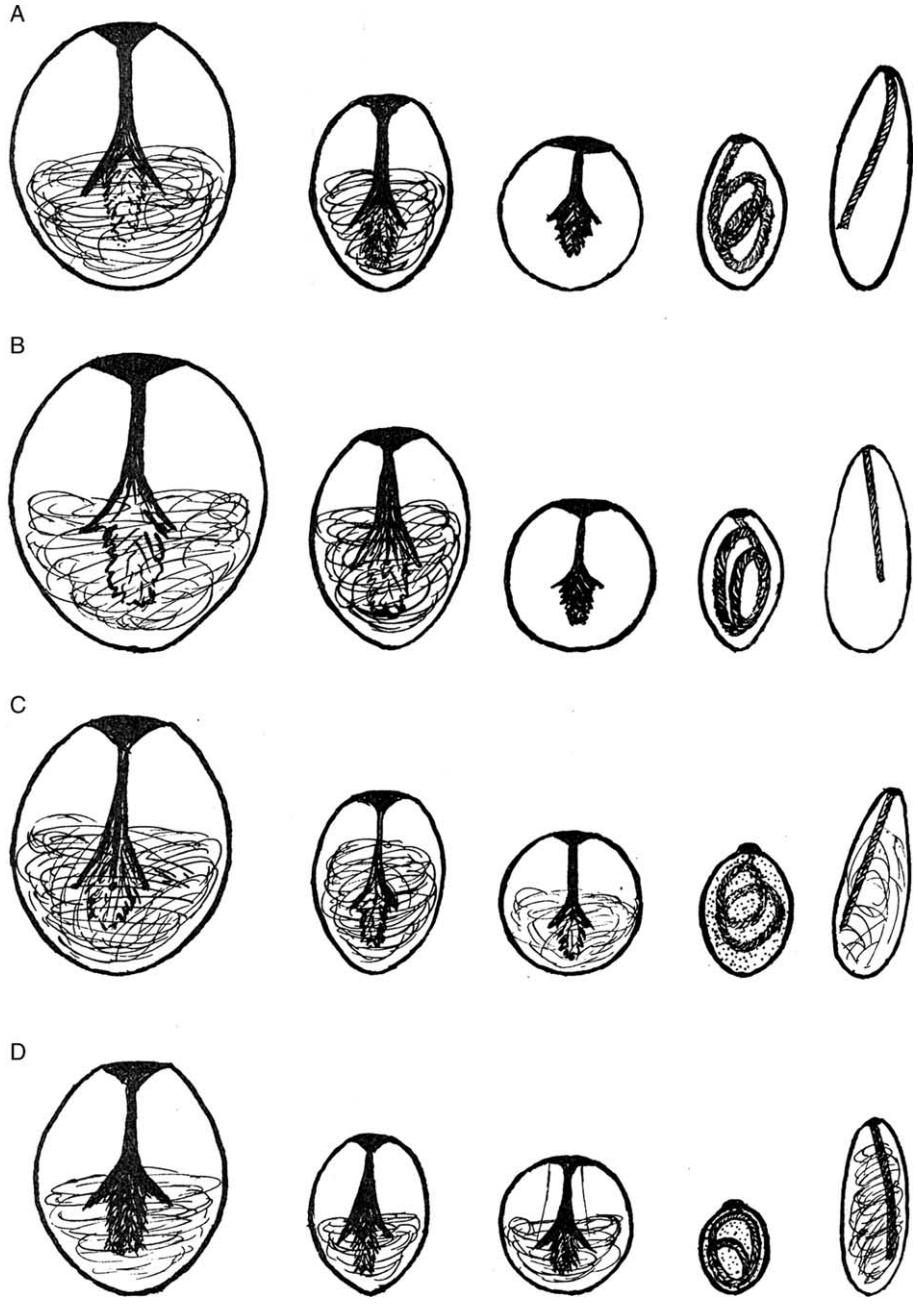

Figure 4. Nematocysts of *Rhabdoon reesi* (schematized). (A) Adult specimen (ZIN RAS, no. 10589, ARK XI/1, station 36-045). (B) Adult specimen (ZIN RAS, No. 10590, ARK 14/1a, station 38). (C) Immature specimen (holotype of *Yakovia polinae* Margulis, ZIN RAS, no. 1/10062). (D) Immature specimen (paratype of *Yakovia polinae* Margulis, ZIN RAS, no. 3/10081).

our young and mature specimens can be related to the medusae's age.

There are presumably some common features in the development of the umbrella shape during the life history of *R. singulare* and *R. reesi*. Thus, Vanucci & Soares Moreira (1966) found that "In the younger specimens [of *Rhizomedusa pomponina*] the tentacle is very short or contracted in such a manner that the knob lies close to the umbrella margin" (p. 9) and "... it [manubrium] ?was found to extend beyond the umbrella margin in single immature specimen, the umbrella of which appears to be rather unusually contracted. Normally it does not reach the umbrella margin" (p. 10).

The major differences between *R. reesi* and *R. singulare* include: the absence of marginal bulbs in the latter and the presence of a single well-developed bulb in *R. reesi*. Keferstein & Ehlers (1861) commented that *R. singulare* had only vacuolated cells but no mesoglea ("...in der Glocke die

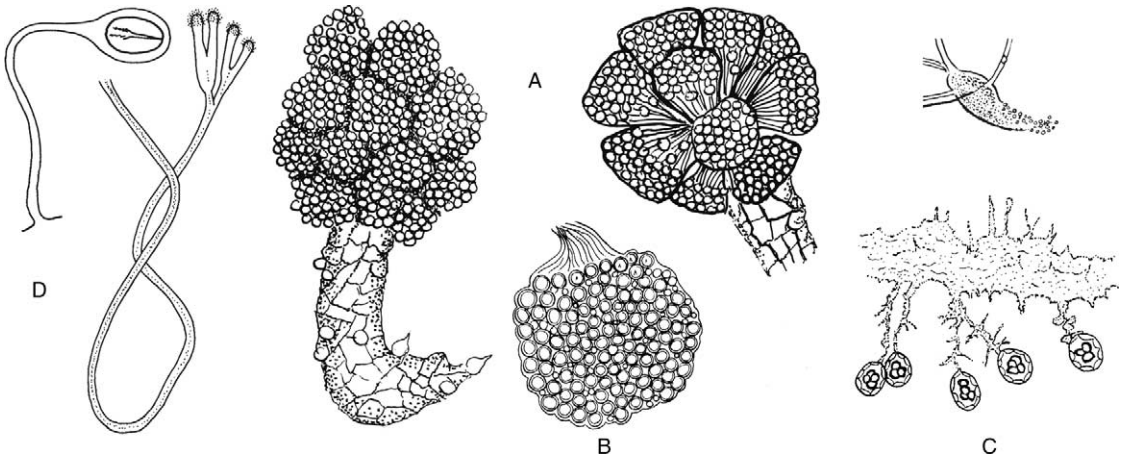

Figure 5. Structure of the terminal part of the tentacle in (A) *Rhabdoon reesi* (schematized); (B) *Yakovia polionae* (after Margulis 1989); (C) *Zanclea costata* (after Russel 1953): marginal tentacle and cnidophores; (D) *Euphysora furcata* (after Schuchert 1996): long furcate marginal tentacle and cnidophore.

Gallertsubstanz fehlt und sie aus grossen rundlichen Zellen besteht . . .", p. 87). Contrary, the umbrella walls of all specimens of *R. reesi* in our collections consisted of a mesogleal substance with separate inclusions of vacuolated cells. It is possible that this parameter is also subject to age variability.

Identification key of *Rhabdoon* species

(1) (2) Marginal bulbs absent..... *R. singulare*
(2) (1) One marginal bulb corresponding to a single marginal tentacle is well developed..... *R. reesi*

Taxonomic status of the genus *Rhabdoon*

Until recently, the genus *Rhabdoon* had been assigned to the superfamily Tubularioidea and family Tubulariidae (Bouillon 1985; Margulis 1989; Bouillon & Boero 2000; Bouillon et al. 2004). At present, certain concerns regarding this relationship have appeared due to the presence in *Rhabdoon* of several features absent in other Tubulariidae. First, the presence of cnidophores in the "pompon" construction. Vannucci & Soares Moreira (1966) were the first who noted that nematocyst-loaded cnidophores in the tentacle "pompon" of their *Rhysomedusa pomponina* (=*Rhabdoon singulare*) were "extremely similar" to the Zancleidae exumbrella nematocyst pads. Nevertheless, they concluded that their new genus "cannot be included in the family Zancleidae mainly on account of the circular shape of the gonad, because they are interradial on the Zancleidae" (Vannucci & Soares Moreira 1966).

One more argument for not including *Rhabdoon* in Zancleidae is the difference in morphology of cnidophores (Figure 5). The Zancleidae are known to be lacking desmonemes (Bouillon 1985; Petersen 1990; Bouillon et al. 2004), whereas they are common in *Rhabdoon*. With regard to the cnidophore structure, there are other Tubularioidea, such as *Euphysora furcata*, with cnidophores on a terminally branched tentacle (Kramp 1961; Schuchert 1996; Bouillon & Barnet 1999). A remarkable feature of the genus *Rhabdoon* is the presence of vacuolated cells. They were found in both known species and, apparently, can be used as a characteristic of the genus.

A feature of *Rhabdoon* as Tubularioidea is the presence of meridional accumulations of nematocysts on the exumbrella parallel to the radial canals. Similar perradial tracks of nematocysts on the exumbrella are also found in Zancleidae, but they usually represent oval or club-shaped patches above the marginal tentacle bulbs (Russel 1953).

Last but not least, *Rhabdoon* has a depleted cnidome composition. As we have shown, only three types of nematocyst are present, whereas anisorhizas and isorhizas, typical for the other Tubulariidae, were not observed.

The four listed features: the presence of cnidophores as a "pompon" construction, longitudinal nematocyst tracks on the exumbrella, vacuolated cells and cnidome depletion suggest that *Rhabdoon*, belonging to the Tubularioidea group, may represent a new family within it. This, subsequently, suggests that a review of Tubularioidea is required based on the collection of new living material, an examination of discharged nematocyst structure, and the development of life cycles involving the polyp and medusa stages.

Distribution of *Rhabdoon reesi*

Specimens of *R. reesi* were found in the area of the continental slope of the Arctic Ocean and in its deep Nansen, Amundsen, Makarov and Canada basins (Figure 1, Table I). They were not present in the shelf areas with depths <100 m. The species' vertical range covers a depth interval between 100 and 3800 m (or the bottom at shallower depths) with maximum numbers below 500 m depth.

Conclusions

(1) Adult one-tentacle anthomedusae collected in the Arctic Basin are attributed to the genus *Rhabdoon* with the species *R. reesi* (Shirley et Leung 1970). The same species was earlier found in the Arctic Ocean and initially described as *P. reesi* by Shirley & Leung (1970).
(2) The small immature hydromedusae described by Margulis (1989) as a new genus and new species *Y. polinae* are regarded here as juvenile stages of *R. reesi.* Accordingly, *Y. polinae* is assumed to be a junior synonym of *R. reesi.*
(3) At present, the two species of the genus *Rhabdoon*, *R. reesi* and *R. singulare*, are registered.

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Note

* Seven issues of "Taxonomic Guides to Arctic Zooplankton" were prepared under the direction of John L. Mohr and distributed in 1970–1971 by the Department of Biological Sciences of the University of Southern California in Los Angeles. Part II, containing the paper by Shirley & Leung (1970), is a Technical Report bearing on the title page a statement that its distribution is not limited and a stamp "This document has been approved for public release and sale; its distribution is unlimited". The paper is cited in Vervoort (1995) and Brunel et al. (1998). Professor W. Pulawski (Californian Academy of Sciences) informed us: "[Our librarians] have found that the Guides are present in 10 USA libraries. Part II is listed under all of them". W. Pulawski specifically confirmed the presence of Part II in the library of the American Museum of Natural History, Washington DC. Hence, the guide by Shirley & Leung (1970) conforms to the criteria of publication (Code, Article 8.1) as it was distributed rather than copied on demand. The method of reproduction was apparently mimeography, as this method is cited for other contemporary publications of the department authored or co-authored by Shirley.

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