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Redescription of Two Antarctic Corymorphidae Species and the Reestablishment of the Genus *Monocaulus* (Cnidaria: Hydrozoa)

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With 2 figures and 4 tables

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Abstract. New material from the Antarctic region offers the opportunity for the redescription of two known Antarctic Corymorphidae species: *Lampra microrhiza* and *L. parvula*. The assignment of these species into genus *Monocaulus* (Allman 1864) (= *Lampra* Bonnevie 1898) is discussed. The Antarctic *Monocaulus* species are compared with the Arctic representatives of this genus.

Problem

There is no agreement between taxonomists concerning genera composition within the Corymorphidae (Petersen, 1990; Silveira & Migotto, 1992; Stepanjants & Svoboda, 1999). In a previous article we presented our position by reference of *Gymnogonos* Bonnevie 1898 to this family and by inclusion of the Antarctic species *Corymorpha ameriensis* Stepanjants 1979 into this genus (Stepanjants & Svoboda, 2001).

Here, we direct our attention towards two Antarctic species described nearly a century ago as *Lampra microrhiza* Hickson & Gravely 1907 and *Lampra parvula* Hickson & Gravely 1907, later placed into the genus *Corymorpha* M. Sars 1859 by Stepanjants (1972, 1979). In 1999, we re-introduced the genus *Lampra* Bonnevie 1898 for *Lampra microrhiza* and *L. parvula* and the Arctic species *Corymorpha glacialis* M. Sars 1859 and *Corymorpha groenlandica* (Allman 1876) (Stepanjants & Svoboda, 1999).

Lampra was established by Bonnevie (1898) for three new Arctic deep-water species: *L. sarsii, L. purpurea* and *L. atlantica*. Later, Broch, (1910, 1916), Spassky (1929) and Naumov (1960) referred these species to *Corymorpha.* Beyond that, Naumov (1960)

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synonymised *L. atlantica* and *L. purpurea* Bonnevie 1898, *Lampra arctica* Jäderholm 1909 and *Corymorpha spitzbergensis* Broch 1916 with *Corymorpha groenlandica* (Allman 1876).

The genus name *Lampra* is preoccupied by genera of Lepidoptera (Hübner, 1821), Coleoptera (Dejean, 1833) and Crustacea (Boeck, 1871). Meanwhile, Allman (1864) established the new genus *Monocaulus* [originally as *Monocaulos*; later (1872, 1876) he emended the spelling to the Latin version *Monocaulus*]. The emendation is justified according to the ICZN (1999: Article 19.2.). According to Allman's description of *M. glacialis,* his own specimens of this species were "bright pink" (1872: 396). *Monocaulus groenlandica* Allman was described later (Allman, 1876) as having gonophores on unbranched blastostyles, but no note on its colour and no comparison with *M. glacialis* are given in his description.

Allman's genus *Monocaulus* is characterized by a whorl of one row of basal tentacles and medusoids "which are borne on all sides of a common peduncle, on which they are sessile" (Allman, 1876: 257–258). These characters coincide with Bonnevie's diagnosis of *Lampra*, especially with regard to the unbranched blastostyles and the pink colour of the preserved specimens (*C. glacialis* excepted). Bonnevie (1898) did not designate a type for the genus *Lampra*; *Lampra sarsii* Bonnevie 1898 is here designated as the type, and the species is here synonymised with *Monocaulus groenlandica* Allman 1876.

Material and Methods

In this paper we discuss and compare all Arctic species which were placed in *Lampra* by Bonnevie (1898, 1899) and the two Antarctic species described as *Lampra microrhiza* and *L. parvula* by Hickson & Gravely (1907). Most of the Arctic *Lampra* species that we examined are from the collections of the Zoological Museum of the University of Oslo and the Zoological Institute of the Russian Academy of Sciences (ZIN RAS), St. Petersburg; the types of the Antarctic species are from the Natural History Museum, London (BMNH), the "Polarstern" ANT VIII/5 specimens from the National Museum of Natural History, Leiden (RMNH), and representatives from both polar regions from the collection of ZIN RAS (Soviet Antarctic expeditions SAE-samples, without collection number).

Anatomy and histology were studied with a Zeiss Axiophot Microscope from microslide preparations. Standard paraffin sections (7 µm) were stained with Azan (according to Heidenhain, 1915) or PAS (according to McManus, 1948); for semi-thin sections (1 µm), polyp parts were embedded in Historesin (Leica), stained by Weigert-Hematoxylin or by Masson's Trichrome staining, modified by Goldener (Romeis, 1989); unstained tissue squashes from oral and aboral tentacles and gonophores were made in glycerol and studied by Nomarski interference contrast.

The photographs aboard "Polarstern" were made as described by Svoboda (1992). Morphological and other characters were compared using a computer data base (Stepanjants, unpublished).

Terminology

I. **Tentacle construction:** filiform, moniliform, capitate. According to Millard (1975) and Petersen (1990).

(a) **Filiform** – the whole tentacle surface is covered more or less uniformly by nematocysts.
(b) **Moniliform** – tentacle is covered by rings of nematocysts.
(c) **Capitate** – nematocysts are concentrated at the terminal tentacle knob. We do not use the term "pseudofiliform" (Petersen, 1990: 109) because it practically does not differ from "filiform".

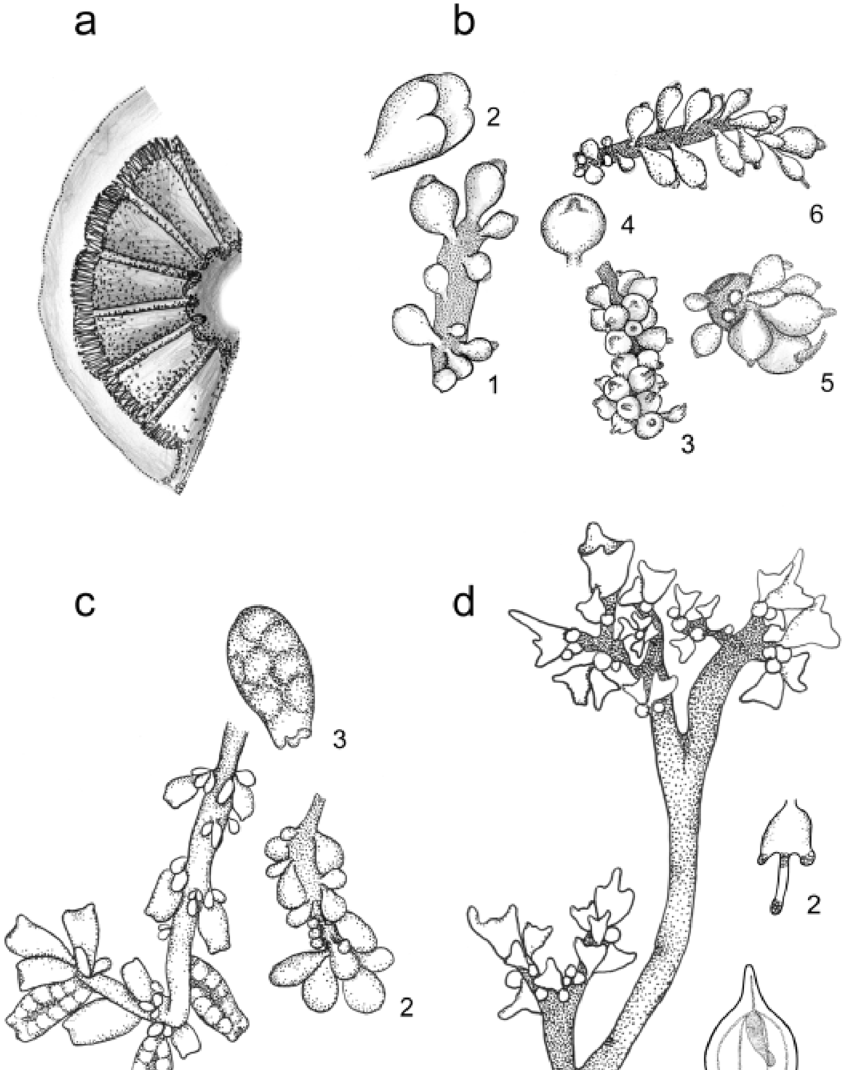

Fig. 1. a. Schematic drawing of diaphragm (*M. sarsii* Bonnevie, type specimen) between oral and aboral tentacle zone in the polyp 'head'. Fragment, view from the oral side. b. Blastostyle constructions of different Arctic *Monocaulus* species described by Bonnevie (1898); 1 – *M. atlantica*, unbranched blastostyle (5 mm); 2 – *M. atlantica*, cryptomedusoid with 4 rudimentary tentacles (1.2 mm); 3 – *M. purpurea*, unbranched blastostyle (2.5 mm); 4 – *M. purpurea*, young cryptomedusoid gonophore (0.3 mm): 5 – *Monocaulus sarsii*, young unbranched blastostyle (2.5 mm); 6 – *Monocaulus* sp., unbranched blastostyle (5.5 mm). c. *Monocaulus glacialis*; 1 – fragment of adult unbranched blastostyle with clusters of young and mature gonophores (10 mm); 2 – young unbranched blastostyle (3.5 mm); 3 – mature cryptomedusoid gonophore with 4 rudimentary tentacles (4 mm). d. *Corymorpha nutans*; 1 – fragment of branched blastostyle (6 mm); 2 – unliberated eumedusoid (1.5 mm); 3 – freshly liberated living medusa (1.5 mm).
All figures drawn from the collections of the Zoological Museum Oslo, May 1999 (except Fig. 1d: 3, redrawn from a micrograph of a living medusa of *C. nutans*).

Fig. 2. ***M. groenlandica;*** a. *in situ* photograph from "Polarstern" Expedition ARK IX, St. 61, by J. Gutt, AWI, in NE Greenland at 260 m depth. The hydranth is filtering downstream, with the mouth turned away from the current. The long stiff marginal tentacles are bent backwards; remarkably, the tentacle tips float with the current, as observed also in *Corymorpha nutans* (Svoboda, 1973) and in *Branchiocerianthus imperator* (Omori & Vervoort, 1986). b. Nearly perfect male specimen collected undamaged with a core sampler by "Polarstern" Expedition ARK XIII at 961 m depth and preserved in formaldehyde. The change of colour to reddish-orange is also typical for *M. parvula* (natural size, RMNH Coel. 29 226). ***M. microrhiza***; c. *in situ* photograph, taken by J. Gutt, "Polarstern" Expedition ANT XIII/3 in the eastern Weddell Sea, at 172 m depth. The polyps are filtering downstream. In contrast to *M. parvula* on the photograph below, the caulus remains unbent upright. The grey perisarc leaves free the black neck region, thus resembling the tubes of *Cerianthus* species (Anthozoa). d. Large specimen collected with the Agassiz trawl by "Polarstern" Expedition ANT VIII/5 and showing the typical partial loss of the black-coloured ectoderm layer with the striped white, thick mesogloea below. The living endoderm is colourless in the caulus and tentacles, but reddish at the proboscis. It stained totally black-brown after preservation (natural size, RMNH Coel. 29 220). ***M. parvula***; e. *in situ* photograph, taken by J. Gutt, "Polarstern" Expedition ANT XIII/3 in the eastern Weddell Sea, at 221 m depth. The slender caulus of this species bends down with the current, the tentacle tips are floating as in the other species. The constriction below the hydranth, allowing its passive rotation, is clearly visible. f. Fully mature male specimen (ANT VIII/5) from the Weddell Sea showing faint colours of the gonophores, proboscis and oral tentacles. After preservation it stained totally reddish-orange (1.5 × enlarged, RMNH Coel. 29 221).

II. We use the terms **"hollow"** and **"solid"** for tentacles as used by Millard (1975: 8).

III. **Diaphragm:** gastric constriction which divides gastral cavity of polyp head between oral and aboral tentacles (Rees, 1957) (see Fig. 1a).

IV. **Gonophore construction**: eumedusoid, cryptomedusoid, styloid (according to Kühn, 1913).

(a) **Eumedusoid** – marginal tentacles reduced, exumbrellar cavity, velum, radial canals, endoderm lamella are present. May produce aborted medusae which cannot feed or normal, viable ones with partly reduced marginal tentacles (see Fig. 1d: 2, 3).

(b) **Cryptomedusoid** – no radial canals, no velum; there is a narrow subumbrellar cavity; thin entodermal lamella and rudiments of tentacles may be present (see Fig. 1b, c).

(c) **Styloid** – radial canals, velum, subumbrellar cavity; endoderm lamella and tentacles are missing; there is only a spadix covered with gastroderm (only in *Gymnogonos*; Stepanjants & Svoboda, 2001).

V. **Types of gonophore attachment: Blastostyles** are reduced gonozooids deprived of tentacles and covered with gonophores. They may be branched or unbranched.

(a) no blastostyles; only solitary gonophore attached to hydranth between oral and aboral tentacles by its own stalk (only in *Gymnogonos*; see Stepanjants & Svoboda, 2001).

(b) no blastostyles; cluster of gonophores attached to hydranth between oral and aboral tentacles by pedicel (only in *Gymnogonos*; see Stepanjants & Svoboda, 2001).

(c, d) unbranched blastostyles covered by gonophores, each attached with its own pedicel (see Fig. 1b, c).

(e) branched blastostyles (see Fig. 1d).

VI. **Nematocyst types**: stenoteles, desmonemes, atrichous isorhiza, anisorhiza, microbasic mastigophores.

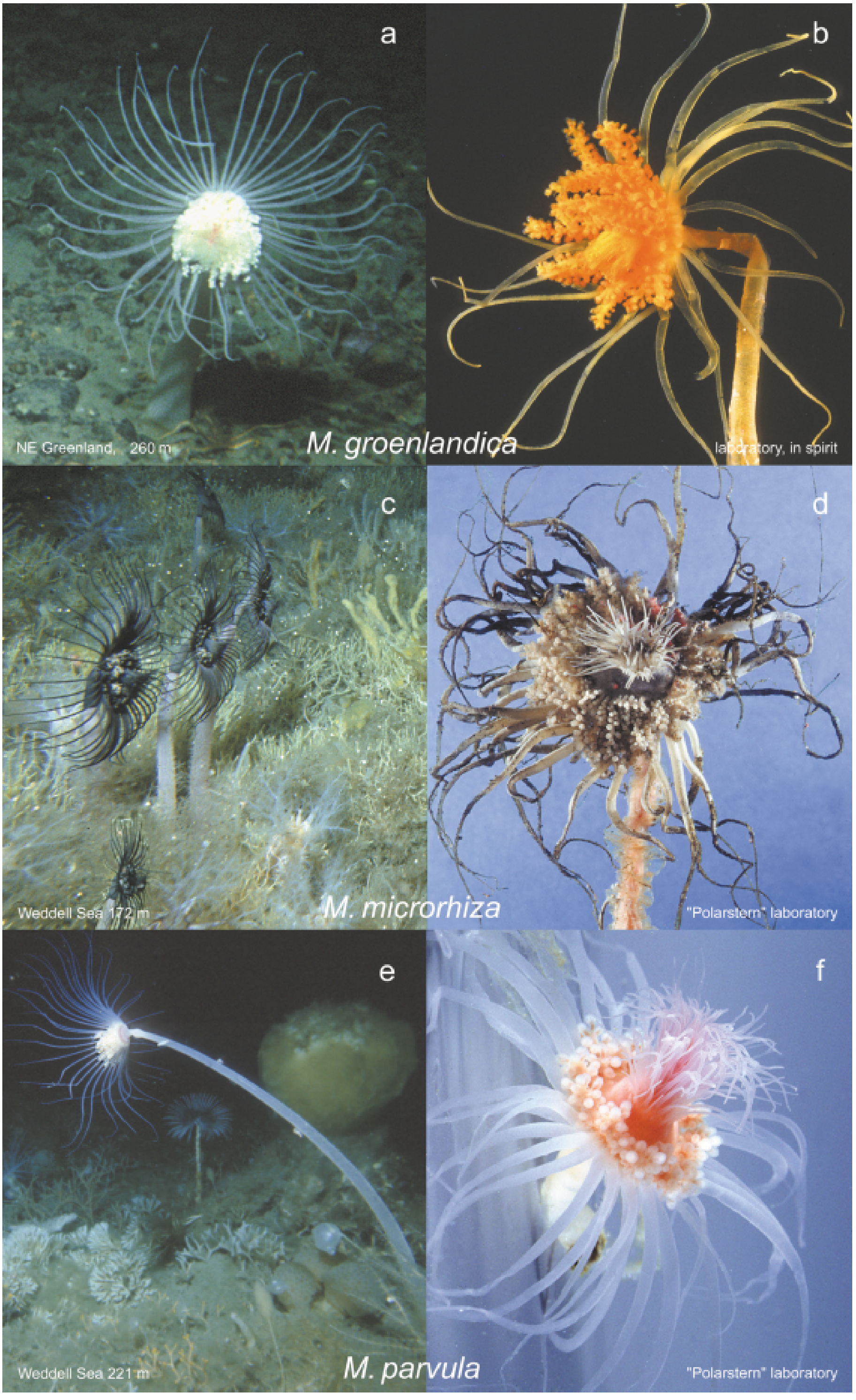
a
b
NE Greenland, 260 m
M. groenlandica
laboratory, in spirit
c
d
Weddell Sea 172 m
M. microrhiza
"Polarstern" laboratory
e
f
Weddell Sea 221 m
M. parvula
"Polarstern" laboratory

Table 1. Data for different species of *Monocaulus* and *Corymorpha.*

species	references	locality, depth, water temperature	polyps				
			total length [mm]	filaments	papillae	canals	perisarc
Monocaulus arctica (Jäderholm)	Jäderholm, 1909; Spassky, 1929	Spitzbergen, about 40 m	?	basal	?	?	?
M. atlantica (Bonnevie)	Bonnevie, 1898	63°22′N-5°29′E; 2222 m; 1.2 °C	80	?	?	?	?
M. glacialis (M. Sars)	Allman, 1872; Broch, 1916; Spassky, 1929; Naumov, 1960; Stepanjants, 1989	White-, Barents-, Cara-, Laptev-, Norwegian-, Greenland Sea; 0–165 m; 0° to +1 °C	50–115	basal	absent	+	–
M. groenlandica Allman	Allman, 1872; Spassky, 1929; Naumov, 1960; Antsulevich & Polteva, 1988; Stepanjants, 1989	Barents-, Laptev-, Greenland Sea; Franz-Josef-Land; 20–375 m; 4 to -1.8 °C	11–125	basal	absent	+	+
M. microrhiza (Hickson & Gravely)	Hickson & Gravely, 1907	Ross-, Weddell Sea; about 500 m; 1 to -2 °C	50–120	basal	absent	+	+
M. parvula (Hickson & Gravely)	Hickson & Gravely, 1907; Stepanjants, 1972, 1979	Ross Sea: McMurdo Bay; Davis Sea; Sodruzestva Sea: Amery Glacier; Weddell Sea; to 500 m; 1 to -2 °C	20–110	basal	absent	visible on basal part	total caulus length
M. purpurea (Bonnevie)	Bonnevie, 1898	67°24′N-8°58′E; 1 °C	100	?	?	?	?
M. sarsii (Bonnevie)	Bonnevie, 1898	67°56′N-4°11′E; 1423 m; 1.28 °C	80	?	?	+	?
M. socia (Swenander)	Swenander, 1904	Trondheim Fjord, 400 m	45	?	?	?	?
M. spitzbergensis (Broch)	Broch, 1910, 1916	Spitzbergen, 1800–1390 m	6	?	?	?	?
Corymorpha? bigelowi (Maas)	Maas, 1905; Petersen, 1990	Japanese waters	20	basal	basal part of caulus	total caulus length	3/4 of caulus length
Corymorpha carnea (Clark)	Clark, 1876; Fraser, 1937; Hirohito, 1988	Alaska, Sagami Bay	150–300	basal 1/4	absent?	anastomoses on total length	total caulus length
C. forbesi Mayer	Brinckmann-Voss, 1970; Petersen, 1990	Mediterranean Sea	20–30	basal	below middle part	total length	below head
C. januari Steenstrup	Steenstrup, 1854; Silveira & Migotto, 1992	Rio de Janeiro, Floria nopolis; Ubatuba; Sao Paolo; intertidal to 18 m, 17.7–28 °C	40–265	basal	basal part of caulus	anostomoses on total length	total caulus length
C. nana Alder	Alder, 1857, 1862; Hincks, 1868	British Isls.	12–20	?	?	?	?
C. nutans (M. Sars)	Russell, 1953; Naumov, 1960; Brinckmann-Voss, 1970; Svoboda, 1973; Petersen, 1990;	Mediterranean-, Adriatic-, Black-, Atlantic-, North Sea, 12–15 °C, Red Sea, 30 °C (G. B. Reinicke, pers. comm.)	50–115	basal	absent?	total caulus length	total caulus length
C. palma Torrey	Torrey, 1902, 1904	North Pacific, San Diego, San Pedro, tidal	140–250	basal	absent?	?	1/2–1/4 of length
C. pendula Agassiz	Fraser, 1944; Calder, 1975	Atlantic coast of N. America, about 300 m	70–100	basal	absent	anastomoses on total length	total caulus length
C. sagamina Hirohito	Hirohito, 1988	Sagami Bay, 120 m	400	below middle of basal part	middle of caulus	upper 1/3 above papillae	total caulus length
C. sarsii (Steenstrup)	Steenstrup, 1854; Allman, 1876	tropical waters	?	?	?	?	?
C. tomoensis Ikeda	Hirohito, 1988; Yamada, 1959	Seto Island, shallow	50	?	?	?	?

Table 2. Tentacle features of the different species of *Monocaulus* and *Corymorpha.*

species	polyp tentacles											
	oral						aboral					
	length [mm]	solid/ hollow	filiform	monili- form	capi- tate	rows	length [mm]	solid/ hollow	filiform	monili- form	capi- tate	rows
M. arctica	?	?	many	?	?	5–6		?	20–25			?
M. atlantica	?	?	?	?	?	many	10–12	?	20	?	?	1?
M. glacialis		?	many	–	–	several	15–30	?	30–50	?	?	1
M. groenlandica	7–10	hollow	60?	–	–	several	17–40	hollow	23–27	–	–	1
M. microrhiza	1.5–10	hollow	about 200	–	–	many	25–75	hollow	30–50	–	–	1
M. parvula	0.3–1.5	hollow	about 200	–	shortest	many	1.5–25	hollow	20–50	–	–	1
M. purpurea	?	?	?	?	?		30–40	?	30	?	?	1?
M. sarsii (Bon.)	?	?	?	?	?	many	18–20	?	20	?	?	1?
M. socia		?	many	?	?	many		?	29–37	?	?	1
M. spitzbergensis		?	many	?	?	4–5		?	25	?	?	?
C.? bigelowi	1–2	?	about 20	–	–	2–3	3–3.5	?	15?	–	–	1
C. carnea		?	200	?	?			?	100	?	?	1
C. forbesi	1–2	?	–	12–14	–		3–3.5	?	16–20	–	–	1
C. januari	5–12	?	up to 353	–	–	several	20–50	?	40–80	–	–	1
C. nana		?	16–18	–	–			?	15–20	–	–	1
C. nutans		hollow	20–80	+ dist	–	many	22–25	hollow	20–50	+ dist	–	1
C. palma	3–4	?	60?	?	?	several	?	?	18–30	?	?	1
C. pendula		?	many	–	–	several	3–6	?	18–30	–	–	1
C. sagamina		?	40	–	–			?	30	–	–	1
C. sarsii Steen.	?	?	many	?	?	many	?	?	?	?	?	?
C. tomoensis	?	?	70	–	–		?	?	38–40	–	–	1

Results

Based on the literature analysis presented in the introduction and the following analysis of the morphogical characters of its species, we substitute here *Lampra* Bonnevie 1898 by the older genus name *Monocaulus* Allman 1864 and designate *Monocaulus groenlandica* Allman 1876 as the type-species of *Monocaulus* on the assumption that Allman (1864) confused his specimens of *Monocaulus glacialis* with that species. This designation is in accordance with Art. 70.3 ICZN (1999).

The pink colour of preserved *Monocaulus* specimens is typical for all Bonnevie's species of *Lampra* and *M. groenlandica*, but not for *M. glacialis,* although Allman (1872) described this species as "bright pink". This gives us a reason to suppose that Allman misidentified his pink coloured specimens as *M. glacialis,* a species insufficiently described by M. Sars, not knowing that he listed characters of a new species, which he described twelve years later as *M. groenlandica*. The second species, *Corymorpha pendula* Agassiz 1862 which Allman (1864) referred to *Monocaulus*, has branched blastostyles and free medusae (this with some doubts, see Kramp, 1949), or at least medusoids. For this species we retain the generic name *Corymorpha* M. Sars 1835, as was also done by Fraser (1944) and Calder (1975) (Table 1).

In order to find specific differences between *Monocaulus* and *Corymorpha* we investigated twenty-one Corymorphinae originally described as new species using eleven groups of morphological characters such as: (1) presence and position of anchoring filaments on caulus; (2) presence or absence and position of solid papillae; (3) presence,

Table 3. Gonophore, blastostyle and nematocyst features of *Monocaulus* and *Corymorpha.*

species	gonophores					blastostyles		nematocysts				
	number	size [mm]	eume-dusoid	crypto-medu-soid	styloid	un-branched	branched	desmo-nemes	steno-teles	atrich. isorhiza	an-isorhiza	micr.bas. mastigo-phores
M. arctica	?	0.6–0.7	–	+	–	22	–	?	?	?	?	?
M. atlantica	60?	1–1.9	–	+?	–	10	–	?	?	?	?	?
M. glacialis	>300	1–1.5	–	+	–	30–35	–	+	+	–	+?	–
M. groenlandica	>300	1?	–	+	–	9–40	–	+?	+	–	+?	–
M. microrhiza	15–40 per blas-tostyle	0.5–1	–	+	–	30–70	–	+	+	–	+?	–
M. parvula	15–40 per blas-tostyle	0.3–1	–	+	–	15–20	–	+	+	–	+?	–
M. purpurea	100?	1–2.4	–	+	–	+	–	?	?	?	?	?
M. sarsii (Bon.)	110?	1–2.5	–	+	–	10	–	?	?	?	?	?
M. socia	8–10 per blas-tostyle	1.2–2	–	+	–	18–32	–	?	?	?	?	?
M. spitzbergensis	?	1?	–	+	–	12	–	?	?	?	?	?
C.? bigelowi	?	?	free	–	–	–	+?	+	+	+?	+	+?
C. carnea	350–500 per blas-tostyle	0.4?	free	–	–	–	40	?	?	?	?	?
C. forbesi	about 10 per blasto style?	1–1.8?	free	–	–	–	+	+	+	+	+	+?
C. januari	30 mature?	0.5–0.8	free	–	–	–	25–63	+	+	+	+	+
C. nana	?	?	free				+					
C. nutans	about 10 per blasto style?	1–2	free	–	–	–	15–20	+	+	–	+	+
C. palma	?	?	free	–	–	–	+	?	?	?	?	?
C. pendula	10? per blas-tostyle	0.3–0.5	free	–	–	–?	10?	?	?	?	?	?
C. sagamina	>100 per blastostyle	0.5?	free	–	–	–	16	?	?	?	?	?
C. sarsii (Steen.)	many	?	+?	–	–	–	+?	?	?	?	?	?
C. tomoensis	?	?	free	–	–	–	+	?	?	?	?	?

position, visibility and length of the endodermal canals within the caulus; (4) perisarc coverage of caulus; (5) internal structure of the tentacles; (6) nematocyst distribution on tentacles; (7) constriction between polyp 'head' and hydrocaulus; (8) presence or absence of gastrodermal diaphragm on level between oral and aboral tentacles within the polyp 'head'; (9) presence or absence of free medusae and type of gonophore construction; (10) presence or absence of blastostyles and, in case there are, whether or not they are branched; (11) types of nematocysts; (see Tables 1–3).

The analysis of these characters allows us to give a new, more detailed diagnosis of the genus *Monocaulus* and to separate it from *Corymorpha*:

(1) From the literature and examination of the specimens listed below, anchoring filaments are present on the basal part of the caulus in both genera (Table 1).

(2) Solid papillae on the caulus are absent in all investigated *Monocaulus* species, but partly present at the middle or at the base of the caulus in *Corymorpha* (Table 1); typically, such papillae are found below the polyp 'head' on the caulus of *Gymnogonos*

ameriensis (Stepanjants, 1979) and other *Gymnogonos* species (Stepanjants & Svoboda, 1999).

(3) Both genera have longitudinal entoderm canals, but in species with strong pigmentation or thick, opaque perisarc they are inconspicuous and therefore not always described (Table 1).

(4) The extent of the perisarc coverage cannot be concluded from preserved specimens, not even from specimens sampled alive, but only from *in situ* observation: in *M. microrhiza* the upper part of the caulus is naked (Fig. 2c), but in *M. parvula* the caulus is covered over its full length (Fig. 2e), as is also the case in *Corymorpha nutans* M. Sars (A. Svoboda, unpublished).

(5) The three species of *Monocaulus* studied histologically – *M. groenlandica, M. microrhiza* and *M. parvula* – have hollow oral and aboral tentacles, as has *C. nutans* (A. Goldschmid & A. Svoboda, unpublished).

(6) Most species have filiform oral and aboral tentacles; exceptionally, *C. nutans* also has moniliform oral and aboral tentacles and *C. forbesi* only moniliform oral tentacles.

(7) Constrictions between hydranth and caulus are known from living and preserved polyps of all *Monocaulus* (more or less developed; Fig. 2e) and *Corymorpha* species (Svoboda, 1973: figs. 1a, b, c).

(8) According to the literature and investigations of thin sections, a diaphragm is present in both genera (different from *Gymnogonos*, see Kramp, 1933) (see Fig. 1a).

(9) The gonophores of all *Monocaulus* species are cryptomedusoid (Figs. 1b, c), the *Corymorpha* species have free medusae or at least eumedusoids (Fig. 1d, Table 3).

(10) All presented species bear blastostyles (different from *Gymnogonos*). In all *Monocaulus* species the blastostyles are unbranched (Figs. 1b-c), but branched in *Corymorpha*, (Fig. 1d, Table 3).

(11) Insufficient data are available to definitively separate both genera based on our present state of knowledge of nematocysts.

The characters presented and their differences in *Monocaulus* and *Corymorpha* allow us to conclude that the general differences between these genera are in (1) unbranched (*Monocaulus*) versus branched (*Corymorpha*) blastostyles and (2) sedentary cryptomedusoids (*Monocaulus*) versus eumedusoids or liberated medusae (*Corymorpha*). The remaining differences are less distinct, as for example the presence of only filiform tentacles in *Monocaulus* and filiform or moniliform tentacles in *Corymorpha,* or the red-orange-brown colour of preserved polyps of *Monocaulus* and the colourless preserved polyps in *Corymorpha*. In connection with the last character there is some doubt concerning inclusion of *M. glacialis* into the genus *Monocaulus,* although most other characters (Tables 1–3) fit satisfactorily: cryptomedusoids, unbranched blastostyles, filiform tentacles. Therefore, for the present, we have decided to include this species into *Monocaulus*.

Family Corymorphidae Allman 1872
Subfamily Corymorphinae Allman 1872

Genus *Monocaulus* (Allman 1864)

Monocaulos Allman, 1864: 370.
Monocaulus Allman, 1872: 395, 1876: 257 (justified emendation).
Lampra Bonnevie, 1898: 478; Bonnevie, 1899: 18.

Type species (by present designation): *Monocaulus groenlandica* Allman, 1876: 257, plate 9: figs. 7, 8.
Type locality: southern Greenland, Arctic.

Polypoid stage represented by solitary polyps. Caulus is covered by a soft perisarc, species-specifically varying in transparency and degree of coverage. For *Gymnogonos* it could be shown (S. D. Stepanjants, A. Svoboda, T. O. Napara & B. A. Anokhin, unpublished data) that the perisarc is secreted by granular epidermis cells of the papillae distributed around the the polyps head base. Such head papillae are absent in *Monocaulus* but similar ones, arranged at the the base of the caulus and producing the anchoring filaments, may additionally supply the saccharids for the perisarcal tube.

The polyp 'head' is more or less clearly demarcated from the hydrocaulus. The oral tentacles are hollow, clearly filiform or slightly moniliform and distributed in several compact whorls. The aboral tentacles are hollow, filiform or slightly moniliform and arranged in one whorl. A diaphragm between polyp's oral and aboral tentacles of the 'head' is present (Fig. 1a). The constriction between the polyp's 'head' and hydrocaulus is not always distinct. Longitudinal canals of the parenchymatic endoderm of the hydrocaulus, distributed along the total hydrocaulus, are more clearly visible at its basal half. The basal part of the hydrocaulus bears many thin rooting filaments. No solid papillae exist on the polyp's 'head'. The reproductive stage is represented by solitary or groups of stalked gonophores attached to unbranched blastostyles (Figs. 1b, c). Blastostyles are distributed along the area between oral and aboral tentacle whorls in several compact rows. Gonophores are cryptomedusoid. Most preserved *Monocaulus* representatives are stained with fading-resistant pigments, although several of them are colourless alive getting stained not until their preservation (Figs. 2a-f). The colour is contained in numerous orange, purple, brown or black pigment granules in ectoderm and endoderm cells, and is resistant against bleaching for at least 100 years. It probably belongs to the phenolic tyrosine-tryptophane group of pigments. Living specimens are mostly colourless and transparent, as for instance *M. groenlandica,* or only faintly pigmented, as for example the proboscis and gonophores of *M. parvula,* or dark brown to black in polyps of *M. microrhiza*. After damage in the trawl ("stone washing"), *M. microrhiza* appears as if smearded by discharged octopus ink (Fig. 2d; Octopoda are very common in the Weddell Sea) – but this black dye originates from its own epidermal cells. Exceptionally, *M. glacialis* polyps (Fig. 1c: 1–3) remain colourless after preservation. Living *M. parvula* and *M. groenlandica* are practically colourless but stain deeply orange after preservation in ethanol or formaldehyde.

Monocaulus species are only known from the Arctic, the Antarctic and high boreal zones with water temperatures between +4° and -1.8 °C. In the Arctic they are found between 0–2000 m depth, but most of them below 100 m; in the Antarctic they mostly were found between 0–160 m, rarely down to 700 m depth.

Two *Monocaulus* species are re-described below: *M. microrhiza* (Hickson & Gravely, 1907) and *M. parvula* (Hickson & Gravely, 1907); the data result from the investigations of old and new Antarctic collections and literature. The Arctic species presented here (without diagnosis) should facilitate the comparison with those from the Antarctic.

1. Antarctic species

Monocaulus microrhiza (Hickson & Gravely 1907) (Figs. 2c, d; Tables 1–3)

Lampra microrhiza Hickson & Gravely, 1907: 18, pl. 2, fig. 14; Stepanjants & Svoboda, 1999: 48, pl. 2, fig. 7.

Material investigated: Syntypes; **BMNH**: No. 1907. 8. 20.30, from 2 specimens [according to Hickson & Gravely (1907)] only 1 was found in the collection. "Discovery" Expedition, McMurdo Bay, off the Barrier, 540 m, 27. 1. 1902. – **RMNH:** Coel. No. 29 217, 1 large specimen, "Polarstern" Expedition ANTVIII/5, Weddell Sea, St. 16–454, 71°4.6′S-11°41.8′W, 278–237 m, 26. 1. 1990. – Coel. No. 29 218, 1 large specimen, "Polarstern" Expedition ANTVIII/5, Weddell Sea, St. 16–468, 74°43.2′S-26°20.3′W, 476–470 m, +0.8 °C, 9. 2. 1990. – Coel. No. 29 219, 1 large and 2 small fragmented specimens, "Polarstern" Expedition ANTVIII/5, Weddell Sea, St. 16–484, 75°17.5′S-55°59.9′W, 441–441 m, -1.7 °C, 16. 2. 1990. – Coel. No. 29 220, 1 specimen, "Polarstern" Expedition ANTVIII/5, Weddell Sea, St. 16–490, 73°42.1′S-22°39.0′W, 629–613 m, -0.2 °C, 21. 2. 1990 (photograph Fig. 2d).

Syntype redescription: The spirit-preserved specimen has a black-brown colour, supporting Bonnevie's opinion that preserved "*Lampra*" maintain their colour for many years. The caulus is covered loosely by 'chitinous' shrunken perisarc. From the base of the caulus arise numerous delicate perisarcal rooting processes for attachment. Endodermal canals are poorly visible. The hydranth 'head', which is not clearly separated from the hydrocaulus by a constriction, has 40–50 aboral filiform and hollow tentacles of about 40 mm length arranged in one row; the oral tentacles (about 7 mm long) are arranged in several indistinct whorls. The few free oral tentacles are also filiform and hollow. The zone between the tentacles whorls is filled with the compressed mass of blastostyles, whether branched or unbranched could not be ascertained.

Measurements (in mm): total length of polyp 65; polyp 'head' 12; maximum diameter of 'head' 15; diameter of hydrocaulus 4–6; length of oral tentacles 3–5; length of aboral tentacles 25–40.

Full description: Living polyps have a greyish to black-brown colour (spirit-preserved specimens) and are tightly covered by greyish, more or less transparent, firm perisarc which only leaves free the black 'neck' region of the caulus. In contrast to *M. parvula,* the perisarc is often covered by small invertebrates and by detritus, resembling the tubes of *Cerianthus* species (Anthozoa). Locally (Cape Norvegia, steep slope between 62–145 m depth), specimens have even a bright pink caulus (M. Rauschert, photographs, pers. comm.). In preserved specimens it is possible to see longitudinal endodermal canals inside the hydrocaulus, appearing more clearly at its basal half. The polyp 'head' is not clearly demarcated from the hydrocaulus. The basal part of the hydrocaulus is covered by many thin perisarcal rooting filaments. The greyish to black polyp 'head' has an oral and aboral set of tentacles. The hollow, filiform, relatively short oral tentacles are arranged in several compact rows; their number ranges, according to polyp size, from 100 to 200; about 30–50 much longer aboral tentacles are arranged in one single row; they are also hollow and filiform. The unbranched blastostyles (30–70) are distributed in the area between oral and aboral tentacles whorls in at least two rows. The largest individuals have up to 4 compact blastostyle rows: the largest, the more mature blastostyles are next to the oral tentacles. Each blastostyle is covered by stalked gonophores (about 15–40 each), which are white to greyish, elongate-oval cryptomedusoids. In specimens with an open oral aperture and in sections of the hydranth a diaphragm is visible.

Measurements (in mm): polyp: total length 100–180; 'head' length 10–20; maximum diameter of 'head' 15–20; diameter of hydrocaulus 4–6; length of oral tentacles 1.5–10; length of aboral tentacles 25–70; blastostyle length 3–12; gonophore length 1.5–2; gonophore diameter 0.5–1.0.

The species is known from the Ross and Weddell Seas; it occurs probably circumantarctic at depths between 200–460 m and temperatures from -1.7 °C to + 0.8 °C. Gutt *et al.* (1998; pers. comm.) found numerous specimens in the eastern Weddell Sea, where around the Atka Iceport the sea floor is heavily scraped by grounded icebergs. Gutt's *in situ* slides show a high population density by recolonization of iceberg scours of up to 1 individual per m. Nothing is known about the seasonality of gonophore ripening or the life span of the individuals. Juveniles settle also occasionally on rooting filaments of mature specimens (photographs by M. Rauschert, pers. comm.).

Monocaulus parvula (Hickson & Gravely 1907) (Figs. 2e, f; Tables 1–4)

Lampra parvula Hickson & Gravely, 1907: 17, pl. 3, figs. 15, 16; pl. 4, fig 35; Stepanjants & Svoboda, 1999: 48, pl. 2, fig. 6.
Corymorpha parvula Stepanjants 1979: 22, pl. 2, fig. 5.

Material investigated: Syntypes; **BMNH**: No. 1907.8.20.10, 6 small and medium-sized specimens, "Discovery" Expedition, McMurdo Bay, off Hut Point and Flagon Point, 27. 9. 1902. **ZIN RAS:** SAE 11, several juvenile specimens, St. A/19, Davis Sea, Isl. Stroiteley, vertical rock, 35 m, 23. 12. 1965. – SAE 11, several juvenile specimens, St. B/-, Davis Sea, Isl.Tokarev, vertical rock, 5 m, 17. 1. 1966. – SAE 11, St. B/68, several juv. specimens, Davis Sea, Isl. Tokarev, 17 m, rock, 22. 1. 1966. – SAE 11, several juvenile specimens, St. G/73, Davis Sea, Mabus Cape, rock, 15 m, 31. 1. 1966. – SAE 11, several juvenile specimens, St. G/75, Davis Sea, Mabus Cape, rock, 10 m, 31. 1. 1966. – SAE 11, several juvenile specimens, St. G/-, Davis Sea, Mabus Cape, rock, depth 3–6 m, 1. 2. 1966. – SAE 11, 2 mature and 6 juvenile specimens attached to rooting filaments, St. D/ 82, Davis Sea, Mabus Cape, vertical rock, 35 m, 12. 2. 1966. – SAE 13, several juvenile specimens, St. 20, Davis Sea, Mirny, Fulmar Isl., vertical rock, 15–40 m, 13. 12. 1967. – SAE 16, several ju-

Table 4. Measurements (all in mm) of the polyps of the type series of *Monocaulus parvula.*

specimen	total length	head length	head diameter	hydranth diameter
1	16	3	4.5	–
2	7.5	1.6	1.8	2.5
3	10	1.2	1.2	2.5
4	6.5	1.0	1.0	2.0
5	10	1.3	1.4	1.5
6	–	1.8	2.0	–

venile specimens, St. 3589, Sodruzestva Sea, Amery Glacier, rock, 20 m, 17. 2. 1972. – SAE 16, several juvenile specimens, St. 3556/161, Sodruzestva Sea, Amery Glacier, shingle, 25 m, 18. 2. 1972. – SAE 16, several juvenile specimens, St. 591/163, Sodruzestva Sea, Amery Glacier, rock, 45 m, 19. 2. 1972. – SAE 16, 7 juvenile specimens, St. 3604/164, Sodruzestva Sea, Amery Glacier, rock, 35 m, 19. 2. 1972. – SAE 16, several juvenile specimens, St. 3639/169, Sodruzestva Sea, Amery Glacier, shingle, 30 m, 20. 2. 1972.

RMNH: Coel. No. 29 221, 6 small specimens, 1 medium-sized specimen, "Polarstern" Expedition ANT VIII/5, Weddell Sea, St. 16–405; 76°31.3′S-52°36.8′W, 377 m; 7. 1. 1990. – Coel. No. 29 222, 1 polyp fragment without base (photograph Fig. 2f), "Polarstern" Expedition ANT VIII/5, St. 16–421, 75°13.6′S-27°45.7′W, 400–430 m, +1.0 °C, 17. 1. 1990. – Coel. No. 29 223, 3 specimens in bad condition, "Polarstern" Expedition ANT VIII/5, St. 16–475, 76°51.4′S-49°27.4′W, 282–281 m, -1.8 °C, 13. 2. 1990. – Coel. No. 29 224. 1 mature specimen, "Polarstern" Expedition ANT VIII/5, St. 16–477, 76°28.2′S-53°2.8′W, depth 440–430 m, 14. 2. 1990. – Coel. No. 29 225, 5 specimens, "Polarstern" Expedition ANT VIII/5, St. 16–486, 76°30.9′S-52°6.7′W, 343–341 m, -1.8 °C; 17. 2. 1990.

Syntypes redescription: We describe here the largest polyp of the series of 6 specimens. It is totally coloured reddish-orange, including the thin, opaque perisarc. The head of the polyp is clearly separated from the hydrocaulus. There are 80–84 filiform oral tentacles in 7 compact rows. Broken tentacles show them to be hollow. Aboral tentacles (24–25 in number) are arranged in 1 row are also hollow. At the zone between oral and aboral tentacles there are about 12–14 short, unbranched blastostyles with 8 immature gonophores of indistinguishable construction. A vague longitudinal pattern can be distinguished on the surface of the hydrocaulus, probably representing endodermal canals. They are more clearly visible along the lower half of the hydrocaulus. Numerous thin rooting filaments originate at the base of the hydrocaulus. The poor state of conservation prohibited preparing sections to check the presence or absence of a diaphragm.

Measurements (in mm): polyp length 16; 'head' length 3; hydrocaulus length 13; maximum diameter of polyp 'head' 4.5; maximum diameter of hydrocaulus 2.5; diameter of the middle part of caulus 1.1; length of broken oral tentacles 0.4; blastostyle length 0.8; immature gonophore length 0.1–0.2.

The other 5 specimens of the type material are smaller and of the same construction (for measurements see Table 4). Specimen No. 6 has remnants of aboral tentacles. They are slightly moniliform, about 1.5 mm in length.

As already mentioned, the type material is in a poor state of preservation. Our more recent formaldehyde-preserved samples are in much better histological condition. Below, we present a fuller description and measurements of this species based on the analysis of all investigated material.

Full description: Solitary polyps with a distinctly demarcated constriction between 'head' and hydrocaulus (see also *in situ* colour photograph). Living polyps white, in fully mature specimens gonophores pale-orange and oral tentacles faintly violet, but completely reddish-orange after formaldehyde or alcohol preservation. According to *in situ* photographs a thin opaque-white perisarc completely covers the hydrocaulus, becoming loose after preservation. As in all Corymorphidae there are oral and aboral tentacles. The first ones (about 50–200) are hollow, filiform (only shortest are capitate) and grouped in several compact whorls around the hypostome. The stiff parenchymatic aboral tentacles (about 20–50) are arranged in one row. No papillae present at the base of polyp 'head'. Longitudinal endodermal gastral canals are not clearly visible. They are distributed along the full length of the hydrocaulus, but sometimes only visible in its basal part. Numerous thin perisarcal rooting filaments originate at the base of the hydrocaulus. Gonophores of immature specimens are arranged in compact clusters on short unbranched blastostyles, distributed in 2 compact rows between oral and aboral tentacle whorls (12–50). Mature specimens have long, unbranched blastostyles with 15–40 gonophores, more or less regularly arranged in different planes on blastostyle surface. The gonophores, each located on a short pedicel, are cryptomedusoid.

Measurements (in mm): polyp length 20–110; polyp 'head' 3–15 ; hydrocaulus length 12–95; maximum 'head' diameter 1.5–10; hydrocaulus diameter at the base 1.5–11; diameter of the middle part of hydrocaulus 0.8–2; oral tentacle length 0.3–1.5; aboral tentacle length 1.5–25; blastostyle length 0.5–6; gonophore length 0.3–1.0.

The distribution can be characterized as circumantarctic (Stepanjants, 1979). The species is known from depths of 3–450 m, at a temperature range from -1.8 °C to +1.0 °C. There is only scarce information concerning the ecology and biology of the species. Surprisingly, all collections yielded numerous young individuals, which are comparatively rare in *M. microrhiza*. Settlement was often observed on the rooting filaments of larger specimens. Hickson & Gravely (1907) figured mature female gonophores from a relatively small polyp of only 13 mm caulus length, showing that maturity is attained before the specimens grow to full size.

2. Arctic species

Monocaulus glacialis (M. Sars 1859) (Fig. 1 c: 1–3, Tables 1–3)

Corymorpha glacialis M. Sars, 1859: 96–105; Broch, 1910: 140; Broch, 1916: 32–33, text-fig. H; Spassky, 1929: 5–6; Naumov, 1960: 212–213, figs. 99, 100 [not *Monocaulos glacialis,* Allman, 1864: 370; Allman, 1872: 396].
Lampra glacialis Stepanjants & Svoboda, 1999: 48, pl. 1, fig. 4.

Material investigated: Syntypes; **Zool. Mus. Oslo**: No. B1195 (?), 2 specimens. – **ZIN RAS:** 2 specimens, "Zarnitsa", Arctic Ocean, Novaya Zemlja, Chernaja Bay, 5–10 m, 5. 9. 1925. – 2 specimens, "Ermak", Franz-Josef Land, St.63, 79°55′N-49°48′E, 49 m, 27. 7. 1901. – 1 specimen, Floating Marine Institute (PlavMorNIn – PMNIN), St. 255, The Barents Sea, 70°30′N-38°51′E, 165 m, 5. 7. 1925.

Monocaulus groenlandica Allman 1876 (Figs. 2a, b)

Monocaulos glacialis Allman, 1864: 370; Allman, 1872: 396.
Monocaulus groenlandica Allman, 1876: 257, pl. 9, figs. 7, 8.
Corymorpha groenlandica Broch, 1916: 33–37, text-fig. 1; Spassky, 1929: 6; Naumov, 1960: 213–214, fig. 101.
Lampra groenlandica Stepanjants & Svoboda, 1999: 48, pl. 1, fig. 5.

Material investigated: ZIN RAS: numerous specimens in bad condition, "Sedov", St. 16, Franz-Josef Land, 36–32.5 m, 17. 8. 1929. – 2 mature specimens in good condition, "Andrey Pervosvannyi", St. 135, 298–293 m, 08. (20.)07.1898. – 1 specimen in bad condition, "SP-3", St. 133. Laptev Sea, 432 m, 30. 8. 1948. – 1 specimen, "NIS-6", St. 64, Norwegian Sea, 425 m, 17. 6. 1954. – 2 specimens in bad condition, "Litke", St. 28; north of Franz-Josef Land, 80°32′N-09°55′E, 749 m, 26. 9. 1955. – several specimens in good condition, "Tichookeanskyi", Kurile Exp., (?)1987, St. 297/53, Isl. Ushishir, 47°30′N-152°50′E, 150 m. – several specimens in good condition, "Tichookeanskyi", Kurile Exp. (?) 1987, St. 389, Severgina Strait, Kurile Islands, 50 m. – **RMNH:** Coel. No. 29 226, 1 mature male specimen, "Polarstern" ARK XIII/22, 81°59.24′N-0.5°44.98′E, St. 44–088, 2. GKG, Stechkasten partiell, 961 m, 26. 7. 1997.

Lampra sarsii Bonnevie 1898 (Fig. 1b: 5, Tables 1–3)

Lampra sarsii Bonnevie, 1898: 478, pl. 26, fig. 21; Bonnevie, 1899: 18, pl. 2, fig. 3.

Material investigated: Syntypes; **Zool. Mus. Oslo**: 2 specimens, St. 248, 8. 8. 1877, 67°56′N-4°11′E, 1423 m, 1.28 °C.

Lampra atlantica Bonnevie 1898 (Fig. 1b: 1, 2)

Lampra atlantica Bonnevie, 1898: 479; Bonnevie, 1899: 21, pl. 2, fig. 4.
Corymorpha groenlandica Naumov, 1960: 213 (part).

Material investigated: Syntypes; **Zool. Mus. Oslo**: 8 specimens, St. 40, 19. 7. 1876. 63°22′N-5°29′E, 2222 m, 1.2 °C.

Lampra purpurea Bonnevie 1898 (Fig. 1b: 3, 4)

Lampra purpurea Bonnevie, 1898: 478; Bonnevie, 1899: 21, pl. 3, fig. 1.
Corymorpha groenlandica Naumov, 1960: 213 (part).

Material investigated: Syntypes; **Zool. Mus. Oslo**: 5 fragments, St. 137, 21. 6. 1877.

Monocaulus sp. (Fig. 1b: 6)

Material investigated: Zool. Mus. Oslo: St. 96. 16. 06.1877.

Discussion

Focussing on the redescription and classification of the two interesting Antarctic species *M. microrhiza* and *M. parvula,* the general differences from the other Corymorphinae are (1) type and (2) arrangement of cryptomedusoid gonophores on blastostyles; (3) unbranched blastostyles; (4) both Antarctic species and the Arctic *M. groenlandica* are brightly coloured in preserved state (only *M. glacialis* remains colourless), whereas all other corymorphid species remain colourless; (5) there may be differences in the nematocyst composition: two types of nematocysts (atrichous isorhiza and microbasic mastigophores) that are absent in *Monocaulus* seem to be present in most *Corymorpha* species as far as this can be concluded from the literature.

We therefore agree with Bonnevie's separation of this species from the other Corymorphinae into her genus *Lampra.* The genus name *Lampra* which she applied is preoccupied and is here replaced by the valid genus name *Monocaulus* Allman 1864. From a detailed study of Bonnevie's material (Oslo Museum) and its comparison with the other Arctic species we conclude that there are only two Arctic species of *Monocaulus*: *M. glacialis* and *M. groenlandica*.

Tables 1–3 demonstrate that there are no substantial morphological differences between the two Antarctic and the two Arctic *Monocaulus* species. Below we present an identification key of the species, based only on specific colour:

1 (2) Preserved polyps are colourless .... *M. glacialis*
2 (1) Preserved polyps are coloured
3 (4) Predominant colouration of living polyps
is black to brown-violet .... *M. microrhiza*
4 (3) Predominant colouration of living polyps is different
5 (6) Gonophores of living polyps are pale-orange .... *M. parvula*
6 (5) Gonophores of the living polyps are white .... *M. groenlandica*

It would be interesting in future studies to search for other differences, for example in chromosome numbers and karyotype structures.

The records of *Monocaulus* from Arctic, Antarctic and high boreal areas indicate that this is a bipolar genus with two species on each hemisphere living at water temperatures between +2 °C to -2 °C (Stepanjants *et al.*, 1996, 1997). On the other hand, all known *Corymorpha* species live in the warmer regions of oceans.

Conclusions

1. The two species *Lampra microrhiza* and *L. parvula*, originally attributed to the genus *Lampra*, later to *Corymorpha*, are here referred to the genus *Monocaulus*.
2. The general characters separating *Monocaulus* from the other corymorphid genera are the distribution of cryptomedusoid gonophores on unbranched blastostyles.
3. Investigation of several species of *Monocaulus* from the Arctic (*M. arctica, M. atlantica, M. glacialis, M. groenlandica, M. purpurea* and *M. spitzbergensis*) indicate that only two species are valid: *M. glacialis* and *M. groenlandica*.
4. The distribution of the above-named Arctic and Antarctic species makes it possible to consider *Monocaulus* as a bipolar genus.

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