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A review of the genus *Muusoctopus* (Cephalopoda: Octopoda) from Arctic waters

Alexey V. Golikov^{1*}, Gudmundur Gudmundsson², Martin E. Blicher^{3,4}, Lis L. Jørgensen⁵, Ekaterina I. Korneeva⁶, Steinunn H. Olafsdottir⁷, Elena I. Shagimardanova⁸, Leyla H. Shigapova⁸, Denis V. Zakharov⁹, Olga L. Zimina^{9,10} and Rushan M. Sabirov⁶

Abstract

We report two Arctic species of incirrate octopods new to science. One is formally described here as *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov **sp. nov.** while the other, *Muusoctopus* sp. 1, is not formally described due to a limited number of samples (all are immature individuals). These two species differ from each other, and from other *Muusoctopus*, especially in: 1) absence of stylets (in *M. aegir* **sp. nov.**); 2) proportions of mantle and head; 3) funnel organ morphology (W-shaped with medial and marginal limbs of equal length in *M. aegir* **sp. nov.**, or medial are slightly longer; VV-shaped with medial limbs slightly longer and broader than marginal in *Muusoctopus* sp. 1); 4) sucker and gill lamellae counts; 5) relative arm length and sucker diameter; and 6) male reproductive system relative size and morphology. Species of *Muusoctopus* now comprise four of 12 known Arctic cephalopods. Additionally, this study provides: a) new data on the morphology and reproductive biology of *M. johnsonianus* and *M. sibiricus*, and a diagnosis of *M. sibiricus*; b) the equations to estimate mantle length and body mass from beak measurements of *M. aegir* **sp. nov.** and *M. johnsonianus*; c) a cytochrome *c* oxidase subunit I gene barcode for *M. sibiricus*; d) new data on the ecology and distribution of all studied species; and e) a data table for the identification of northern North Atlantic and Arctic species of *Muusoctopus*.

Keywords Biogeography, *COI*, Deep-sea, Ecology, Incirrata, Morphology, North Atlantic, Reproduction, Slope, Taxonomy

*Correspondence:

Alexey V. Golikov
golikov.ksu@gmail.com

¹ GEOMAR Helmholtz Centre for Ocean Research Kiel, Dusternbrooker Weg 20, 24105 Kiel, Germany

² Collections and Systematics Department, Icelandic Institute of Natural History, Urriðaholtssræti 6–8, 210 Gardabaer, Iceland

³ NIRAS A/S, Ceres Allé 3, 8000 Aarhus, Denmark

⁴ Greenland Institute of Natural Resources, Greenland Climate Research Centre, Kivioq 2, 3900 Nuuk, Greenland

⁵ Institute of Marine Research, Tromsø Department, P.O. Box 6606 Langnes, 9294 Tromsø, Norway

⁶ Department of Zoology, Kazan Federal University, Kremlyovskaya Str. 18, 420008 Kazan, Russia

⁷ Marine and Freshwater Research Institute, Demersal Division, Fornubúðir 5, 220 Hafnarfjörður, Iceland

⁸ Kazan Federal University, Extreme Biology Laboratory, Volkova Str. 18, 420021 Kazan, Russia

⁹ Zoological Institute of Russian Academy of Sciences, Laboratory of Marine Research, Universitetskaya Nab. 1, 199034 Sankt-Petersburg, Russia

¹⁰ Murmansk Marine Biological Institute, Laboratory of Zoobenthos, Vladimirska Str. 17, 183010 Murmansk, Russia



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Background

The majority of octopods of the suborder Incirrata Grimpe, 1916 [1] are carnivorous benthic animals with fast growth rates and short life cycles. This group is an important component of the seafloor ecosystems from polar to tropical areas, from littoral to bathyal depths [2, 3]. Most incirrate octopods belong to the superfamily Octopodoidea Orbigny, 1840 [4], in which five of six families are benthic [5, 6]. These include the Bathypolypodidae Robson, 1929 [7], Eledonidae Rochebrune, 1884 [8], Enteroctopodidae Strugnell, Norman, Vecchione, Guzik & Allcock, 2014 [9], Megaleledonidae Taki, 1961 [10] and Octopodidae Orbigny, 1840 [4–6]. There are more than 300 species of Octopodoidea, many of which have not been formally described [5, 6]. The commercial importance and catch rates of octopods are increasing worldwide [11], along with an upsurge in other anthropogenic influences on the oceans [12]. This can potentially lead to species extinction outpacing biodiversity assessment and description [13], especially given the global decrease in taxonomic studies [14]. Moreover, these five families of benthic octopods include many deep-sea representatives [3, 5, 15], which are particularly understudied and prone to environmental and anthropogenic stresses, such as those described in [16, 17].

The taxonomy, life histories, and distributions of deep-sea North Atlantic cephalopods are not well known [18]. Deep-sea octopods of the genera *Bathypolypus* Grimpe, 1921 [19] and *Muusoctopus* Gleadall, 2004 [20] (formerly *Benthooctopus* Grimpe, 1921 [19]) and *Graneledone verrucosa* (Verrill, 1881) [21] are the most common incirrate octopods in North Atlantic lower shelf and slope areas [22–25]. All lack an ink sac, and *Bathypolypus* and *Muusoctopus* have biserial suckers, whereas *G. verrucosa* has uniserial suckers [23, 26]. Following Muus [23], three of the five species of *Bathypolypus* from North Atlantic waters occur in Arctic waters: *B. arcticus* (Prosch, 1847) [27], *B. bairdii* (Verrill, 1873) [28] and *B. pugniger* Muus, 2002 [23]. Voss and Percy [29] suggested that the holotype of *Benthooctopus piscatorum* (Verrill, 1879) [30], which is the type species of the genus (Grimpe, 1921) [19], belongs to the genus *Bathypolypus*. It was later confirmed to be a junior synonym of *B. bairdii* by Muus [23] and Allcock et al. [26]. The transition of *Benthooctopus* to a junior synonym of *Bathypolypus* resulted in all deep-sea non-*Bathypolypus* biserial inkless octopods lacking a valid genus name [20]. Later, most of them were listed in the genus *Muusoctopus* Gleadall, 2004 [31, 32], which currently includes 27 species [33]. Octopods caught in the North Atlantic and Arctic which were previously assigned to the species *Be. piscatorum* became impossible to assign to any known species [22, 34–54]. Two species of *Muusoctopus*, one new and one resurrected,

were described from the northeast Atlantic by Allcock et al. [26]: *Muusoctopus normani* (Massy, 1907) [37] and *M. johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]. These species are known from slope areas of the North Atlantic from 38°N (*M. johnsonianus* was recently found at 15°N by Luna et al. [55]) to 60°N in the eastern Atlantic, and apparently at about the same latitudes in the western Atlantic and along the Mid-Atlantic Ridge [22, 24–26, 32, 56] [M. Vecchione, pers. comm.; C. Nozères, pers. comm.]. Records in the western Atlantic are largely unpublished, excepting Pratt et al. [25]. The northernmost record of *Muusoctopus* spp. in the northwest Atlantic is the entrance of Ungava Bay at about 60°N [C. Nozères, pers. comm.: photos checked by A.V.G.]. Depth records for *M. normani* and *M. johnsonianus* are 500–1843 m and 797–2540 m, respectively [22, 25, 26, 32, 55–57]. Data on the associated bottom temperatures are absent. Also, *M. normani* is sometimes synonymized with *M. januarii* (Hoyle, 1885) [58] [32]. However, only a single individual of *M. januarii* was analysed in Gleadall [32], whose characteristics do not fully fit *M. normani* [25, 32, 58, 59], and no genetic analysis has been performed on *M. januarii*. Moreover, the known geographical range of *M. januarii* is much further south, i.e., from the Gulf of Mexico to Brazil, and the depth ranges of these species do not coincide [25, 32, 58, 59]. Thus, after comparing *M. januarii* from Toll [59] and *M. normani* from Allcock et al. [26] and Gleadall [32], the present study treats *M. normani* as a separate species.

The northern distributional limits of both *M. normani* and *M. johnsonianus* are the Canada–Greenland and Greenland–Iceland–Faroe Ridges, which coincide with natural borders between biogeographic provinces of the boreal Atlantic and Arctic deep-seas [60, 61]. Records of these species to the north of that border do not exist. An inventory of accepted *Muusoctopus* from Arctic waters includes *M. sibiricus* (Løynning, 1930) [62], which inhabits the Laptev, East Siberian, Chukchi and Beaufort Seas [49–52, 63], and *M. leioderma* (Berry, 1911) [64], found in areas of the Chukchi Sea, adjacent to the Bering Strait [49, 50, 65–67]. Records of other *Muusoctopus* species from the Pacific Arctic are considered misidentifications: 1) *M. profundorum* (Robson, 1932) [43] from the Chukchi Sea [66, 68] is considered to be *M. sibiricus* [50, 63] [I. G. Gleadall, pers. comm.]; 2) *M. hokkaidensis* (Berry, 1921) [69] from the Chukchi Sea [68, 70, 71] is considered to be *Muusoctopus* sp. or *M. sibiricus* [50, 63], with *Muusoctopus* sp. later considered to be *M. sibiricus* as well [I. G. Gleadall, pers. comm.]; 3) ‘Octopus’ from the Chukchi Sea [72] is considered to be *M. sibiricus* in the present study, as it occurs far from the Bering Strait. *Muusoctopus leioderma* records from the Chukchi Sea by Feder et al. [73] are also distant from the Bering Strait. They

most likely belong to *M. sibiricus* and are treated as such in this study. Depth records of *M. sibiricus*, 30–220 m, are associated with bottom temperatures of -1.4 – -1.6 °C [51, 62, 63, 70–72, 74]. Depth records for *M. leioderma*, 38–1760 m (40–80 m in the Arctic) are associated with bottom temperatures of -1.0 – -4.9 °C [50, 65–67].

Records of what had previously been considered *Be. piscatorum* within the Arctic and Subarctic areas are known along the northern slope of the Greenland–Iceland–Faroe Ridge, in the Faroe–Shetland Channel, along the Norwegian slope, at the deep-sea sides of the Svalbard slope, and at the deep-sea side of the Severnaya Zemlya slope [34–36, 40–47, 49–52]. The depth records are 86–2000 m and are associated with a bottom temperature of -0.9 °C [34, 36, 41, 42, 44, 51, 57]. This species was found to be an undescribed species of *Muusoctopus* [75]. We herein describe this species on the basis of a large collection of individuals ($n=37$) and present information on its biology, ecology, and distribution. We also report a second Arctic species to the genus *Muusoctopus*, but refrain from describing it further because of limited material ($n=4$ immature individuals). Additionally, this study provides: a) new data on the morphology and reproductive biology of *M. johnsonianus* and *M. sibiricus*, and a diagnosis of *M. sibiricus*; b) equations for estimation of mantle length (ML) and body mass from beak measurements of the new species of *Muusoctopus* and *M. johnsonianus*; c) a cytochrome *c* oxidase subunit I gene (*COI*), i.e. DNA barcode for *M. sibiricus*; d) new data on the ecology and distribution of all studied species; and e)

a table for identifying northern North Atlantic and Arctic *Muusoctopus* species.

Materials and methods

Sample collection, fixation and storage

Octopuses were collected off Iceland in 1991–2017 by the Icelandic Institute of Natural History, Reykjavik (IINH) and Marine and Freshwater Research Institute, Reykjavik (MFRI); off East and West Greenland in 2016 by the Greenland Institute of Natural Resources, Nuuk (GINR); in the Barents Sea in 2007–2018 by the Institute of Marine Research, Bergen (IMR) and Polar Branch of All-Russian Fisheries Research Institute of Fisheries and Oceanography, Murmansk (PINRO); in the Kara Sea in 2007–2013 by PINRO; and in the Laptev and East Siberian Seas in 2014 by the Murmansk Marine Biological Institute, Murmansk (MMBI) (Fig. 1). Additionally, hitherto unpublished data for one individual referred to *Muusoctopus* sp. from the United States National Museum of Natural History, Smithsonian Institution, Washington (USNM) were provided by A. L. Allcock [A. L. Allcock, unpublished data]. Additional collection acronyms include: Eduard Eversman Zoological Museum of Kazan Federal University, Kazan (ZM KFU); Laboratory of Hydrobiology, Department of Zoology, Kazan Federal University, Kazan (LH KFU); and Zoological Institute of Russian Academy of Sciences, Sankt-Petersburg (ZIAS). Exact locations and associated environmental parameters of stations and details of individuals are provided in ‘Material examined’ sections for each species.

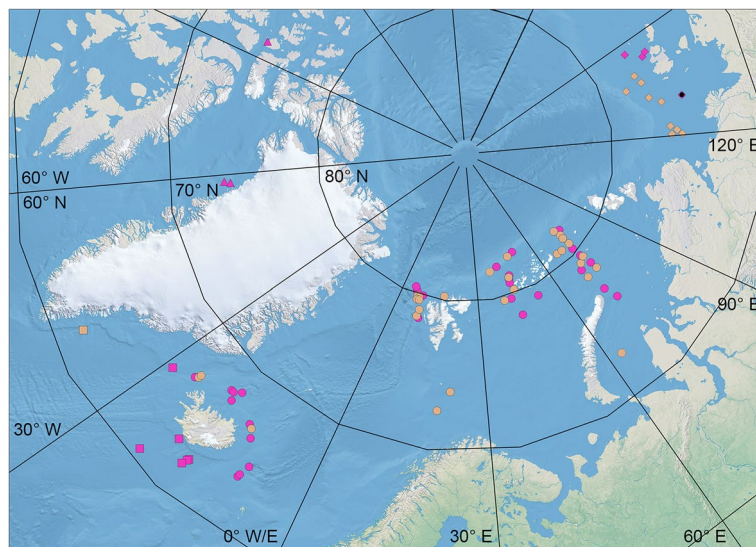


Fig. 1 Sampling locations of *Muusoctopus* Gleadall, 2004 [20] in the Arctic and North Atlantic. Circles = *M. aegir* Golikov, Gudmundsson & Sabirov, **sp. nov.**; squares = *M. johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]; triangles = *Muusoctopus* sp. 1; rhombs = *M. sibiricus* (Løyning, 1930) [62]. Bright magenta color indicates the stations where individuals were analyzed. Pale brown color indicates stations where no individuals were analyzed. The black dot indicates the station where the sample was taken for cytochrome *c* oxidase subunit I gene

Individuals were collected either as bycatch during annual bottom trawl surveys of ground fish stocks (MFRI and GINR), or during scientific research cruises (IINH, IMR, PINRO, and MMBI). Octopods were fixed in 10% formalin onboard. Tissue sample was taken prior to that for DNA analysis from one individual of *M. sibiricus* (LS-L-3). The tissue sample was kept in 96% ethanol in the freezer (-20°C).

Morphological and statistical analyses

Counts, measurements, and indices were made following the general guidelines for cephalopods [76] and previous studies on *Muusoctopus* morphology: in particular, total arm sucker count was employed, not basal half [26, 31, 32, 77]. The beak measurements follow Clarke [78]. The right side was chosen for arms, eyes, and gills, and the left side was used as a substitute in case the right one was unavailable. Values are given as minimum to maximum (mean \pm SE), unless otherwise stated. All indices are related to ML unless otherwise stated, and are always detailed when used for the first time. Maturity stages were assigned on a scale modified from Sauer & Lipinski [79] and Nigmatullin et al. [80], where:

0=juvenile (reproductive system so small it can not be seen without stereomicroscope and is not fully developed; translucent in color);

I=early immature (reproductive system still very small, but fully formed, and visible without stereomicroscope; still translucent in color);

II=late immature (reproductive system is larger than on previous stage and not translucent; in females, ovary is full of similar-sized oocytes);

III=early maturing (reproductive system is large, it occupies 1/3 to half of the volume of the mantle cavity; in males, spermatophoric complex has no sperm inside; in females, oocytes of two different size groups present in the ovary);

IV=late maturing (reproductive system large, it occupies more than a half of the volume of the mantle cavity; in males, spermatophoric complex has sperm inside sperm duct and proximal spermatophoric glands, which can be recognized by their whitening, and tentative spermatophores can be present; in females, large vitellogenic oocytes present in the ovary);

V₁=pre-mature (reproductive system large, it may be even larger than at the previous stage; up to five normal spermatophores present in males; first ripe oocytes present in females);

V₂=mature (reproductive system large, it is proportionally the largest of all the stages; more than five spermatophores present in males; ripe oocytes and possibly post-ovulatory follicles present in females);

V₃=pre-spent (gonad is degraded and of reduced size, the size is roughly as in early maturing individuals; number of spermatophores is equal to that in mature males; residual ripe oocytes present in the ovary or oviducts of females);

and VI=spent (gonad is degraded and of reduced size, the size is roughly as in early maturing individuals or even smaller; residual spermatophores can be present in males; only post-ovulatory follicles and resorbing oocytes present in females).

The products of tentative spermatophorogenesis are treated following Nigmatullin et al. [80]: 1) spermatophore-like structures resemble fragments of spermatophores and do not contain sperm; and 2) tentative spermatophores remind normal spermatophores but are smaller and with different proportions, and either do not contain sperm at all or have lowered sperm concentration. In the main text, sex and maturity stage of the respective individual are reported as a sign (♀ or ♂) and a roman digit.

Radulae were carefully washed with distilled water, dehydrated using ascending ethanol concentrations (70%, 80%, 90%, 96%, and 100%), CO₂ critical-point dried and examined using a Hitachi TM Series SEM scanning electron microscope at the Department of Zoology, Kazan Federal University, Kazan. A regression analysis was used to find equations fitting our data [81], with $\alpha=0.05$ regarded as significant. Analyses were performed in PAST 4.02 [82].

Barcoding COI DNA sequences and analyses

Samples for genetic analyses were only available from single individual of *M. sibiricus* (see 'Species description' below for individual's details). Total DNA was extracted from mantle muscle tissue using a QIAamp DNA Mini Kit (Qiagen GmbH, Hilden, Germany) following manufacturer instructions. Primers used for the COI barcode were 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' and 5'-GGTCAA CAAATCATAAAGATATTGG-3' [83]. The PCR mixture included 12.5 μL of Q5 High-Fidelity 2X Master Mix, 1.25 μL of each primer (10 μM), 7 μL of nuclease-free water and 2 μL of DNA template. Amplification included 30 s denaturation at 98 $^{\circ}\text{C}$ followed by 35 cycles each consisting of 10 s denaturation at 98 $^{\circ}\text{C}$, 15 s of annealing at temperature of 52 $^{\circ}\text{C}$ and 1 min extension at 72 $^{\circ}\text{C}$. A final extension was carried out at 72 $^{\circ}\text{C}$ for 5 min. PCR products were electrophoresed on 1% agarose along with appropriate negative controls and DNA ladder. After purification using a QIAquick PCR Purification Kit (Qiagen GmbH, Hilden, Germany), amplicons were sequenced by Sanger Sequencing using ABI Prism 3 500 (Applied Biosystems, CA, USA).

A phylogenetic tree was constructed using the neighbor-joining method in MEGA 11 [84]. All sequences of *Muusoctopus*, *Benthoctopus*, and *Vulcanoctopus* available in GenBank (<https://www.ncbi.nlm.nih.gov/genbank>) and BOLD (<https://www.boldsystems.org/>) databases

on 18 August 2023 were used; *Octopus vulgaris* (accession number MW560654) was used as an outgroup. All accession numbers are provided on a phylogenetic tree (SM.01 Fig. S1). The most suitable evolutionary model for analysis, as determined in MEGA 11 based on the lowest Bayesian information criterion scores, is Tamura–Nei substitution model with gamma distribution (TN93+G). Bootstrapping was used to verify the validity of trees constructed based on results of multiple sequence alignment with MUSCLE option. Nodes are supported by 100 bootstrap replicates. Because single gene cladograms are unreliable for phylogenetic inferences, e.g. [85], we use them here solely to differentiate the species.

Results

Species descriptions

Family

Enteractopodidae Strugnell, Norman, Vecchione, Guzik & Allcock, 2014 [9].

Genus

Muusoctopus Gleadall, 2004 [20].

Muusoctopus aegir Golikov, Gudmundsson & Sabirov, sp. nov.

(Tables 1, 2, 3, 4 and 5, 9; SM.01 Tables S1, S2; Figs. 2, 3, 4, 5 and 6).

Synonymy *Octopus piscatorum* Verrill, 1879 [30] – Hoyle, 1886 [34]: 91 (partim); Lønneberg, 1892 [35]: 8 (partim); Appelløf, 1893 [36]: 3 (partim).

Polypus piscatorum (Verrill, 1879) [30] – Pfeffer, 1908 [40]: 19, Figs 9, 10 (partim); Russel, 1909 [41]: 446 (partim); Russel, 1922 [42]: 7, pl. II Fig 7 (partim).

Benthooctopus piscatorum (Verrill, 1879) [30] – Robson, 1932 [43]: 224, figs 31, 34, 35 (partim); Grieg, 1933 [44]: 8 (partim); Grimpe, 1933 [45]: 496 (partim); Stephen, 1944 [46]: 253 (partim); Muus, 1959 [47]: 218, fig. 111 (partim); Nesis, 1987a [49]: 316, figs 84G, 84H (partim); Nesis, 1987b [50]: 124 (partim); Nesis, 2001 [51]: 7, fig. 4 (partim).

Muusoctopus sp. – Golikov et al., 2018 [75]: 1; Xavier et al., 2018 [86]: 5; Taite et al. (in press): 8 (in draft).

Not *Octopus piscatorum* Verrill, 1879 [30]: 470; Verrill 1881 [87]: 377, pl. XXXVI figs. 1, 2; Verrill 1884 [88]: 248; Verrill 1885 [89]: pl. XLII fig 5.

Not *Polypus normani* Massy, 1907 [37]: 379.

Not *Polypus piscatorum* (Verrill, 1879) [30] – Massy, 1909 [38]: 13, pl. II figs. 2–4.

Not *Benthooctopus piscatorum* (Verrill, 1879) [30] – Massy, 1928 [39]: 27; Aldrich & Lu, 1968 [48]: 70, pl. 8 figs 1, 2; Nixon, 1991 [53]: 499; O’Shea, 1999 [77]: 192, figs 115A, 115B; Collins et al. 2001 [22]: 112; Nixon & Young, 2003 [54]: 321, figs 31.58, 31.59, 31.61, 31.62.

Not *Benthooctopus* sp. – Collins et al. 2001 [22]: 112; Bar-rat et al. 2007 [90]: 392.

ZooBank urn:lsid:zoobank.org:act:7110DA04-B684-452D-B285-24B38A63E013.

Material examined Holotype: ZM KFU ZMG SC-9 INV-1 (ЗМиГ КП-9 БП-1): ♀IV, ML 43 mm, BS-319–2012, Stn 319, 82.07°N, 40.42°E, 677 m, bottom temperature (BT) 0.44 °C, 22 September 2012. Paratypes: ZM KFU ZMG SC-9 INV-2 (ЗМиГ КП-9 БП-2): ♀VI, ML 26 mm, BS-304–2012, Stn 304, 80.77°N, 44.02°E, 280.5 m, BT 0.31 °C, 20 September 2012; ZIAS ZIN 1/306 522–2022: ♂V₁, ML 29 mm, BS-70–1-2018, Stn 70, 79.26°N, 52.32°E, 321 m, BT –0.27 °C, 27 September 2018; ZM KFU ZMG SC-9 INV-3 (ЗМиГ КП-9 БП-3): ♂V₂, ML 30 mm, KS-189–2010, Stn 189, 81.82°N, 75.92°E, 367 m, BT –1.26 °C, 9 September 2010; IINH 37,493: ♀V₃, ML 24 mm, ICL-A13-570–2017, Stn 570, 67.80°N, 19.15°W, 793.5 m, 21 October 2017.

Other material examined Iceland: IINH 37,824, ♂III, ML 27 mm, BIOICE Stn 2789, 67.31°N, 18.39°W, 535 m, BT –0.29 °C, 5 August 1995; IINH 37,828, ♂I, ML 12 mm, BIOICE Stn 2369, 64.67°N, 9.57°W, 970 m, 8 May 1993; IINH 37,819, 2♀IV, ML 32, 28 mm, BIOICE Stn 2516, 66.62°N, 25.39°W, 683 m, BT –0.50 °C, 13 July 1993; IINH 37,821, ♀IV, ML 38 mm, BIOICE Stn 2322, 63.92°N, 10.06°W, 628 m, 3 May 1993; IINH 37,820, ♀III, ML 29 mm, BIOICE Stn 2326, 63.73°N, 10.15°W, 563 m, BT –0.48 °C, 3 May 1993; IINH 37,822, ♀III, ML 21 mm, BIOICE Stn 2033, 66.91°N, 13.50°W, 556.5, BT –0.54 °C, 23 July 1991; IINH 37,825, ♀II, ML 19 mm, BIOICE Stn 3124, 68.16°N, 17.99°W, 875 m, BT 0.33 °C, 22 August 1999; IINH 37,823, ♀II, ML 16 mm, BIOICE Stn 3242, 66.22°N, 11.97°W, 418 m, BT –0.20 °C, 14 July 2001; IINH 37,827, ♀I, ML 8 mm, juvenile (sex indet.), ML 4.5 mm, BIOICE Stn 3659, 67.79°N, 19.61°W, 800 m, BT –0.53 °C, 24 July 2004.

Barents Sea (Laboratory of Hydrobiology (LH), Department of Zoology, KFU): ♂V₂, ML 50 mm, BS-JM-539–2009, Stn 539, 80.22°N, 5.70°E, 704 m, BT –0.55 °C, 15 September 2009; ♂V₂, ML 36 mm, BS-HH-244–2012, Stn 244, 78.49°N, 9.01°E, 534 m, 23 August 2012; ♂V₂, ML 46 mm, BS-HH-264–2012, Stn 264, 80.03°N, 8.44°E, 495 m, 25 August 2012; ♂V₂, ML 28 mm, BS-255–2010,

Table 1 Data on maturing and mature male individuals of *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, **sp. nov.** Immature individuals detailed in SM.01 Table S1

Individual/ character	BIOICE- 2789	BS-JM- 539–2009	BS-HH- 244–2012	BS-HH- 264–2012	BS-255- 2010	BS-70- 1-2018 ^a	BS-70- 2-2018	BS-176- 2017	KS-189- 2010 ^a	KS-27- 1-2007	KS-15- 1-2007
Area	ICL	BS	BS	BS	BS	BS	BS	BS	KS	KS	KS
Maturity stage	Early maturing (III)	Mature (V ₂)	Mature (V ₂)	Mature (V ₂)	Mature (V ₂)	Pre-mature (V ₁)	Late maturing (IV)	Early maturing (III)	Mature (V ₂)	Mature (V ₂)	Pre-mature (V ₁)
ML, mm	27	50	36	46	28	29	24	22	30	46	32
TL, mm	126	n/a	n/a	n/a	134	152	118	102	167	235	139
Ventral ML, mm	26	49	n/a	n/a	21	26	21	18	28	40	28
Mantle width, mm	28	n/a	n/a	n/a	34	32	29	24	40	41	33
Head length, mm	13	n/a	n/a	n/a	12	14	10.5	9	15.5	18	12
Head width, mm	22	n/a	n/a	n/a	25	24	21	18	23	32	26
Eye diameter, mm	11.0	n/a	n/a	n/a	10.0	9.0	7.5	7.5	12.0	16.0	9.0
Lens diameter, mm	2.5	n/a	n/a	n/a	2.8	3.5	2.2	2.0	4.1	4.3	3.2
Funnel length, mm	11.0	n/a	n/a	n/a	10.0	13.5	12.0	9.0	17.0	18.0	14.0
Free funnel length, mm	6.0	n/a	n/a	n/a	5.3	7.5	6.6	4.5	9.0	10.1	7.4
Web depth, mm (min – max)	n/a	n/a	n/a	n/a	17–28	20–26	19–26	14–20	33–36	32–44	24–29
Web formula	n/a	n/a	n/a	n/a	c>b>d>a>e	b>a>c>d>e	b>c>a>d>e	a=c>b=d>e	a=c>b>d>e	c>b=d>a>e	a>b>d>c>e
Arm length, mm (min – max)	82–86	147 ^b	115–117	168–170	89–94	86–104	76–83	67–71	101–111	162–171	86–95
Arm formula	2=3>1>4	n/a	1>2=3>4	1=2>3=4	2>1=3>4	2>1>3>4	1=2>3>4	1=2>3>4	2>3>1=4	1>2>3>4	1>2>3>4
Sucker count (min – max)	94–102	n/a	108–120	n/a	84–90	90–98	84–88	90–98	92–100	100–110	96–100
Sucker diameter (max), mm	3.0	n/a	n/a	n/a	2.5	2.5	2.5	1.7	3.5	3.0	3.3
Gill length, mm	9.0	n/a	n/a	n/a	8.5	9.0	9.0	9.0	10.5	18.0	9.5
Gill lamellae count, outer/inner	8/7	n/a	n/a	n/a	8/7	8/8	8/7	8/7	9/8	8/7	8/7
Hectocotylized arm length, mm	62	113	64	130	63	67	61	50	73	113	71
Hectocotylized arm sucker count	56	n/a	54	n/a	46	54	52	50	54	54	48
Ligula length, mm	5.5	11.0	9.0	11.0	7.0	6.0	5.8	4.0	9.0	12.0	8.0
Ligula width, mm	3.0	n/a	5.0	6.6	4.4	3.8	3.6	1.8	4.8	6.0	3.8
Calamus length, mm	2.2	n/a	3.8	3.9	2.9	1.8	2.1	1.1	3.2	5.2	2.9

Table 1 (continued)

Individual/ character	BIOICE- 2789	BS-JM- 539–2009	BS-HH- 244–2012	BS-HH- 264–2012	BS-255- 2010	BS-70- 1-2018 ^a	BS-70- 2-2018	BS-176- 2017	KS-189- 2010 ^b	KS-27- 1-2007	KS-15- 1-2007
Number of spermatophores	Normal	11	13	22	7 ^c	5	Normal	Spermatophores	20	17	5
Spermatophore length, mm (min – max)	absent ^d	39.0 ^e	36.0–39.1	41.0–45.4	28.1–38.0	35.3–39.4	spermatophores absent	absent	30.3–40.5	41.00–48.0	27.9–34.9

ML mantle length, *TL* total length, *ICL* Iceland, *BS* Barents Sea, *KS* Kara Sea, *n/a* not analyzed

^a paratype; ^b third left arm measured only

^c also had three tentative spermatophores, not measured

^d one tentative spermatophore, length 20.9 mm

^e one spermatophore measured only

^f one fragmented tentative spermatophore

Table 2 Data on maturing, mature and spent female individuals of *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, **sp. nov.** Immature individuals are detailed in SM.01 Table S1

Individual/ character	ICL-A13- 570-2017 ^a	ICL Late maturing (IV)	ICL Late maturing (IV)	ICL Late maturing (IV)	BIOICE- 2516-1	BIOICE- 2516-2	BIOICE- 2322	BIOICE- 2326	BIOICE- 2033	BS-304- 2012 ^a	BS-305- 2012	BS-246- 2010	BS-322- 2014	BS-HH- 259- 2012-1	BS-319- 2012 ^b	KS-201- 2010	KS-28- 2009
Area	ICL	Pre-spent (V ₃)	ICL	ICL	ICL	ICL	ICL	ICL	ICL	BS	BS	BS	BS	BS	BS	KS	KS
Maturity stage										Spent (VI)	Spent (VI)	Spent (VI)	Spent (VI)	Mature (V ₂)	Late maturing (IV)	Spent (VI)	Spent (VI)
ML, mm	24	32	28	38	29	21	110	137	20	25	25	36	20	44	43	52	30
TL, mm	101	135	114	171	137	110	137	137	110	122	122	153	96	n/a	173	218	138
Ventral ML, mm	19	26	24	35	28	20	20	24	20	21	21	31	17	n/a	33	48	28
Mantle width, mm	25	28	28	34	27	25	25	25	25	31	31	40	28	n/a	54	51	36
Head length, mm	10	12	12	17	12	10	10	12	10	12	12	11	8	n/a	14	22	10
Head width, mm	12	24	20	29	23	14	14	14	14	22	22	26	20	n/a	32	31	28
Eye diameter, mm	7.0	11.0	8.0	13.0	10.0	7.0	7.0	7.0	7.0	7.5	7.5	9.5	7.0	n/a	12.0	16.5	9.0
Lens diameter, mm	1.5	2.5	2.0	3.0	2.0	1.4	1.4	1.4	1.4	2.3	2.3	3.2	2.2	n/a	4.5	5.5	2.9
Funnel length, mm	9.5	10.5	12.0	14.0	11.0	11.0	11.0	11.0	11.0	13.0	13.0	14.0	8.0	n/a	15.0	15.0	12.0
Free funnel length, mm	5.0	5.0	6.0	8.0	5.5	5.0	5.0	5.0	5.0	7.2	7.2	7.5	4.0	n/a	8.5	8.5	6.2
Web depth, mm	7-11	16-26	12-18	22-30	n/a	16-18	16-18	16-18	16-18	25-28	25-28	19-33	14-20	n/a	28-37	34-41	22-26
(min - max)																	
Web formula	a=b>c>d>e	a=b>c>d>e	a>b=c>d>e	a>b=c>d>e	a>b=c>d>e	a=b>c>d>e	a=b>c>d>e	a=b>c>d>e	a=b>c>d>e	b>a=c>d>e	b>a=c>d>e	b>c>a>d>e	a>b=c>d>e	n/a	a=b=c>d>e	b=c>c>a>e	b=c>d>a>e

Table 2 (continued)

Individual/ character	ICL-A13- 570-2017 ^a	BIOICE- 2516-1	BIOICE- 2516-2	BIOICE- 2322	BIOICE- 2326	BIOICE- 2033	BS-304- 2012 ^a	BS-305- 2012	BS-246- 2010	BS-322- 2014	BS-HH- 259- 2012-1	BS-319- 2012 ^b	KS-201- 2010	KS-28- 2009
Arm length, mm	61–67	84–91	79–84	98–116	92–96	70–79	85–91	79–83	98–106	64–68	n/a	107–116	122–144	92–98
(min – max)														
Arm formula	2 > 3 > 4 > 1	1 = 2 = 3 > 4	1 > 2 > 3 > 4	2 > 1 > 3 > 4	1 > 2 = 3 = 4	1 > 2 > 3 > 4	1 > 3 > 2 > 4	1 > 2 > 3 > 4	1 > 2 > 3 > 4	1 = 2 > 3 > 4	n/a	1 = 2 > 3 > 4	1 > 2 > 3 > 4	1 = 2 > 3 > 4
Sucker count	94–96	88–92	84–90	90–96	92–98	96–100	88–98	86–90	100–104	88–100	n/a	102–106	92–102	84–96
(min – max)														
Sucker diameter (max), mm	1.5	2.5	2.5	3.5	3.0	2.0	2.2	2.0	3.1	1.4	n/a	4.0	4.0	3.0
Gill length, mm	8.0	7.0	8.0	11.5	12.0	9.0	9.5	11.0	10.5	8.0	n/a	16.5	12.0	10.5
Gill lamel- lae count, outer/ inner	8/8	8/7	8/7	8/7	8/8	9/8	9/8	8/7	9/8	8/7	n/a	8/7	8/7	8/7
Fecundity	71 ^c	121	101	168	112	130	74	89	93	65	n/a	78	73	93

ML mantle length, *TL* total length, *ICL* Iceland, *BS* Barents Sea, *KS* Kara Sea, *n/a* not analyzed

^a paratype

^b holotype

^c this is the only individual for which ripe oocyte length is available, = 12.8 mm

Table 3 Spermatophore number and measurements in *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, *sp. nov.* and *M. sibiricus* (Løyning, 1930) [62]. Values are minimum – maximum (mean ± SE), where applicable

Species/measurement, index or count		<i>Muusoctopus aegir</i> <i>sp. nov.</i>	<i>Muusoctopus sibiricus</i>
# spermatophores		5–22 (12.5 ± 2.4); 7–22 (15.0 ± 2.3) excluding V ₁ males	49 (V ₂), 52 (V ₃)
SL	mm	27.9–48.0 (39.8 ± 0.5)	46.3–63.5 (57.9 ± 1.1)
	% ML	78.0–135.9 (108.1 ± 1.8)	118.7–167.1 (150.6 ± 3.3)
Spermatophore W	mm	0.8–1.4 (1.2 ± 0.04)	0.6–0.8 (0.7 ± 0.03)
	% ML	2.8–3.8 (3.1 ± 0.1)	1.1–1.3 (1.2 ± 0.03)
Head L	mm	0.7–2.6 (1.5 ± 0.1)	0.8–1.3 (1.1 ± 0.1)
	% SL	2.4–6.7 (4.0 ± 0.3)	1.3–2.8 (1.9 ± 0.3)
Ejaculatory apparatus L	mm	14.0–26.2 (19.4 ± 0.7)	26.3–38.2 (32.6 ± 2.5)
	% SL	44.1–58.1 (52.5 ± 0.9)	49.6–61.6 (57.0 ± 2.2)
Cement body L	mm	2.5–7.6 (4.3 ± 0.3)	5.5–6.8 (6.3 ± 0.2)
	% SL	6.7–21.5 (11.7 ± 0.8)	10.4–14.7 (11.2 ± 0.7)
Seminal reservoir L	mm	9.2–15.4 (11.6 ± 0.4)	11.8–21.0 (16.7 ± 1.3)
	% SL	26.1–36.4 (31.4 ± 0.6)	25.5–37.4 (29.5 ± 2.3)
Seminal reservoir W	mm	0.7–1.3 (1.1 ± 0.04)	0.55–0.70 (0.63 ± 0.03)
	% SL	2.5–3.5 (2.9 ± 0.1)	1.0–1.2 (1.1 ± 0.03)
Seminal reservoir volume, mm ³		3.6–20.4 (10.9 ± 1.0)	2.8–6.2 (5.2 ± 0.6)
# of sperm cord whorls		65–98 (77.2 ± 2.7)	59–92 (79.2 ± 5.8)
Sperm cord W, mm		0.10–0.20 (0.16 ± 0.01)	0.15–0.20 (0.19 ± 0.01)
Posterior hollow part	mm	0.1–0.2 (0.11 ± 0.1)	0.1–0.3 (0.2 ± 0.04)
	% SL	0.2–0.5 (0.3 ± 0.02)	0.2–0.5 (0.3 ± 0.1)

ML mantle length, SL spermatophore length, L length, W width

Stn 255, 81.05°N, 44.23°E, 343 m, BT –0.28 °C, 19 October 2010; ♂IV, ML 24 mm, BS-70–2-2018, Stn 70, 79.26°N, 52.32°E, 321 m, BT –0.27 °C, 27 September 2018; ♂III, ML 22 mm, BS-176–2017, Stn 176, 78.47°N, 44.74°E, 226.5 m, BT 0.67 °C, 25 September 2017; ♀VI, ML 25 mm, BS-305–2012, Stn 305, 81.25°N, 44.83°E, 183.5 m, BT 0.34 °C, 20 September 2012; ♀VI, ML 36 mm, BS-246–2010, Stn 246, 79.75°N, 42.70°E, 354 m, 18 September 2010; ♀VI, ML 20 mm, BS-322–2014, Stn 322, 82.84°N, 50.41°E, 529 m, 23 September 2014; ♀V₂, ML 44 mm, BS-HH-259–1-2012 and ♀II, ML 31 mm, BS-HH-259–2-2012, Stn 259, 79.87°N, 6.76°E, 834 m, 24 August 2012; ♀II, ML 31 mm, BS-HH-269–2012, Stn 269, 80.45°N, 4.80°E, 730 m, 25 August 2012.

Kara Sea (LH KFU): ♂V₂, ML 46 mm, KS-27–1-2007, ♂II, ML 29 mm, KS-27–2-2007, ♀II, ML 21 mm, KS-27–3-2007, Stn 27, 75.98°N, 71.90°E, 201 m, BT –1.08 °C, 21 September 2007; ♂V₁, ML 32 mm, KS-15–1-2007, ♂II, ML 19 mm, KS-15–2-2007, Stn 15, 79.64°N, 73.51°E, 423 m, BT –0.28 °C, 17 September 2007; ♂II, ML 27 mm, KS-25–2007, Stn 25, 76.95°N, 70.93°E, 429.5 m, BT 0.07 °C, 20 September 2007; ♀VI, ML 52 mm, KS-201–2010, Stn 201, 78.90°N, 69.95°E, 490.5 m, 11 September 2010; ♀VI, ML 30 mm, KS-28–2009, Stn 28, 80.33°N,

73.47°E, 398 m, BT –0.69 °C, 18 August 2009; ♀II, ML 17 mm, KS-16–2007, Stn 16, 78.80°N, 74.08°E, 383.5 m, BT –0.25 °C, 17 September 2007.

Additional material examined See SM.01.

Type locality Off the Barents Sea slope, Stn 319, 82.07°N, 40.42°E, 677 m, BT 0.44 °C.

Etymology Named after Ægir (Old Norse for ‘sea’, latinized and anglicized to ‘aegir’; noun in apposition, masculine), a sea giant associated with the ocean in Norse mythology [91], because the distribution of this species extends along the slope of Scandinavia and Iceland, and to underscore the senior author’s appreciation of ancient Norse culture, history, and mythology.

Diagnosis Small (maximum ML 52 mm) violet-brown octopods, paler ventrally, and with white area orally. Skin smooth, body rounded, arms ~3.1 times ML. Suckers closely set, small, not enlarged in either sex. From 84 to 120 suckers on unmodified arms, and 46–56 suckers on hectocotylus. Ligula moderately large and broad, tapering gradually, without transverse ridges, but with 8–14 low indistinct rugae; calamus large, pointed. Funnel of

Table 4 Fecundity and oogenesis in *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, **sp. nov.**, *M. johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26] and *M. sibiricus* (Løyning, 1930) [62]. Values are minimum – maximum (mean ± SE), where applicable

Species/maturity stages and characters	<i>Muusoctopus aegir</i> sp. nov.	<i>Muusoctopus johnsonianus</i>	<i>Muusoctopus sibiricus</i>
Fecundity (all stages)	65–168 (99.5 ± 6.8)	227–300 (259.0 ± 21.5)	136
Realized fecundity, %	10.8–58.1 (44.7 ± 6.2); 39.4–58.1 (50.4 ± 3.0) if outlier is excluded	No data	No data
Early Immature (I)	Fecundity 96 Oocytes Only pre-vitellogenic, 0.4–0.6 mm	No data	136 Only pre-vitellogenic, 0.2–0.3 mm
Late immature (II)	Fecundity 98 and 130 Oocytes Only pre-vitellogenic, 0.4–1.6 mm	250 and 300 Only pre-vitellogenic, 0.3–0.6 mm	No data
Early maturing (III)	Fecundity 112 and 130 Oocytes Pre-vitellogenic oocytes: ~61%; ~57% of them 0.4–0.7 mm and ~43% of them 0.9–1.1 mm; Small vitellogenic oocytes: ~2%; 2.2–2.5 mm; Medium vitellogenic oocytes: ~37%; 2.6–4.5 mm	No data	No data
Late maturing (IV)	Fecundity 78–168 (117.0 ± 19.1) Oocytes Pre-vitellogenic oocytes: 0–63%; 18–75% of them 0.2–0.5 mm and 25–82% of them 0.6–1.2 mm; Small vitellogenic oocytes: 7–39%; 2.5–5.0 mm; Medium vitellogenic oocytes: 12–34%; 3.0–7.0 mm; Large vitellogenic oocytes: 0.2–44%; 6.0–12.0 mm; 17–24 folds; Resorbing oocytes: 0.6–28%; 0.5–4.8 mm	227 Small vitellogenic oocytes: 47%; 2.0–5.0 mm; Medium vitellogenic oocytes: 11%; 10.0–13.0 mm; Large vitellogenic oocytes: 42%; 17.0–22.0 mm; 18–20 folds	No data
Pre-mature (V₁)	Fecundity No data Oocytes	No data	No data
Mature (V₂)	Fecundity No data Oocytes Analyzed onboard: only ripe oocytes counted (18)	No data	No data
Pre-spent (V₃)	Fecundity 71 Oocytes Ripe oocytes: 2.8%; 12.5 and 13.0 mm without capsules, 13.0 and 14.0 mm in capsules; Post-ovulatory follicles: 37%; 1.1–4.2 mm; Resorbing oocytes: 61%; 0.5–3.0 mm	No data	No data
Spent (VI)	Fecundity 65–93 (81.2 ± 4.9) Oocytes Post-ovulatory follicles: 11–58% (without outlier 44–58%); 2.0–5.1 mm; Resorbing oocytes: 42–89% (without outlier 42–56%); 0.2–2.6 mm	No data	No data

moderate length, free from ventral surface of head for slightly more than half its length. Funnel organ W-shaped, with medial and marginal limbs of the same length (or medial limbs are slightly longer), and with broad marginal limbs. Gills long, with eight or nine outer and seven

or eight inner lamellae per demibranch. Stylets, anal flaps, ink sac, and ink duct absent. Multicuspid rachidian with 5–7 cusps, located asymmetrically with seriation of 4–6. Long and slender spermatophores, up to 22 (mean: 13 ± 2). Female with up to 168 oocytes (mean: 100 ± 7).

Table 5 Equations to estimate mantle length and body mass from upper and lower hood length of the beak in *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, **sp. nov.** and *M. johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]

Species/ measurement	<i>Muusoctopus aegir</i> sp. nov.	<i>Muusoctopus johnsonianus</i>
UHL	ML ML = 1.92UHL ^{1.67} n = 28, r ² = 0.82, p < 0.0001	ML = 2.61UHL ^{1.49} n = 6, r ² = 0.82, p = 0.0179
	BM BM = 0.03UHL ^{4.35} n = 28, r ² = 0.79, p < 0.0001	BM = 0.03UHL ^{4.28} n = 6, r ² = 0.18, p = 0.41
LHL	ML ML = 7.37LHL ^{0.97} n = 28, r ² = 0.63, p < 0.0001	ML = 3.57LHL ^{1.61} n = 6, r ² = 0.92, p = 0.0243
	BM ML = 0.91UHL ^{2.57} n = 28, r ² = 0.63, p < 0.0001	ML = 0.07UHL ^{4.67} n = 6, r ² = 0.93, p = 0.0013

Significant *p*-values are in bold. *n*, number of individuals; *r*², determination coefficient

ML mantle length, BM body mass, UHL upper beak hood length, LHL lower beak hood length

Description Counts and measurements for the species are given in Tables 1, 2 and 3 and SM.01 Table S1, and indices are given in Table 9.

Description based on 25 individuals (all studied individuals, excluding the immature ones, i.e., 11 males (♂) and 14 females (♀)), additionally data for 2♂ (late maturing and mature) are from Nesis [51]. Species small, ML 20–52 mm (32.3 ± 1.8 mm), total length (TL) 96–235 mm (141.6 ± 7.8 mm) (Fig. 2; Tables 1, 2, 9); ventral ML 1–10 mm shorter than dorsal ML. Mantle wider than long, appearing round; width 111.3% ± 3.4% ML. Head narrower (71.3% ± 2.2%) than mantle (Fig. 2). Eyes relatively prominent in comparison to other North Atlantic and Arctic *Muusoctopus* (Table 9); diameter 32.5% ± 0.8% ML (Fig. 2). Funnel moderately long (42.1% ± 1.6% ML), tapered. Funnel free from ventral surface of head for slightly more than a half its length (mean 52.9% ± 0.7% funnel length). Funnel organ W-shaped, with medial and marginal limbs of similar length, or with medial limbs slightly longer; marginal limbs broad (Fig. 3a–d). Arms relatively long, ~3.1 times ML (Fig. 2), their length subequal, of formula typically 1.2.3.4. Suckers: number 84–120 (95.5 ± 1.5) per arm, biserial from base of arms to arm tips, small (8.9% ± 0.3% ML), closely set (Fig. 2); none enlarged in either sex. Web medium deep (25.5% ± 1.1% longest arm length); all web sectors are approximately subequal, with sectors B and C deepest, and D and E most shallow.

Gills long (34.4% ± 1.3% ML), with eight or nine (mode: 8) outer and seven or eight (mode: 7) inner lamellae per demibranch. Stylets absent. Upper beak with hooked rostrum (Fig. 4a–c); lower beak with straight rostrum (Fig. 4d–f); both typically *Muusoctopus*. Anterior salivary

glands moderate (21.5% ± 2.6% ML), discoid. Posterior salivary glands large (28.8% ± 2.8% ML), almost triangular. Crop diverticulum well developed (Fig. 3e). Rectum with a loop. Ink sac, ink duct and anal flaps absent (Fig. 3e). Radula with nine elements per transverse row; rachidian with 5–7 cusps, the central largest, with asymmetric lateral cusps with 4–6 seriation (Fig. 4g–k). Marginal and lateral teeth unicuspid, marginal teeth curved. Marginal plates well developed (Fig. 4g–k).

Male third right arm hectocotylized (Fig. 2d, j), length 233.8% ± 6.5% ML, 71.5% ± 2.2% that of the opposite arm, with 46 to 56 (52.0 ± 1.1) suckers. Ligula moderately large, 8.0–14.1% (10.3% ± 0.5%) of hectocotylized arm length, broad, 45.0–63.3% (55.4% ± 2.1%) ligula length, tapering gradually, with distinct margins and well-marked shallow, narrow groove without transverse ridges, but with 8–14 low indistinct rugae (Fig. 5a–c). Calamus large, 27.5–43.3% (36.8% ± 1.4%) ligula length, pointed (Fig. 5a–c). Spermatophoric complex accessory gland longer than spermatophoric sac (Fig. 5d), both longer than ML. Length of terminal organ with diverticulum 30–56% ML. Spermatophoric sac with 5–22 (12.5 ± 2.4) spermatophores (Tables 1, 3); spermatophores long, 27.9–48.0 mm (39.8 ± 0.5 mm) and 78.0–135.9% (108.1% ± 1.8%) ML, slender (Fig. 5e), of width 0.8–1.4 (1.2 ± 0.04) mm. Sperm cord width 0.1–0.2 mm, forming 65–98 (77.2 ± 2.7) whorls. Seminal reservoir length 26.1–36.4% (31.4% ± 0.6%) spermatophore length (Table 3); ejaculatory tube comprises longest part of spermatophore (Fig. 5e; Table 3). Oviducal glands large (length 17.0% ± 2.0% ML and width 17.8% ± 2.4% ML), broader than long, dark-colored, but paler in spent females (Fig. 6a–c). Fecundity 65–168 (99.5 ± 6.8) oocytes (Tables 2, 4; SM.01 Table S1). Ripe oocyte length 12.5 and 13.0 mm (*n* = 2; in pre-spent female), and 13.0 and 14.0 mm in capsules, respectively (Fig. 6d; Table 4). Large vitellogenic oocytes range from 6.0 to 12.0 mm with 17–24 follicular folds (Fig. 6g; Table 4).

Skin smooth, without papillae, and minute folds can appear in some fixed individuals (Fig. 2). Live color violet-brown, paler ventrally, and white around the mouth (Fig. 2e–j). Some fixed individuals turn darker, while others turn lighter of which some eventually lose color.

Distribution In the Faroe–Shetland Channel, along the northern slope of the Greenland–Iceland–Faroe Ridge, farther to the east along the Norwegian slope and the continental slopes of the Barents and Kara Seas (Fig. 1): the easternmost location is to the north of the Severnaya Zemlya Archipelago, 96.94°E [34–36, 40–47, 49–52, 57] [the present study]. The species enters the



Fig. 2 *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, *sp. nov.* External view. **a–c**, holotype BS-319–2012 (late maturing female, mantle length (ML) 43 mm, off the Barents Sea slope, fixed): dorsal (**a**), ventral (**b**) and lateral (**c**) view; **d**, paratype KS-189–2010 (mature male, ML 30 mm, the Kara Sea, fixed): lateral view; **e, f**, paratype ICL-A13-570–2017 (pre-spent female, ML 24 mm, off Iceland, fixed): ventral (**e**) and lateral (**f**) view; **g, h**, ICL-A11-640–2016 (not analyzed; off Iceland, fresh): dorsal (**g**) and ventral (**h**) view; **i, j**, BS-HH-244–2012 (mature male, ML 36 mm, off Svalbard, fresh (**j**) and fixed (**i**)): dorsal (**i**) and ventral (**j**) view; **k**, BIOICE-2322 (late maturing female, ML 38 mm, off Iceland, fixed): dorsal view. Arrowheads indicate the hectocotylus in males. Scale bars = 10 mm

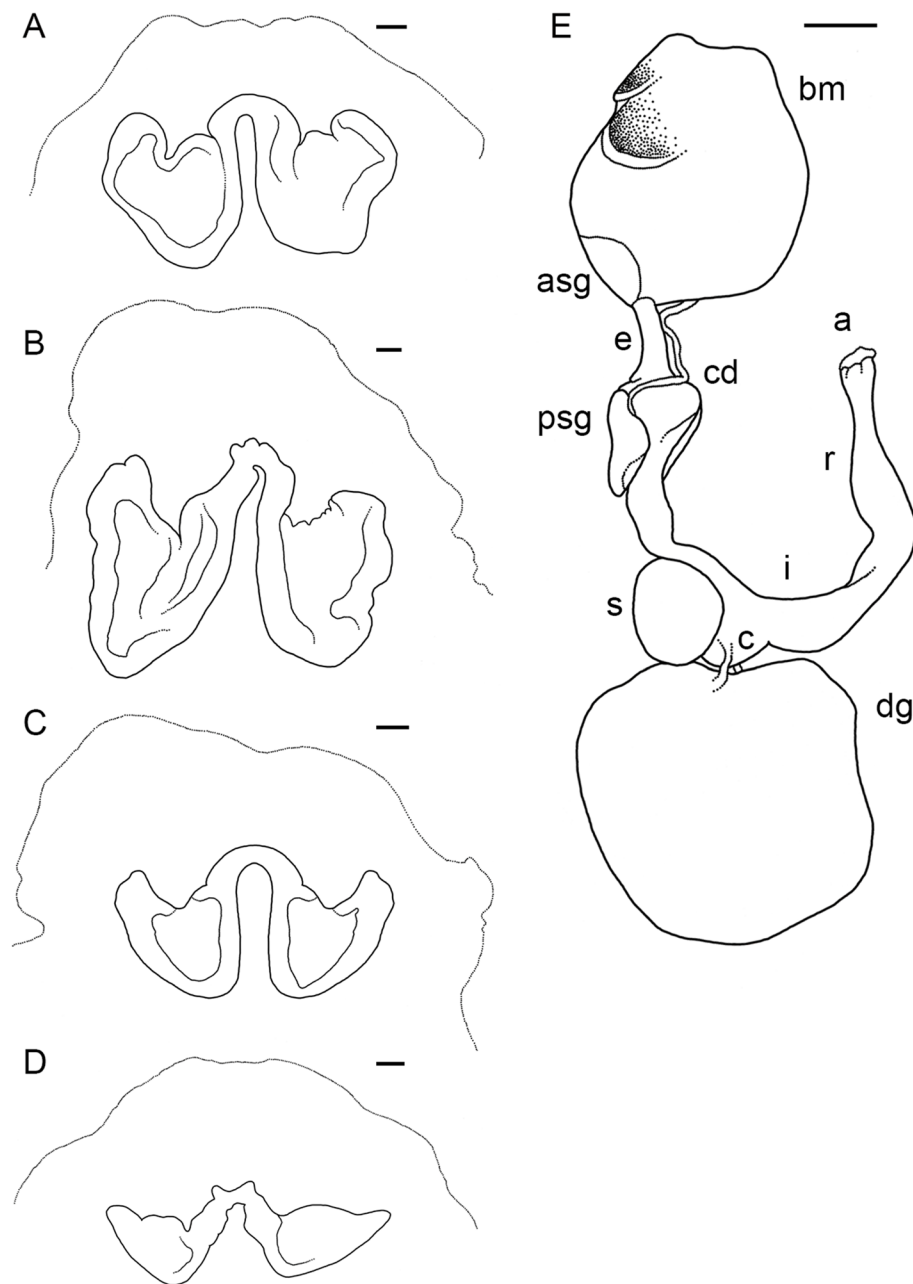


Fig. 3 *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, *sp. nov.* General anatomy. **a**, holotype BS-319–2012 (late maturing female, mantle length (ML) 43 mm, off the Barents Sea slope): funnel organ; **b**, paratype KS-189–2010 (mature male, ML 30 mm, the Kara Sea): funnel organ; **c**, BS-70–2–2018 (late maturing male, ML 24 mm, the Barents Sea): funnel organ; **d**, BIOICE-2516–2 (late maturing female, ML 28 mm, off Iceland): funnel organ; **e**, paratype BS-304–2012 (spent female, ML 26 mm, off the Barents Sea slope): digestive tract, rectum loop untangled. Scale bars: **a–d** = 1 mm, **e** = 5 mm. Abbreviations: a, anus; asg, anterior salivary gland; bm, buccal mass; c, caecum; cd, crop diverticulum; dg, digestive gland; e, esophagus; i, intestine; psg, posterior salivary gland; r, rectum; s, stomach

Barents and Kara Seas via deep-sea troughs (Fig. 1). It is not known how far north the distribution of *M. aegir* extends along the East Greenland slope. Habitat depth is 86–2000 m judging from literature, with the associated bottom temperature -0.9°C [34, 36, 41, 42, 44, 51,

57], and 86–2442 m (579.4 ± 52.4 m) and -1.31 – 6.90°C ($0.41 \pm 0.30^{\circ}\text{C}$), respectively, according to our data.

Biology and ecology Among the characters studied, only the following increase without significant correlation

to ML in *M. aegir*: relative width of mantle and ligula; relative diameter of eye and sucker; relative length of arm, gill, hectocotylized arm, opposite arm, ligula, and calamus; spermatophore number; and fecundity (SM.01 Table S2).

Pre-mature males of *M. aegir* are found in the Barents and Kara Seas, and both individuals have five spermatophores. Mature males found in the same areas have 7–22 spermatophores. There is an ontogenetic increase in the size of normal spermatophores in *M. aegir*: of six males with spermatophores in both the spermatophoric sac and terminal organ, older spermatophores (in the terminal organ) were smaller than younger spermatophores (in the spermatophoric sac) in five males, while in one male they were of similar size. Thus, the ontogenetic increase in spermatophore length is 0.0–35.2% ($18.1\% \pm 6.3\%$). Spermatophore width increases by 0.0–25.0% ($12.4\% \pm 5.6\%$). Among spermatophore parts, the most significant ontogenetic increase is shown by the head ($71.4\% \pm 27.2\%$), and for other parts the increase is less pronounced: ejaculatory apparatus ($19.5\% \pm 10.0\%$), cement body ($14.6\% \pm 6.2\%$), and seminal reservoir ($13.6\% \pm 7.3\%$). The posterior cavity does not show ontogenetic size changes. The seminal reservoir width and volume show a larger ontogenetic increase than its length, $14.0\% \pm 6.4\%$ and $48.9\% \pm 18.6\%$, respectively.

Tentative spermatophores were found in one early maturing male off Iceland, one late-maturing male, and two mature males from the Barents Sea, in addition to which a spermatophore-like structure was found in one of the mature males. Tentative spermatophores are 25–50% shorter than normal spermatophores, and have a relatively longer cement body and a relatively shorter ejaculatory apparatus and seminal reservoir (Fig. 5f). The latter is semi-translucent, seemingly containing a lower sperm concentration. The spermatophore-like structure is represented by a heavily coiled and largely empty tube (Fig. 5g).

Sperm is present in the oviducal glands of mature, pre-spent and spent females, and is not found in females at the

late maturity or earlier. Oogenesis starts synchronously, but two separate portions of different-sized oocytes are clearly visible throughout the ovary from the early maturing stage: one portion remains at the pre-vitellogenic stage with no further development (Fig. 6h), while the other portion is already at least at the small vitellogenic stage and continues development (Table 4). Oocytes from both portions occasionally undergo resorption from the late maturing stage of females (0.6–28% of fecundity), and all remaining oocytes are resorbing in pre-spent and spent females, except for post-ovulatory follicles (Fig. 6e, f) and residual ripe oocytes, if any of the latter remain in the ovary (Table 4). Two residual ripe oocytes in capsules (thus, obviously fertilized) in the ovary of pre-spent female represent an abnormal state, as they should be in the distal oviduct(s). The realized fecundity of the species is 10.8–54.1% ($44.7\% \pm 6.2\%$). A Barents Sea spent female (BS-322–2014) of ML 20 mm has a fecundity of 65 oocytes, which is the lowest recorded, and it is constituted by seven post-ovulatory follicles and 58 resorbing oocytes with a diameter less than 1 mm, indicating that this female realized less than 11% of its fecundity. If this female is excluded as an abnormal individual, the realized fecundity of the species is 39.4–58.1% ($50.4\% \pm 3.0\%$).

The equations to estimate ML and body mass of *M. aegir* from upper and lower beak hood lengths are provided in Table 5.

Remarks Muus [23] recognized three species of *Bathypolypus* (*B. arcticus*, *B. bairdii* and *B. pugniger*) from the Arctic Atlantic. These three species differ from *Muusoctopus aegir* in being larger, and in having: 1) different funnel organs (V V- or II II-shaped); 2) proportionally shorter arms with fewer and proportionally smaller suckers (including on the hectocotylized arm); 3) proportionally larger and more prominent eyes; 4) fewer gill lamellae; 5) stylets; 6) different female fecundity; 7) papillose skin and supraocular cirri, with paler ventral mantle pigmentation; 8) different radula characteristics, especially rachidian dentition; 9) ligula morphology; and 10) spermatophore number and morphology [23, 90]. Likewise, *M. aegir* fits the amended diagnosis of *Benthooctopus*

(See figure on next page.)

Fig. 4 *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, **sp. nov.** Beak and radula. **a, d**, paratype BS-70–1-2018 (pre-mature male, mantle length (ML) 29 mm, the Barents Sea): upper (**a**) and lower (**d**) beaks; **b, e**, KS-201–2010 (spent female, ML 52 mm, the Kara Sea): upper (**b**) and lower (**e**) beaks; **c, f**, BIOICE-2789 (early maturing male, ML 27 mm, off Iceland): upper (**c**) and lower (**f**) beaks; **g, j**, holotype BS-319–2012 (late maturing female, ML 43 mm, off the Barents Sea slope): older (**g**) and younger (**j**) unworn sections of radula; **h, k**, BS-255–2010 (mature male, ML 28 mm, off the Barents Sea slope): older (**h**) and younger (**k**) unworn sections of radula; **i**, BIOICE-2516–2 (late maturing female, ML 28 mm, off Iceland): older unworn section of radula. Scale bars: **a–f** = 1 mm, **g–k** = 100 μ m. Abbreviations: l1, first lateral tooth; l2, second lateral tooth; m, marginal tooth; r, rachidian tooth



Fig. 4 (See legend on previous page.)

(widely recognized as *Muusoctopus* now [31, 32]) from Strugnell et al. [56] in having: 1) a fitting relative arm length; 2) a crop diverticulum and a fitting radula; and 3) a ligula with small indistinct rugae.

The holotype of *Be. piscatorum* has twice been stated to be a synonym of *B. bairdii* [23, 26]. Using the photos of the holotype provided by I. G. Gleadall and in O'Shea [77] and its measurements [30, 77, 87], we again demonstrate it is indeed rather a *Bathypolypus*: it fits *Bathypolypus* in mantle and head proportions, and having large prominent eyes; proportional length of arms and sucker count are lower than in *Muusoctopus*, and suckers are proportionally smaller than in all Arctic and North Atlantic *Muusoctopus*, except for *M. normani*; funnel length and free funnel length are shorter than in all Arctic and North Atlantic *Muusoctopus*, except for *M. normani*; it lacks a crop diverticulum, which is present in Arctic and North Atlantic *Muusoctopus*; and coloration fits *Bathypolypus*. Muus [23] described remains of an eye cirrus (a character of *Bathypolypus*) over the right eye in this individual; and this individual has stylets [A. L. Allcock, pers. comm.]. Unfortunately, Verrill [30, 87] did not provide any measurements of the other *Be. piscatorum* female he described from Northwest Atlantic. The male of *Be. piscatorum* from Verrill [88, 89] also does not have any measurements provided, and its hectocotylus, as estimated from Verrill's drawing [89] [Pl. XLII, Fig. 5], is small and resembles that of *M. normani*. Another individual referred to as *Be. piscatorum* even after the suggested synonymy [23] is a large female from Placentia Bay [48, 53, 54]. Its large size, mantle and head proportions, proportional web depth and sucker diameter, gill lamellae count, and ripe oocyte size and count fit those of *M. normani*; however, its arms are proportionally shorter, and sucker count, funnel measurements, and funnel organ morphology are not reported.

Individuals from the Faroe–Shetland Channel [34, 41–43] are of globular shape, which is the case for *M. aegir* described here, and are very different from the individuals of Verrill [30, 87–89] and those from Placentia Bay [48, 53, 54]. Moreover, these individuals from the

Faroe–Shetland Channel have their mantle and body proportions, hectocotylized arm sucker count, sucker diameter, free funnel length, and gill lamellae count fitting *M. aegir*, and also have a crop diverticulum [34, 41–43]. Funnel organ morphology, W-shaped with medial limb longer, according to Robson [43], can be seen as fitting those of *M. aegir*: in *M. aegir*, medial limbs are also sometimes longer than marginal limbs (but generally are of similar length). The radula illustrated by Robson [43] [Fig. 35] is typical for *M. aegir*, with a rachidian with seven cusps—a character state not reported for other North Atlantic and Arctic species of *Muusoctopus* [26, 63] [this study, *M. johnsonianus* below]. Ligula length from Hoyle [34], reported in Massy [38], and from Robson [43] fit *M. aegir*. Ligula width and ligula rugae count from Russell [41, 42] fit those of *M. aegir*. Ligula length from Russell [41, 42] is shorter, and ligula width from Hoyle [34], reported in Massy [38], is narrower than in *M. aegir*. Small sizes and proportionally longer arms in Russell [41, 42] fit immature *M. aegir* (SM.01 Table S1), which can explain their shorter ligula. Overall, the individuals from the Faroe–Shetland Channel [34, 41–43] are very different from Verrill's [30, 87–89] *Be. piscatorum* but conform fully to the morphology of *M. aegir*. Finally, '*Muusoctopus* sp.' was recently reported from the Faroe–Shetland Channel and that it did not coincide with any known species (with COI barcode, but no morphological description of the species provided) [57]. The locations are very close to the old individuals reported from the area [34, 41–43] (SM.01 Fig. S2). The depths of older (908–1112 m [34, 41–43]) and newer (704–1198 m [57]) records coincide, and are close to mean depth of our Iceland records of *M. aegir* (418–2442, 950.9 ± 173.4 m). Based on the morphological similarity of the old Faroe–Shetland Channel individuals [34, 41–43] and our individuals, and similar depths and location of the older [34, 41–43] and newer [57] Faroe–Shetland Channel individuals, we suppose the latter are also *M. aegir*. As such, COI barcode of '*Muusoctopus* sp.' from the Faroe–Shetland Channel reported in Taite et al. [57] is applicable to *M. aegir* described here. Biogeography also supports this view particularly well for the Icelandic and Faroese waters: 1) during the extensive sampling around Iceland

(See figure on next page.)

Fig. 5 *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, **sp. nov.** Hectocotylus and male reproductive anatomy. **a**, paratype BS-70-1-2018 (pre-mature male, mantle length (ML) 29 mm, the Barents Sea): hectocotylus; **b, d, e**, BS-HH-244-2012 (mature male, ML 36 mm, off Svalbard): hectocotylus (**b**), fresh, spermatophoric complex (**d**), dissected, ventral view, and spermatophore (**e**); **c**, BIOICE-2789 (early maturing male, ML 27 mm, Iceland): hectocotylus; **f, g**, BS-255-2010 (mature male, ML 28 mm, off the Barents Sea slope): tentative spermatophore (**f**) and spermatophore-like structure (**g**). Scale bars: **a–c, e–g** = 1 mm, **d** = 5 mm. Abbreviations: ag, accessory gland; ca, calamus; cb, cement body, di, diverticulum; ea, ejaculatory apparatus; he, head; sd, sperm duct; sg, spermatophoric glands; sr, seminal reservoir; ss, spermatophoric sac; th, thread; to, terminal organ

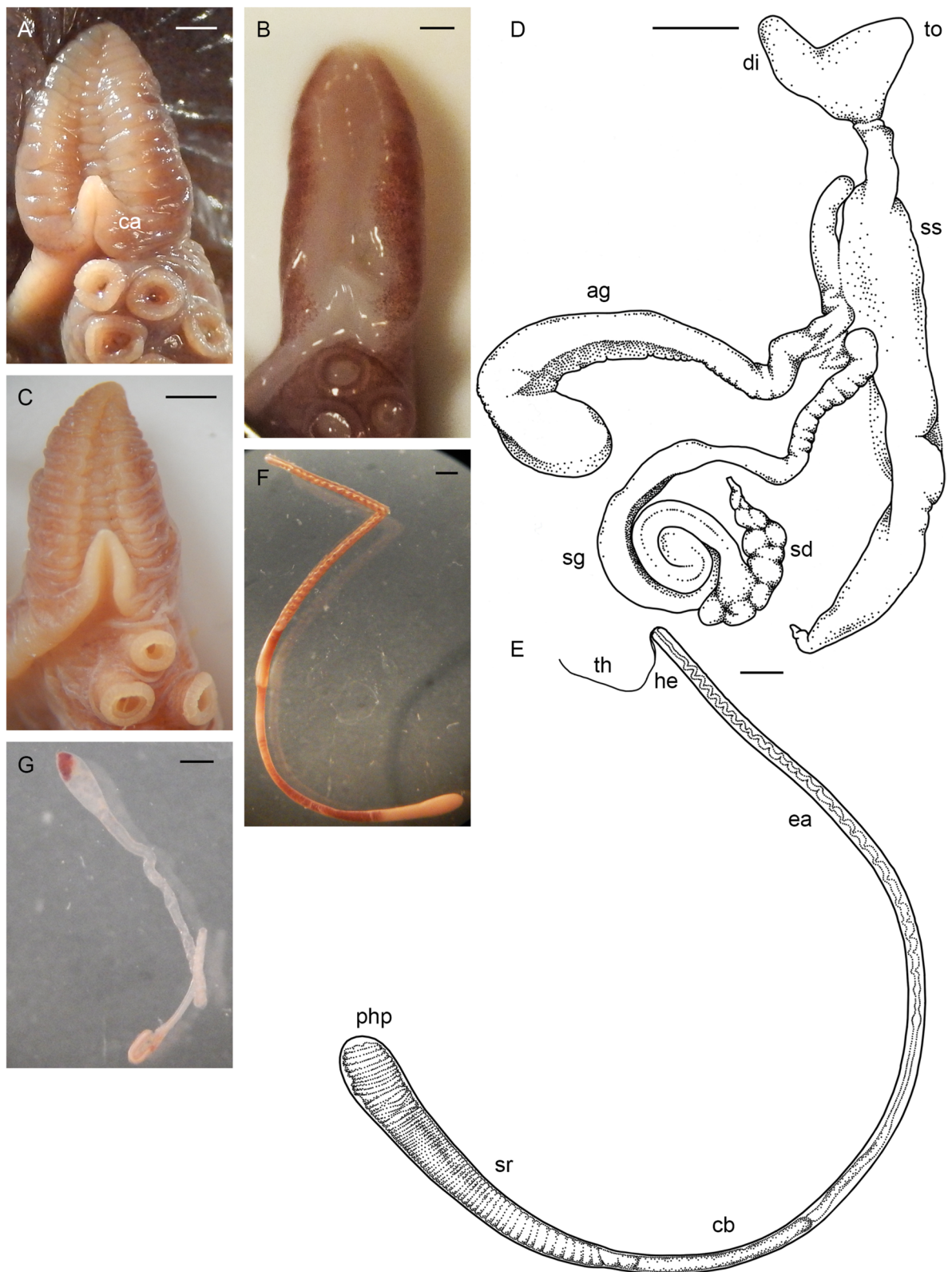


Fig. 5 (See legend on previous page.)



Fig. 6 *Muusoctopus aegir* Golikov, Gudmundsson & Sabirov, *sp. nov.* Female reproductive anatomy. **a**, holotype BS-319-2012 (late maturing female, mantle length (ML) 43 mm, off the Barents Sea slope): female reproductive tract; **b**, paratype BS-304-2012 (spent female, ML 26 mm, off the Barents Sea slope): female reproductive tract; **c**, BIOICE-2033 (early maturing female, ML 21 mm, off Iceland): dissected female reproductive tract; **d–f**, paratype ICL-A13-570-2017 (pre-spent female, ML 24 mm, off Iceland): ripe ova in shell (**d**), post-ovulatory follicles (**e**) and part of the ovary with post-ovulatory follicles and resorbing oocytes (**f**); **g, h**, BIOICE-2516-1 (late maturing female, ML 32 mm, off Iceland): late vitellogenic oocytes (**g**) and part of the ovary with pre-vitellogenic oocytes (**h**). Scale bars: **a** = 5 mm, **b–h** = 1 mm. Abbreviations: do, distal oviduct; ev, early vitellogenic oocyte; lv, late vitellogenic oocyte; mv, mid-vitellogenic oocyte; o, ovary; og, oviducal gland; oo, oviduct opening; pf, post-ovulatory follicle; po, proximal oviduct; pr, pre-vitellogenic oocyte; re, resorbing oocyte; s, stalk

(579 bottom stations) during BIOICE program, *M. aegir* was only recorded to the north of the Greenland–Iceland–Faroe Ridges. In the extensive sampling reported

by Taite et al. [57], '*Muusoctopus sp.*' was only found in the Faroe–Shetland Channel, where individuals exhibiting characters fitting those of *M. aegir* were recorded

previously [34, 41–43]; and 2) only *M. johnsonianus* was found in the BIOICE samples south of the Greenland–Iceland–Faroe Ridges, but *M. aegir* was absent. In Taite et al. [57], *M. johnsonianus* and *M. normani* were found to the south of the Faroe–Shetland Channel, but never ‘*Muusoctopus* sp.’ (SM.01 Fig. S2). It is clear that the Arctic species, *M. aegir*, is separated from the North Atlantic species, *M. johnsonianus* and *M. normani*, by the Canada–Greenland and Greenland–Iceland–Faroe Ridges.

Other historical records of *Be. piscatorum* are discussed below. There is an individual from Massy [37], caught near Ireland and initially described as *Polypus normani* Massy, 1907 [37], but later reconsidered to be *Be. piscatorum* [38, 39]. Measurements of this individual fit *M. normani*, which is shown by Allcock et al. [26], who reinstated this species as *M. normani*. Regarding the Arctic records of *Be. piscatorum*: in Appelløf [36], one individual off Ranen fits *M. aegir* and individuals off Isfjord fit *Bathypolypus*; in Grieg [44], all Svalbard individuals fit *M. aegir*, except for the large female from North Atlantic, which is rather one of the Atlantic species of *Muusoctopus*; and high Arctic individuals from Nesis [51] fit *M. aegir* so well, that they were used in species description here, to complement our samples. To summarize, studies that reported *Be. piscatorum* in the North Atlantic and Arctic [22, 34–54] were in fact mixing Verrill’s *Bathypolypus*, two Atlantic species of *Muusoctopus* (*M. johnsonianus* and *M. normani*), and Arctic *M. aegir*, which reaches the Faroe–Shetland Channel as a southernmost part of its range. This means that the published records of *Be. piscatorum* in the Faroe–Shetland Channel, along the northern slope of the Greenland–Iceland–Faroe Ridge, farther to the east along the Norwegian slope and the continental slopes of the Barents and Kara Seas [34–36, 40–47, 49–52] are in fact *M. aegir*.

No other known *Muusoctopus* species occur within the recognized distribution of *M. aegir*. *Muusoctopus aegir* differs from both *M. johnsonianus* and *M. normani* most notably in: 1) being smaller and in having a more rounded mantle; 2) having relatively more of the funnel free from the ventral surface of head than in *M. normani*, and less than in *M. johnsonianus*; 3) having proportionally shorter arms with fewer, larger suckers (including hectocotylyzed arms), and fewer gill lamellae than *M. johnsonianus* (but largely overlapping with *M. normani*); 4) lacking stylets; 5) having a rachidian with 5–7 cusps, with differing seriation (vs. five cusps in the other two species); 6) and differing in coloration (Table 9) [26, 32] [this study, section on *M. johnsonianus* below]. Proportionally, the ligula of *M. aegir* is longer than that in either of the other species, and broader than that in *M. johnsonianus* (no data

are available for *M. normani*); the calamus is shorter than that in *M. normani*, but similar to that of *M. johnsonianus*; the spermatophores are shorter than that in *M. normani* (insufficient data on *M. johnsonianus* to compare); and females have fewer and relatively larger ripe oocytes (large vitellogenic oocytes used as a proxy for *M. johnsonianus*) (Table 9) [26, 32, 90] [this study, section on *M. johnsonianus* below]. The funnel organ enables unambiguous differentiation of these species; in *M. normani* it is V V-shaped; and while it is similarly W-shaped in *M. johnsonianus*, with the marginal limbs of comparable length or slightly longer than the medial limbs, in *M. aegir* the medial limbs are usually slightly longer than the marginal, and the marginal limbs are broader than in *M. johnsonianus* (Figs. 3a–d, 11; Table 9) [26, 32] [this study, section on *M. johnsonianus*, below].

For differences from *Muusoctopus* sp. 1 from the northern Baffin Bay and Canadian Arctic Archipelago and *M. sibiricus* from the Siberian, Chukchi and Beaufort Seas, see Remarks sections for each species, below. *Muusoctopus leioderma* from the Chukchi Sea, adjacent to the Bering Strait 1) seems to be larger and to have a narrower mantle than *M. aegir*; 2) has a W-shaped funnel organ with medial limbs always longer than marginal limbs; 3) has stylets; 4) has more gill lamellae; 5) has a proportionally longer ligula and shorter calamus; 6) has different coloration; and 7) has a lateral skin fold and small papillae (Table 9) [65–67, 92].

***Muusoctopus* sp. 1**

(Table 6; Figs. 7, 8 and 9).

Material examined Baffin Bay (individuals no longer extant): ♂II, ML 30 mm, GRL-PA-7–20-1–2016 and ♂I, ML 23 mm, GRL-PA-7–20-2–2016, Stn 20, 74.11°N, 57.94°W, 450.5 m, BT 2.00 °C, 23 September 2016; ♀I, ML 22 mm, GRL-7–117-2016, Stn 117, 73.72°N, 58.39°W, 393 m, BT 1.97 °C, 30 September 2016.

Canadian Arctic Archipelago (USNM 574859, examined by Dr. A. Louise Allcock, with data provided to A.V.G.): ♀II, ML 31 mm, USNM 574859, 74.72°N, 94.70°W, 101 m, 8 August 1950.

Description Counts and measurements for the species are given in Table 6, and indices are given in Table 9.

The following description is based on all individuals studied. Species small, ML 22–31 (26.5 ± 2.3) mm, TL 99–148 mm (121.7 ± 14.3 mm) mm; ventral ML 5 mm shorter than dorsal ML in Baffin Bay individuals. Mantle width and length similar (102.0% ± 5.1% ML); head

Table 6 Data on individuals of *Muusoctopus* sp. 1

Individuals/ character	GRL-PA-7- 20–1-2016	GRL-PA-7- 20–2-2016	GRL-PA-7- 117–2016	USNM 574859 ^a
Area	GRL	GRL	GRL	CAN
Sex	Male	Male	Female	Female
Maturity stage	Late immature (II)	Early immature (I)	Early immature (I)	Late immature (II) (?)
ML, mm	30	23	22	31
TL, mm	148	118	99	n/a
Ventral ML, mm	26	19	17	n/a
Mantle width, mm	32	20	23	34
Head length, mm	13	9	8	n/a
Head width, mm	26	19	17	n/a
Eye diameter, mm	8.5	7.0	6.0	n/a
Lens diameter, mm	3.0	2.0	2.0	n/a
Funnel length, mm	13.0	9.0	9.0	14.0
Free funnel length, mm	7.0	5.5	6.0	11.0
Web depth, mm (min – max)	20–27	12–16	13–17	13–21
Web formula	a > c > b > d > e	b > c > d > a > e	b > c = d > e > a	c = d > b > a > e
Arm length, mm (min – max)	79–105	69–86	54–69	80–85
Arm formula	1 > 2 = 4 > 3	1 > 2 > 3 > 4	1 > 2 > 3 > 4	3 > 1 = 2 = 4
Sucker count (min – max)	102–118	88–108	84–100	81
Sucker diameter (max), mm	3.0	2.0	2.0	3.0
Gill length, mm	13.5	9.6	8.6	n/a
Gill lamellae count, outer/inner	10/9	10/9	9/9	8/8
Hectocotylized arm length, mm	74	59	–	–
Hectocotylized arm sucker count	66	56	–	–
Ligula length, mm	4.8	2.7	–	–
Ligula width, mm	3.0	1.5	–	–
Calamus length, mm	1.8	1.8	–	–

ML mantle length, TL total length, GRL north Baffin Bay (West Greenland), CAN Canadian Arctic Archipelago; n/a not analyzed

^a examined by A. L. Allcock (A. L. Allcock, unpubl. data)

width $79.5\% \pm 5.9\%$ mantle width (Fig. 7). Eyes relatively prominent, of diameter $28.7\% \pm 0.9\%$ ML (Fig. 7). Funnel of moderate length $42.1\% \pm 1.3\%$ ML, tapered, free from ventral surface of head for $\sim 50\text{--}80\%$ its length. Funnel organ V V-shaped, with medial limbs slightly longer and broader than marginal limbs (Fig. 8a). Arms ~ 2.9 times ML (Fig. 7), of subequal length, and typically formula is 1.2.3.4. Suckers biserial, closely set from base of arms to arm tips, moderately sized ($9.4\% \pm 0.3\%$ ML). Suckers: number 81–118 (99.9 ± 5.3) per arm, none enlarged in either sex; with 81 (USNM 574859) and 84–110 (Baffin

Bay individuals) on arm pair 3. Web relatively shallow, depth $20.1\% \pm 2.2\%$ longest arm length; all web sectors are approximately subequal, with sectors C and B deepest, and A and E most shallow.

Gills very long ($41.9\% \pm 1.7\%$ ML), with 8–10 (mode: 10) outer and eight or nine (mode: 9) inner lamellae per demibranch. Presence of stylets not examined. Upper beak with hooked rostrum (Fig. 9a); lower beak with broad, straight rostrum (Fig. 9c); both typically *Muusoctopus*. Anterior salivary glands small

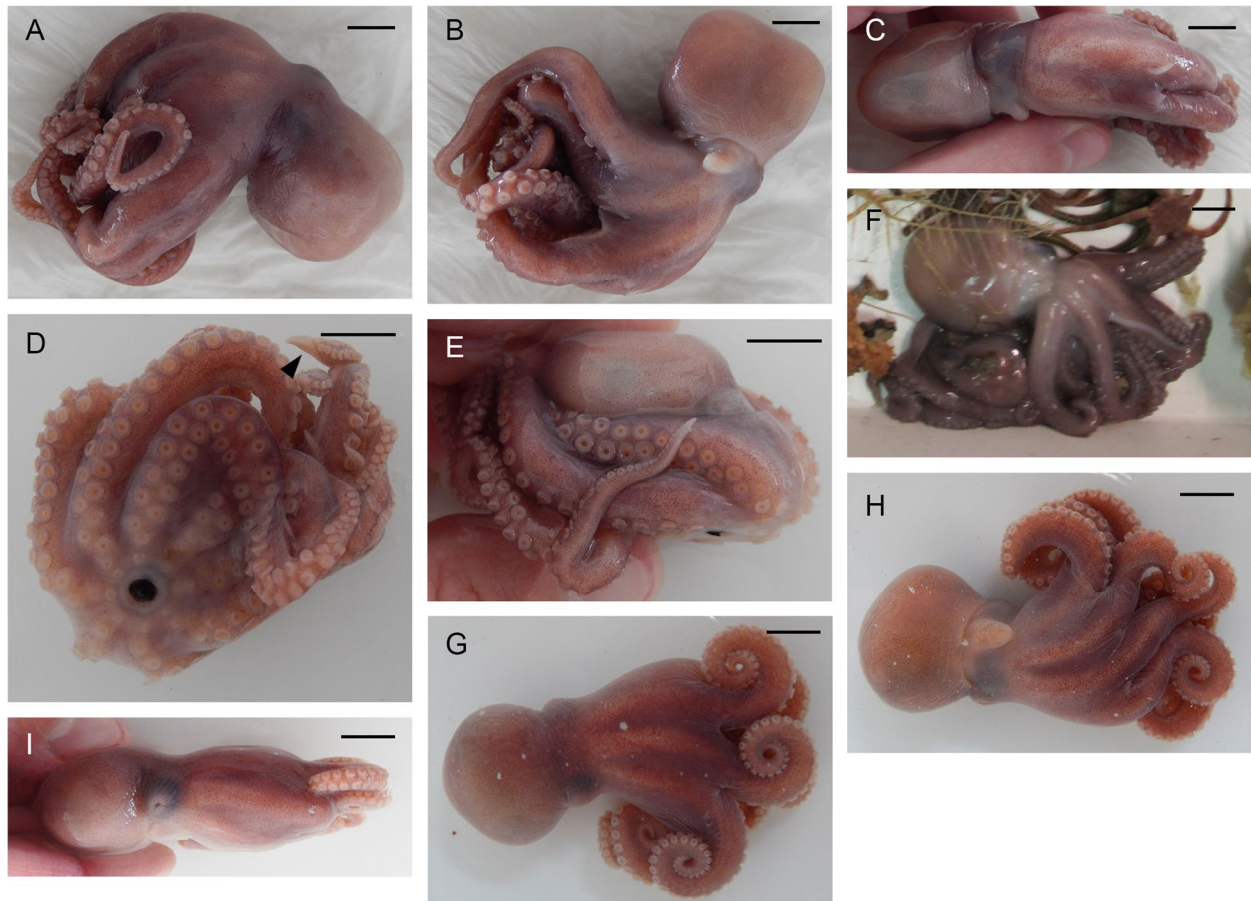


Fig. 7 *Muusoctopus* sp. 1. External view. **a–c**, GRL-PA-7–20-1–2016 (late immature male, mantle length (ML) 30 mm, northern Baffin Bay, fixed): dorsal (**a**), ventral (**b**) and lateral (**c**) view; **d, e**, GRL-PA-7–20-2–2016 (early immature male, ML 23 mm, northern Baffin Bay, fixed): ventral (**d**) and lateral (**e**) view; **f**, GRL-PA-7–20-1–2016 and GRL-PA-7–20-2–2016 in bottom trawl catch, showing fresh coloration; **g–i**, GRL-7–117-2016 (early immature female, ML 22 mm, northern Baffin Bay, fixed): dorsal (**g**), ventral (**h**) and lateral (**i**) view. Arrowhead indicates the hectocotylus in male. Scale bars = 10 mm

(19.2% \pm 0.7% ML), discoid. Posterior salivary glands very large (31.4% \pm 0.3% ML), approximately triangular. Crop diverticulum well developed (Fig. 8b). Presence of rectum loop not examined. Ink sac and well-developed ink duct absent (presence of vestigial ink duct not examined). Anal flaps absent. Radula with nine elements per transverse row; rachidian pentacuspoid, the central largest, with asymmetrical lateral cusps with 4 or 5 seriation (Fig. 9b, d); marginal and lateral teeth unicuspid, marginal teeth curved. Marginal plates well developed (Fig. 9b, d).

Male third right arm hectocotylized (Fig. 7d), of length 246.7% and 256.5% ML ($n=2$) and 79.7% and 93.7% the opposite arm, with 56–6 suckers. Ligula small, 4.6% and 6.5% of hectocotylized arm length, broad, 55.6% and 62.5% ligula length, tapering acutely. Ligula with

distinct margins and well-marked shallow groove without transverse ridges, but with 12 or 13 low indistinct rugae; groove and margins of similar width for 2/3 of ligula length basally (Fig. 8c). Calamus very large, 37.5% or 66.7% ligula length, and pointed (Fig. 8c). Spermatic complex in males is translucent due to immaturity, but fully formed (Fig. 8d); not measured. Female reproductive tract not examined.

Skin smooth, without papillae (Fig. 7). Live color is violet-brown, paler ventrally, with no white area around the mouth (Fig. 7).

Distribution Known from the Canadian Arctic Archipelago and northern Baffin Bay (Fig. 1), at 101–450.5 m (314.8 \pm 108.2 m), with the associated bottom temperatures 1.97–2.00 °C.

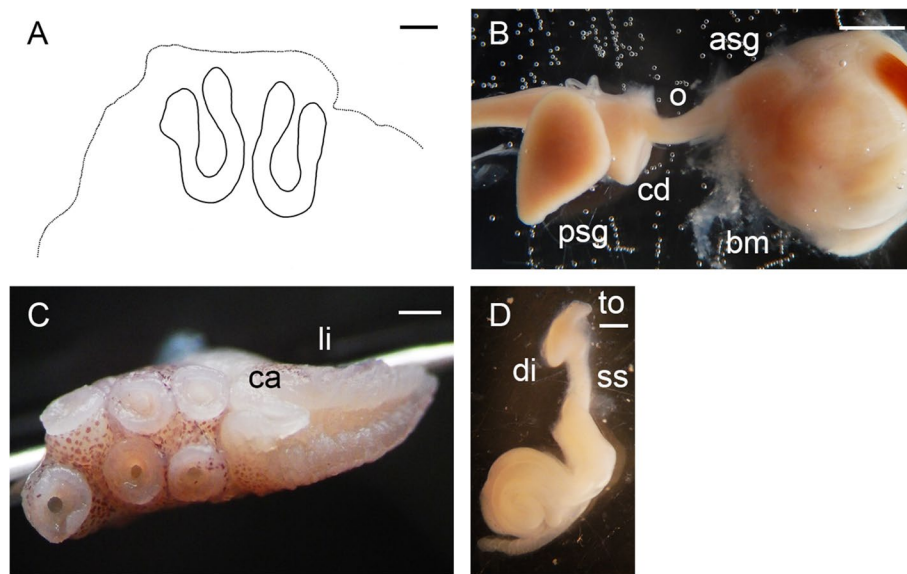


Fig. 8 *Muusoctopus* sp. 1. General anatomy, hectocotylus and male reproductive anatomy. **a, d**, GRL-PA-7–20–2–2016 (early immature male, mantle length (ML) 23 mm, northern Baffin Bay): funnel organ (**a**) and spermatophoric complex (**d**), in situ, ventral view; **b, c**, GRL-PA-7–20–1–2016 (late immature male, ML 30 mm, northern Baffin Bay): anterior part of digestive tract (**b**) and hectocotylus (**c**). Scale bars: **a, c, d** = 1 mm, **b** = 5 mm. Abbreviations: asg, anterior salivary gland; bm, buccal mass; ca, calamus; cd, crop diverticulum; di, diverticulum; e, esophagus; li, ligula; psg, posterior salivary gland; ss, spermatophoric sac; to, terminal organ

Biology and ecology Unknown.

Remarks It is unknown whether the ranges of *M. aegir* and *Muusoctopus* sp. 1 overlap to the north of Greenland, or if the ranges of *M. sibiricus* and *Muusoctopus* sp. 1 overlap in the western marginal area of the Canadian Arctic Archipelago. *Muusoctopus* sp. 1 differs from *M. aegir* in having: 1) a slightly larger body size (immature individuals are larger than the respective maturity stages of *M. aegir*); 2) a relatively longer free funnel length; 3) funnel organ shape (V V- vs. W- in *M. aegir*); 4) larger sucker counts (sucker counts on immature individuals exceed those of mature *M. aegir*); 5) relatively longer gills with more gill lamellae (the values are overlapping though); 6) a pentacuspoid rachidian with reduced seriation (4–5 vs. 4–6 in *M. aegir*); and 7) a ligula of different shape and size, judging by morphology of immature individuals of *Muusoctopus* sp. 1 (Table 9). Coloration also differs slightly: *Muusoctopus* sp. 1 is slightly darker than *M. aegir* and lacks a whitish area around the mouth (Figs. 2, 7).

Muusoctopus sp. 1 is differentiated from *M. sibiricus* in the remarks section for *M. sibiricus*, below. While limited data exist for both *Muusoctopus* sp. 1 and *M. leioderma* (see [65–67, 92] for *M. leioderma*), they differ in: 1) funnel organ shape (V V- vs. W- in *M. leioderma*); 2) *M. leioderma* has relatively shorter gills with more gill lamellae

(non-overlapping values); 3) size and shape differences in ligula present, as can be judged from immature *Muusoctopus* sp. 1; and 4) *M. leioderma* has a different coloration, and a lateral skin fold and small papillae (Table 9).

North Atlantic species (*M. johnsonianus* and *M. normani*) differ from *Muusoctopus* sp. 1 in being larger, and in having a proportionally narrower mantle. *Muusoctopus* sp. 1 also differs from *M. normani* in having a proportionally shorter portion of free funnel, from *M. johnsonianus* in funnel organ shape, and from both *M. johnsonianus* and *M. normani* in having relatively shorter arms with fewer and larger suckers (including hectocotylized arms), and relatively longer gills (with more lamellae than *M. normani*, although values overlap); and size and shape differences in ligula present, as can be judged from immature *Muusoctopus* sp. 1 (Table 9) [26, 32] [the following section on *M. johnsonianus*, below].

***Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]**

(Tables 4, 5, 7; SM.01 Table S3; Figs. 10, 11, 12 and 13).

Synonymy *Benthoctopus johnsoniana* Allcock, Strugnell, Ruggiero & Collins 2006 [26]: 379, Figs. 6–9.

Muusoctopus johnsonianus (Allcock, Strugnell, Ruggiero & Collins, 2006) [26] – Gleadall, 2013 [32]: 113, fig. 3.

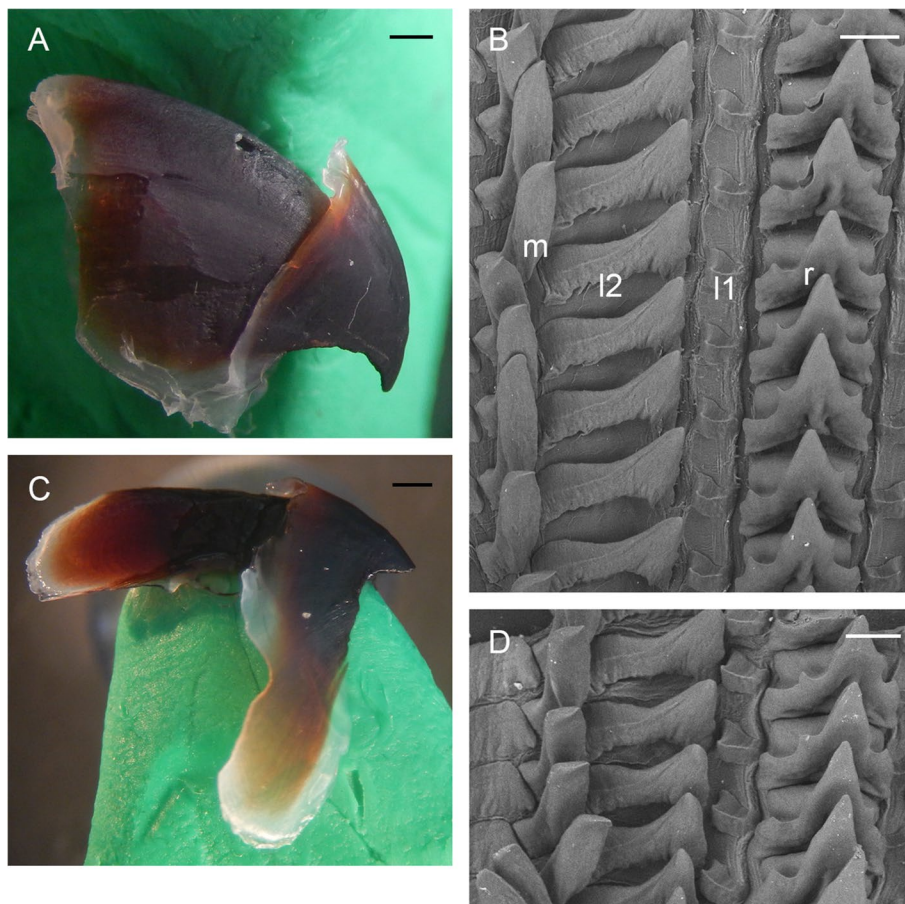


Fig. 9 *Muusoctopus* sp. 1. Beak and radula. GRL-PA-7-20-1-2016 (late immature male, mantle length 30 mm, northern Baffin Bay): upper (a) and lower (c) beak, and unworn sections of radula (b, d). Scale bars: a, c = 1 mm, b, d = 100 μ m. Abbreviations: i1, first lateral tooth; i2, second lateral tooth; m, marginal tooth; r, rachidian tooth

Benthoctopus sp. – Collins et al. 2001 [22]: 112; Barrat et al. 2007 [90]: 392.

Material examined Iceland: IINH 37,816, ♂III, ML 49 mm, BIOICE Stn 3524, 62.64°N, 17.05°W, 1919.5 m, BT 2.37 °C, 7 September 2002; IINH 37,815, ♂III, ML 47 mm, BIOICE Stn 3168, 60.92°N, 22.78°W, 1899.5 m, BT 2.98 °C, 26 July 2000; IINH 37,829, ♂I, ML 8.5 mm, BIOICE Stn 2427, 63.16°N, 20.06°W, 778 m, BT 5.50 °C, 3 July 1993; IINH 38,040, ♀IV, ML 89 mm, BIOICE Stn 3520, 62.26°N, 17.54°W, 1957 m, BT 2.70 °C, 5 September 2002; IINH 37,817, ♀II, ML 49 mm, BIOICE Stn 3520, 62.26°N, 17.54°W, 1957 m, BT 2.70 °C, 5 September 2002; IINH 37,818, ♀II, ML 36 mm, BIOICE Stn 3521, 62.52°N, 17.17°W, 1937.5 m, BT 2.34 °C, 7 September 2002; IINH 37,826, ♀I, ML 13 mm, BIOICE Stn 2926, 65.86°N, 28.78°W, 540 m, 27 August 1996.

Additional material examined See SM.01.

Description Counts and measurements for the species are given in Table 7 and SM.01 Table S3, and indices are given in Table 9.

Description based on individuals of maturity stages III and IV (two males and one female), and reports only ‘what-is-new’ in relation to [26, 32]; reference to ‘combined data’ includes values from [26, 32]. Mantle from wide oval to rounded, of width to 100.0% ML. Head width occasionally exceeds mantle width, to 106.1% mantle width, mean $88.4\% \pm 4.8\%$ mantle width (combined data). Eyes very prominent, their diameter $47.0\% \pm 7.2\%$ ML (Fig. 10). Funnel organ W-shaped, with medial and marginal limbs of similar length, or with moderately broad marginal limbs slightly longer (Fig. 11). Arms relatively

Table 7 Data on maturing individuals of *Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]. Immature individuals are detailed in SM.01 Table S3. All individuals are from Iceland

Individuals/character	BIOICE-3524	BIOICE-3168	BIOICE-3520-1
Sex	Male	Male	Female
Maturity stage	Early maturing (III)	Early maturing (III)	Late maturing (IV)
ML, mm	49	47	89
TL, mm	256	255	425
Ventral ML, mm	41	40	66
Mantle width, mm	49	46	74
Head length, mm	29	29	33
Head width, mm	52	43	58
Eye diameter, mm	27.0	25.0	29.0
Lens diameter, mm	8.0	7.0	9.0
Funnel length, mm	23.0	26.0	39.0
Free funnel length, mm	14.0	16.0	28.0
Web depth, mm (min – max)	42–53	46–58	56–85
Web formula	b > c > a > d > e	a = d > b > c > e	b > c > a > d > e
Arm length, mm (min – max)	154–178	148–179	242–303
Arm formula	2 > 1 > 3 > 4	2 > 1 > 3 > 4	1 > 2 > 3 > 4
Sucker count (min – max)	128–136	130–136	146–164
Sucker diameter (max), mm	4.0	4.0	8.0
Gill length, mm	14.5	15.0	28.0
Gill lamellae count, outer/inner	10/9	10/9	10/9
Hectocotylized arm length, mm	137	129	–
Hectocotylized arm sucker count	68	68	–
Ligula length, mm	7.0	5.0	–
Ligula width, mm	4.0	2.4	–
Calamus length, mm	2.0	2.0	–
Fecundity	–	–	227

ML mantle length, TL total length

long; in our individuals ~350% ML compared with 400% ML in combined data, with arm formula typically 2.1.3.4 (combined data). Arms with 128–164 (140.3 ± 3.3) suckers. Web medium deep (combined data, 25.1% ± 1.3% longest arm length), with sectors B and C deepest, and A and E most shallow.

New material has 10 lamellae per outer and 9 lamellae per inner demibranch; in combined data, it is 8–11

(mode: 10) outer and 8–10 (mode: 9) inner lamellae per demibranch. Rostra of both upper and lower beaks broad, and upper one hooked (Fig. 12a, c). Rachidian pentacuspoid, with large central cusp and smaller asymmetrical lateral cusps with 4 or 5 seriation (Fig. 12b).

Hectocotylized arm relatively long, 268.6% ± 12.9% ML, and 78.5% ± 4.2% opposite arm (combined data), with 68 suckers in new material (67–71 in combined data). Ligula of medium size, 3.9–10.6% (6.3% ± 1.0%) hectocotylized arm length (combined data), broad, 48.0% and 57.1% ligula length ($n=2$), tapering gradually. Ligula with distinct margins and well-marked shallow groove without transverse ridges, but with 15 and 18 low indistinct rugae ($n=2$); with groove and margins of the same width for a half of ligula length basally (Fig. 13a, b). Calamus large, 28.0–43.5% (36.9% ± 2.8%) ligula length (combined data), and pointed (Fig. 13a, b). Length of terminal organ with diverticulum 17.0% and 22.4% ML ($n=2$). Spermatophores absent in both studied early maturing males. Oviducal glands dark, broader than long, large (length 12.4% ML and width 15.7% ML in late maturing female) (Fig. 13c). Fecundity 227–300 (259.0 ± 21.5) oocytes (Tables 4, 6; SM.01 Table S3). Large vitellogenic oocytes range 17.0–22.0 mm with 18–20 follicular folds (Fig. 13c; Table 4).

Skin smooth (Fig. 10). Animals reverse-countershaded when alive, paler dorsally, darker (violet-brown) ventrally (Fig. 10) [26]; two of seven fixed individuals uniformly violet-brown over all body surfaces.

Distribution North Atlantic slope, 15–66°N, reaching the Canada–Greenland and Greenland–Iceland–Faroe Ridges [22, 24–26, 32, 55–57] [M. Vecchione, pers. comm.; this study]. While the northernmost record is Davis Strait (65.86°N) from this study, this species may reach the Greenland–Scotland Ridge, as other deep-sea cephalopods do in the area [86, 93]. This species is reported from 797–2540 m, but the associated bottom temperatures not reported [22, 25, 26, 55–57]; we report this species from 540–1957 m (1470.6 m ± 230.4 m) and 2.34–5.50 °C (3.18 ± 0.48 °C).

Biology and ecology The most mature of the studied females is at the late maturing stage. It has no sperm in the oviducal glands. In late immature females, all oocytes are pre-vitellogenic (Fig. 13d). Late maturing female has similar proportions of small vitellogenic (47% of fecundity) and medium and large vitellogenic (53% of fecundity) oocytes (Table 4). No evidence for oocyte resorption is found.

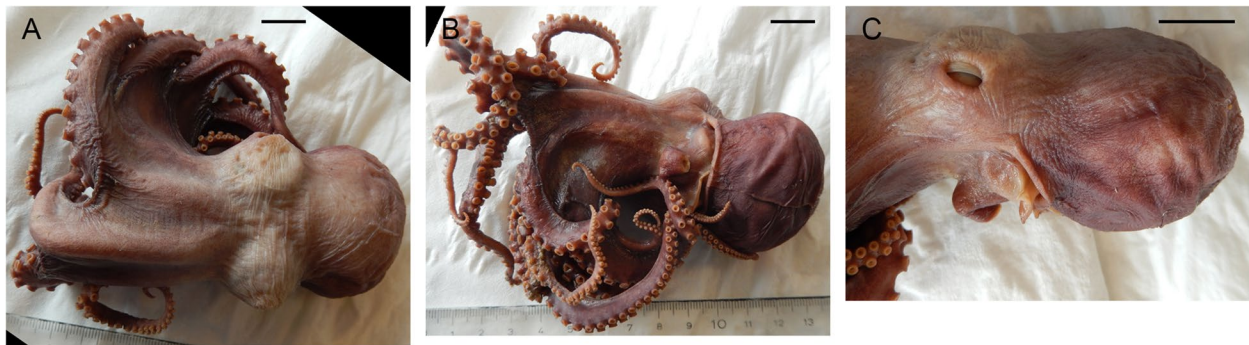


Fig. 10 *Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]. External view. BIOICE-3520-1 (late immature female, mantle length 41 mm, off Iceland, fixed): dorsal (a), ventral (b) and lateral (c) view. Scale bars = 10 mm

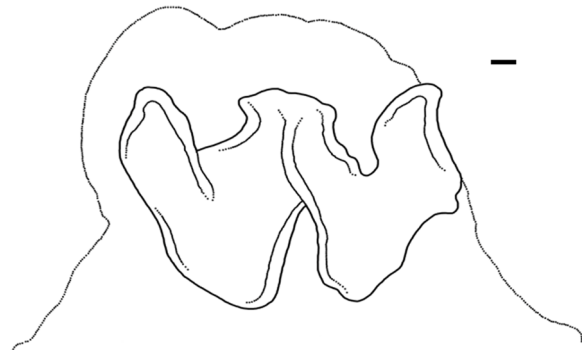


Fig. 11 *Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]. Funnel organ. BIOICE-3168 (early maturing male, mantle length 47 mm, off Iceland). Scale bar = 1 mm

The equations to estimate ML and body mass of *M. johnsonianus* from upper and lower beak hood length are provided in Table 5.

Remarks Presence of vestigial ink duct, stated for *M. johnsonianus* in [32], but not in another study of the species [26], has not been examined in IINH individuals.

The distribution ranges of *M. johnsonianus* and *M. normani* are largely similar [22, 26]. *Muusoctopus normani* differs from *M. johnsonianus* in having: 1) a relatively narrower mantle and head; 2) a shorter funnel and free part of the funnel; 3) longer arms with more and smaller suckers; 4) a longer ligula and calamus; 5) V V-shaped funnel organ (as opposed to W-shaped); and 6) in coloration, being uniformly violet-brown, whereas *M. johnsonianus* is reverse countershaded (Table 9) [26, 32] [this study]. Suckers in *M. normani* being more widely spaced than in *M. johnsonianus* is reported as a diagnostic character in [26], but dismissed in [32]; we lack *M. normani* in our samples to examine this character. Additionally, *M. normani*

may have relatively longer spermatophores and larger ripe oocytes, and lower female fecundity (Table 9) [26, 32, 90] [this study]; more studies needed to analyse these characters. The indistinct rugae on ligula are ignored by [26, 32] in both species, presumably with the assumption they are simply artifacts of the preservation process.

Muusoctopus johnsonianus is differentiated from *M. aegir*, *Muusoctopus* sp. 1 and *M. sibiricus* in ‘Remarks’ sections for these species. From *M. leioderma* (see [65–67, 92] for *M. leioderma*), *M. johnsonianus* differs in being larger and in having: 1) a broader mantle; 2) relatively longer arms with more, and smaller, suckers (including hectocotylized arms); 3) more gill lamellae; 4) different funnel organ morphology (*M. leioderma* has medial limbs of its funnel organ longer than broad marginal limbs); 5) a relatively shorter ligula with longer calamus; and 6) in coloration, and lacking of a lateral skin fold and papillae (Table 9) [26, 32] [this study].

***Muusoctopus sibiricus* (Løyning, 1930) [62]**

(Tables 3, 4, 8; SM.01 Table S4; Figs. 14, 15, 16 and 17).

Synonymy *Benthoctopus sibiricus* Løyning, 1930 [62]: 1, pls. I, II, text-figs 1, 2; Robson, 1932 [43]: 230; Grimpe, 1933 [45]: 496; Kondakov et al., 1981 [63]: 42, figs 1–3a; Nesis, 1987a [49]: 316, figs 84A, 84B; Nesis, 1987b [50]: 125; Nesis, 2001 [51]: 7.

Muusoctopus sibiricus (Løyning, 1930) [62] – Xavier et al., 2018 [86]: 5.

Not *Benthoctopus sibiricus* Løyning, 1930 [62] – Bizikov, 2004 [94]: 35, Figs. 23A, 23B, 24, 25.

Material examined Laptev Sea (LH KFU): ♂V₃, ML 38 mm, LS-L-3, Stn L-3, 74.91°N, 130.28°E, 33 m, 9 September 2014, sequenced for *COI*.

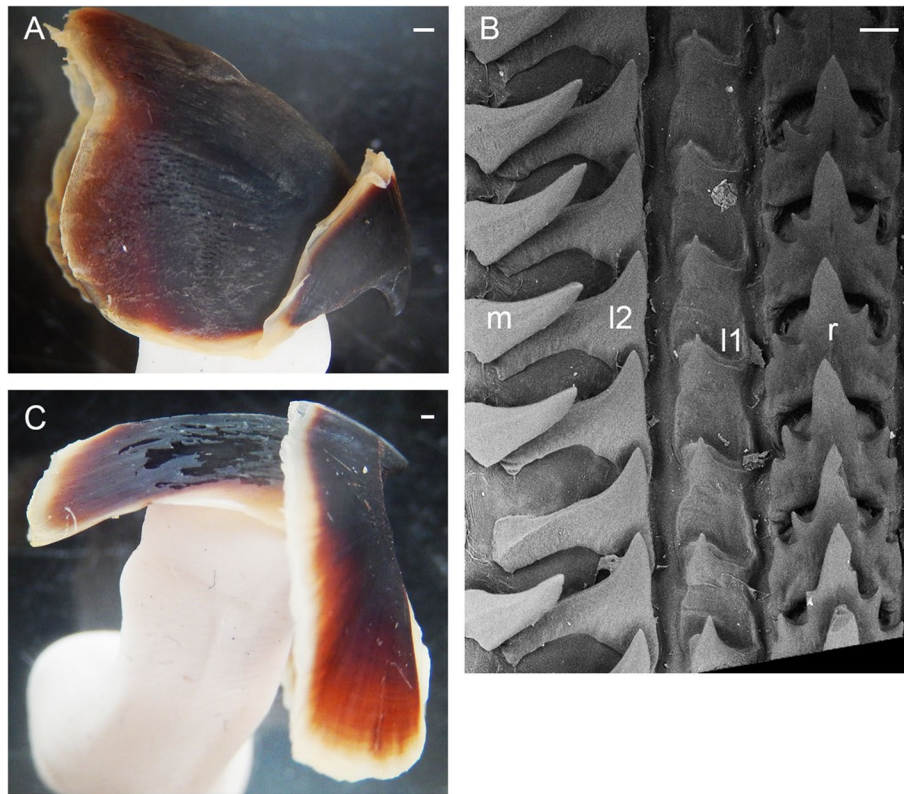


Fig. 12 *Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]. Beak and radula. BIOICE -3520-2 (late maturing female, mantle length 89 mm, off Iceland): upper (a) and lower (c) beak, and unworn section of radula (b). Scale bars: a, c = 1 mm, b = 100 μ m. Abbreviations: l1, first lateral tooth; l2, second lateral tooth; m, marginal tooth; r, rachidian tooth

East Siberian Sea (LH KFU): ♂V₂, ML 39 mm, ESS-A-19, Stn A-19, 76.09°N, 174.69°E, 36 m, 21 August 2014; ♀I, ML 14 mm, ESS-A-51, Stn A-51, 77.35°N, 146.89°E, 38 m, BT -0.82 °C, 25 August 2014; ESS-A-27, juvenile, ML 10 mm, Stn A-27, 76.40°N, 143.80°E, 29 m, BT -1.00 °C, 30 August 2014 (ex stomach contents of *Gymnocanthus tricuspis* (Reinhardt, 1830) [95], length 175 mm, weight 72 g, age 6+; partially digested).

Additional material examined See SM.01.

Diagnosis Small (maximum ML 59 mm), brick-red or bright orange octopods. Smooth skin with minute folds dorsally on mantle and head, visible in both live and fixed individuals; with ovoid body, and arms ~3.0 times ML. Suckers large, biserial, closely set, with pairs 7–12 enlarged in mature males; with 84–104 suckers on unmodified arms, and 60–64 on hectocotylus. Hectocotylized arm as long as or longer than opposite arm. Ligula large, narrow, tapering gradually, without transverse ridges, but with 27–29 low rugae. Calamus small and pointed. Funnel long, free from ventral surface of head for about half its length. Funnel organ W-shaped,

with medial limbs much longer than very broad marginal limbs. Gills very long, with 10 or 11 (mode 10) outer and 10 inner lamellae per demibranch. Stylets vestigial. Anal flaps and ink sac absent; ink duct vestigial. Rachidian with 4–5 asymmetrical cusps, with 3–6 seriation; second lateral occasionally with small secondary cusp. Very long and slender spermatophores, up to 52. Female with up to 136 oocytes.

Description Counts and measurements for the species are given in Tables 8 and S4, and indices are given in Table 9.

The following description is based on two studied males (mature and pre-spent), and maturing to mature individuals from Løyning [62] ($n=1$), MacGinitie GE [70] and MacGinitie N [71] ($n=1$; the same individual), Kondakov et al. [63] ($n=2$) and Nesis [51] ($n=1$). Species small, ML 26–55 mm (39.5 ± 6.0 mm), TL 94–253 mm (187.6 ± 27.8 mm) (Fig. 14; Tables 8, 9). Ventral ML 1 and 3 mm shorter than dorsal ML ($n=2$). Mantle ovoid, width $85.8\% \pm 11.1\%$ ML. Head width $68.9\% \pm 6.1\%$ mantle width (Fig. 14). Eyes less prominent than in other

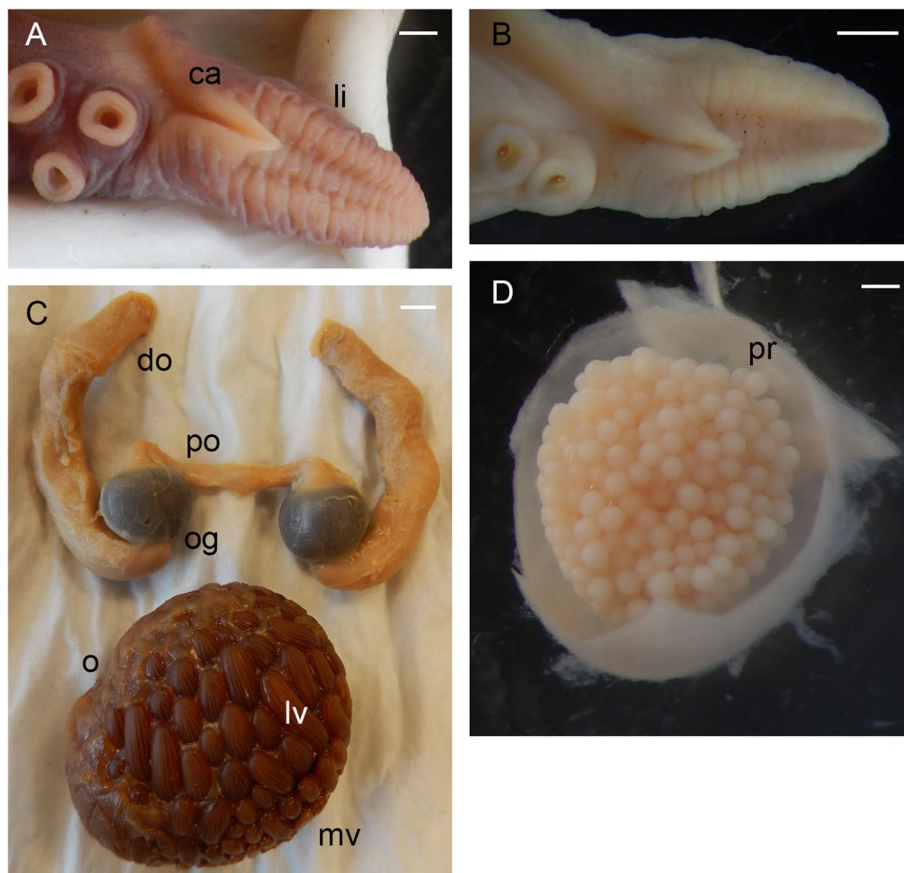


Fig. 13 *Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero & Collins, 2006) [26]. Hectocotylus and female reproductive anatomy. **a**, BIOICE-3524 (early maturing male, mantle length (ML) 49 mm, off Iceland): hectocotylus; **b**, BIOICE-3168 (early maturing male, ML 47 mm, off Iceland): hectocotylus; **c**, BIOICE -3520-2 (late maturing female, ML 89 mm, off Iceland): dissected female reproductive tract; **d**, BIOICE-3521 (late immature female, ML 36 mm, off Iceland): dissected ovary. Scale bars: **a**, **b** = 1 mm, **c** = 5 mm, **d** = 0.5 mm. Abbreviations: ca, calamus; do, distal oviduct; li, ligula; lv, late vitellogenic oocyte; mv, mid-vitellogenic oocyte; o, ovary; og, oviducal gland; po, proximal oviduct; pr, pre-vitellogenic oocyte

North Atlantic and Arctic *Muusoctopus*; their diameter 21.1% and 23.1% ML ($n=2$) (Fig. 14). Funnel long (53.8% and 63.2% ML; $n=2$), strongly tapered, free from ventral surface of head for almost half its length (45.8% and 52.4% funnel length; $n=2$). Funnel organ W-shaped, with medial limbs much longer than marginal limbs, and marginal limbs very broad (Fig. 15a). Arms ~3.0 times ML (Fig. 7), subequal in length, with formula 2.1.4.3. Suckers (84–104 (88.1 ± 1.4)) biserial to arm tip, large (11.3% \pm 1.9%, to 16.7% ML), closely set (Fig. 14); pairs 7–12 enlarged in mature and pre-spent males: 23.1% \pm 1.3% ML (Fig. 14); enlarged suckers absent in maturing female [63]. Web deep (27.3% \pm 1.1% longest arm length), with sectors B and C deepest, and D and E most shallow.

Gills very long (42.1% and 48.7% ML; $n=2$), with 10 or 11 (mode: 10) outer and 10 inner lamellae per demibranch. Stylets non-calcareous, vestigial (Fig. 15b, c), of length 4.4

and 4.6 mm (12.2% and 12.4% ML), width 0.8 and 0.9 mm (2.2% and 2.4% ML) ($n=2$). Upper beak with hooked, broad rostrum (Fig. 16a); lower beak with straight and relatively small rostrum (Fig. 16c); both typically *Muusoctopus*. Anterior salivary glands medium-sized (21.1% and 22.1% ML; $n=2$), discoid. Posterior salivary glands large (28.0% and 28.6% ML; $n=2$), approximately triangular. Crop diverticulum well developed. Presence of rectum loop not examined. Ink sac absent; vestigial ink duct present on ventral surface of digestive gland, connects to distalmost rectum. Anal flaps absent. Radula with nine elements per transverse row. Rachidian with 4–5 cusps, the central largest; lateral cusps asymmetrical, with 4–6 seriation (Fig. 16b, d) (3–4 according to [63]). Marginal and lateral teeth mostly unicuspid: small second cusp found in one individual on second right lateral, and the same is known in one individual on second left lateral in Løyning [62]; marginal teeth curved. Marginal plates well developed (Fig. 16b, d).

Table 8 Data on mature and pre-spent male individuals of *Muusoctopus sibiricus* (Løyning, 1930) [62]. Immature individuals are detailed in SM.01 Table S4. Both individuals are males

Individuals/character	LS-L-3	ESS-A-19
Area	LS	ESS
Maturity stage	Pre-spent (V ₃)	Mature (V ₂)
ML, mm	38	39
TL, mm	179	177
Ventral ML, mm	37	36
Mantle width, mm	40	35
Head length, mm	11	10
Head width, mm	30	22
Eye diameter, mm	8.0	9.0
Lens diameter, mm	2.0	2.4
Funnel length, mm	24.0	21.0
Free funnel length, mm	11.0	11.0
Web depth, mm (min – max)	26–38	26–44
Web formula	c > a = b > d > e	b > d > a = c > e
Arm length, mm (min – max)	122–130	112–128
Arm formula	2 > 1 = 3 > 4	1 > 2 > 3 > 4
Sucker count (min – max)	84–88	84–94
Normal sucker diameter (max), mm	4.0	4.0
Enlarged suckers, diameter (min – max), mm and location	6.0–9.0; 7–12 pairs	5.0–8.0; 8–12 pairs
Gill length, mm	16	19.0
Gill lamellae count, outer/inner	10/10	10/10
Gill lamellae count, inner	10	10
Hectocotylized arm length, mm	123	112
Hectocotylized arm sucker count	60	64
Ligula length, mm	14.5	15.0
Ligula width, mm	3.5	3.0
Calamus length, mm	2.5	2.3
Number of spermatophores	52	49
Spermatophore length, mm (min – max)	61.1–63.5	46.3–56.2

ML, mantle length; TL, total length; LS, Laptev Sea; ESS, East Siberian Sea

Male third right arm hectocotylized (Fig. 14e), of length 287.2% and 323.7% ML ($n=2$) or $102.6\% \pm 7.2\%$ opposite arm, with 60 to 64 (62.7 ± 1.3) suckers. Ligula large, 9.0–13.4% ($11.5\% \pm 0.9\%$) of arm length, narrow, 20.0% and 24.1% ligula length ($n=2$), tapering gradually. Ligula with distinct margins, well-marked shallow groove

without transverse ridges, but with 27 or 29 low rugae; with groove and margins basally of comparable width (Fig. 17a, b). Calamus small, 14.3–17.2% ($15.6\% \pm 0.9\%$) ligula length, and pointed (Fig. 17a, b). Spermatophoric complex accessory gland longer than spermatophoric sac (Fig. 17c), both longer than ML (accessory gland $> 2 \times$ ML). Length of terminal organ with diverticulum 40% and 45% ML ($n=2$). Spermatophores 49 (in mature male) and 52 (in pre-spent male) (Tables 3, 8), very long, 118.7–167.1% ($150.6\% \pm 3.3\%$) ML; slender, width 0.6–0.8 (0.7 ± 0.03) mm (Fig. 17d). Sperm cord width 0.15–0.20 mm, forming 59–92 (79.2 ± 5.8) whorls. Seminal reservoir length 25.5–37.4% ($29.5\% \pm 2.3\%$) spermatophore length (Table 3); ejaculatory tube comprises longest part of spermatophore (Fig. 17d; Table 3). Immature female reproductive system (Fig. 15d) with 136 oocytes (Table 4; SM.01 Table S4).

Skin smooth, with minute folds on live individuals dorsally on mantle and head, more apparent when fixed (Fig. 14). Live animal color from brick-red or bright orange with small whitish spots (Fig. 14f) (also see [63]) to uniformly pale (Fig. 14a). Fixed individuals light violet-brown (Fig. 14) (also see [63]).

COI barcode The sequence for individual LS-L-3 is deposited in GenBank, accession number OM791385.

Distribution The Laptev, East Siberian, Chukchi, and Beaufort Seas (Fig. 1), east of 105.63°E (southwestern Laptev Sea); how far east this species occurs in the Beaufort Sea, and whether it reaches the western margin of the Canadian Arctic Archipelago, are unknown [49–52, 63] [this study]. Habitat depth is 30–220 m judging from literature, with the associated bottom temperatures -1.4 – -1.6 °C [51, 62, 63, 70–72, 74], and 29–255 m (58.2 ± 16.6 m) and -1.74 – -0.28 °C (-1.23 ± 0.18 °C), respectively, according to our data.

Biology and ecology Mature male with 49 spermatophores, and pre-spent male with 52 spermatophores. An ontogenetic increase in the spermatophore size observed in mature male: older spermatophores (in the terminal organ) were shorter than younger spermatophores (in the spermatophoric sac) by 21.4%, while spermatophore width remained the same. Among spermatophore parts, the seminal reservoir increases most (46.7%), followed by the ejaculatory apparatus, 6.1%, with the head and posterior hollow part remaining similarly sized; the cement body decreases by 13.2%. Seminal reservoir width does not show an ontogenetic increase, and seminal reservoir volume increases by 78.6%.

Table 9 Comparison of the Arctic and northern North Atlantic species of *Muuscoctopus* Gleadall, 2004 [20]. Immature individuals are not used (except for *Muuscoctopus* sp. 1, where only immature individuals are known, and *M. leioderma* (Berry, 1911) [64], where it is impossible to separate them from the rest in Akimushkin (1965) [66], Hochberg (1998) [67] and Ibanez et al. (2016) [92]). Values are minimum to maximum (mean \pm SE), where applicable (except for *M. leioderma* (Berry, 1911) [64], where values from Akimushkin (1965) [66], Hochberg (1998) [67] and Ibanez et al. (2016) [92] are impossible to recalculate due to lack of individuals' details). ML, mantle length

Species/character	<i>Muuscoctopus aegir</i> sp. nov.	<i>Muuscoctopus johnsonianus</i>	<i>Muuscoctopus leioderma</i>	<i>Muuscoctopus sp. 1</i>	<i>Muuscoctopus normani</i>	<i>Muuscoctopus sibiricus</i>
Habitat depth, m	Original data	540–1957 (1470.6 \pm 230.4)	No data	101–450.5 (314.8 \pm 108.2) ^a	No data	29–255 (58.2 \pm 16.6)
Literature data	86–2000 ^b	797–2540 ^c	38–1760 ^d	No data	500–1843 ^f	30–220 ^g
Habitat temperature, °C	Original data	2.34–5.50 (3.18 \pm 0.48)	No data	1.97–2.00 ^e	No data	–1.74 to 0.28 (–1.23 \pm 0.18)
Literature data	–0.9 ^h	No data	–1.0 to 4.9 ⁱ	No data	No data	–1.4 to 1.6 ^g
Sources of information on morphology	This study ($n = 25$); Nesis (2001) ($n = 2$)	This study ($n = 3$); Allcock et al. (2006) ($n = 3$); Gleadall (2013) ($n = 1$)	Kondaikov (1941) ($n = 3$; 2 = juv.); Akimushkin (1965) (n not stated); Nesis (1987) (n not stated); Hochberg (1998) (n not stated); Ibanez et al. (2016) (n not stated)	This study ($n = 3$); A. L. Allcock (unpubl. data) ($n = 1$)	Allcock et al. (2006) ($n = 16$); Barrat et al. (2007) ($n = 5$); Gleadall (2013) ($n = 1$)	This study ($n = 2$); Løyning (1930) ($n = 1$); MacGinitie GE (1955) + MacGinitie N (1959) ($n = 1$); Kondakov et al (1981) ($n = 2$); Nesis (2001) ($n = 1$)
ML, mm	20–52 (32.3 \pm 1.8)	47–113 (78.6 \pm 10.2)	42–100	22–31 (26.5 \pm 2.3)	50–107 (73.1 \pm 3.2)	26–59 (43.4 \pm 6.0)
TL, mm	96–235 (141.6 \pm 7.8)	255–510 (354.2 \pm 49.8)	Up to 210	99–148 (121.7 \pm 14.3)	320–648 (431.6 \pm 21.8)	94–253 (187.6 \pm 27.8)
Ventral ML, mm	17–49 (27.8 \pm 1.9)	40–89 (64.7 \pm 8.5)	No data	17–26 (20.7 \pm 2.7)	43–61 (50.5 \pm 2.1)	36–37 ^e
Mantle width, % ML	87.5–140.0 (111.3 \pm 3.4)	83.1–100.0 (91.0 \pm 2.4)	63.0–89.0	87.8–109.7 (102.0 \pm 5.1)	43.3–78.8 (69.7 \pm 2.2)	54.0–105.3 (85.8 \pm 11.1)
Head width	50.0–100.0 (78.7 \pm 2.6)	63.7–106.1 (81.0 \pm 6.1)	No data	74.2–86.7 (80.2 \pm 2.8)	36.4–69.4 (56.4 \pm 2.0)	54.0–78.9 (62.3 \pm 5.7)
% mantle width	48.0–85.7 (71.3 \pm 2.2)	75.8–106.1 (88.4 \pm 4.8)	78.1–105.0	67.6–95.0 (79.5 \pm 5.9)	67.7–127.6 (81.8 \pm 3.3)	62.9–75.0 (68.9 \pm 6.1)
Eye diameter, % ML	26.4–40.7 (32.5 \pm 0.8)	32.6–55.1 (47.0 \pm 7.2)	No data	27.3–30.4 (28.7 \pm 0.9)	No data	21.1–23.1 ^e
Lens diameter, % eye diameter	20.0–38.9 (28.8 \pm 1.3)	28.0–31.0 (29.6 \pm 0.9)	No data	28.6–35.3 (32.4 \pm 2.0)	No data	25.0–26.7 ^e
Funnel length, % ML	28.8–56.7 (42.1 \pm 1.6)	39.8–55.3 (46.8 \pm 2.2)	30.0–58.0	39.1–45.2 (42.1 \pm 1.3)	20.9–46.3 (35.1 \pm 1.5)	53.8–63.2 ^e
Free funnel length, % funnel length	45.5–57.1 (52.9 \pm 0.7)	50.0–75.0 (64.3 \pm 3.5)	No data	53.8–78.6 (65.0 \pm 5.2)	19.2–66.7 (40.2 \pm 2.9)	45.8–52.4 ^e
Funnel organ shape	W; medial and marginal limbs of same length, or medial can be slightly longer; marginal limbs broad	W; medial and marginal limbs of same length, or marginal can be slightly longer; marginal limbs moderately broad	W; medial limbs longer than marginal limbs; marginal limbs broad	W; medial limbs slightly longer than marginal limbs; marginal limbs relatively narrow	W; medial and marginal limbs of same length, or medial can be slightly longer; marginal limbs relatively narrow	W; medial limbs much longer than marginal limbs; marginal limbs very broad
Web depth, % longest arm	10.4–35.6 (25.5 \pm 1.1)	17.9–32.4 (25.1 \pm 1.3)	14.0–24.0	14.0–25.7 (20.1 \pm 2.2)	10.8–25.0 (17.7 \pm 0.6)	20.0–34.4 (27.3 \pm 1.1)
Web formula	b > c > a > d > e	b > c > d > a > e	b > a = c > d > e or c > b > d > a > e or a > b > c > d > e	c > b > d > a > e	c > b > a > d > e	b > c > a > d > e

Table 9 (continued)

Species/character	<i>Muusoctopus aegir</i> sp. nov.	<i>Muusoctopus johnsonianus</i>	<i>Muusoctopus leioderma</i>	<i>Muusoctopus</i> sp. 1	<i>Muusoctopus normani</i>	<i>Muusoctopus sibiricus</i>
Arm length, % ML	234.6–376.2 (313.7 ± 6.8)	271.9–456.9 (351.3 ± 14.4)	224.0–374.0	245.5–373.9 (293.2 ± 17.7)	328.1–541.6 (417.5 ± 12.6)	230.0–350.0 (303.6 ± 28.4)
Arm formula	1 > 2 > 3 > 4	2 > 1 > 3 > 4	1 > 2 > 3 > 4	1 > 2 > 3 > 4	1 > 2 > 3 > 4	2 > 1 > 4 > 3
Sucker count	84–120 (95.5 ± 1.5)	128–164 (140.3 ± 3.3)	80–102	81–118 (99.9 ± 5.3)	134–199 (170.0 ± 4.8)	84–104 (88.1 ± 1.4)
Sucker diameter, % ML	6.3–11.7 (8.9 ± 0.3)	7.1–9.0 (8.4 ± 0.3)	7.0–11.0	8.7–10.0 (9.4 ± 0.3)	4.5–10.6 (7.0 ± 0.4)	7.8–16.7 (11.3 ± 1.9)
Enlarged suckers, diameter (% ML) and location	Enlarged suckers absent	Enlarged suckers absent	Enlarged suckers absent	No data (as only immature individuals are known)	Enlarged suckers absent	7–12 pairs; 20.5–25.0 (23.1 ± 1.3)
Gill length, % ML	21.9–44.0 (34.4 ± 1.3)	25.8–31.9 (29.4 ± 0.8)	27.0	39.1–45.0 (41.9 ± 1.7)	20.9–32.0 (25.3 ± 0.7)	42.1–48.7 ^e
Gill lamellae, outer/inner	8–9 (mode 8)/7–8 (mode 7)	8–11 (mode 10)/8–11 (mode 9)	11–12/? (whole gill 16–20)	8–10 (mode 10)/8–9 (mode 9)	7–10 (mode 9)/6–9 (mode 8)	10–11 (mode 10)/10
Stylets	Absent	Present	Present (vestigial?)	No data	Present	Vestigial
Vestigial link duct	Absent	Present	Present	No data	Present	Present
Hectocotylized arm length	177.8–282.6 (233.8 ± 6.5)	208.0–299.0 (268.6 ± 12.9)	127.0–139.0	246.7–256.5 ^e	189.0–261.2 (220.3 ± 6.3)	287.2–323.7 ^e
Hectocotylized arm sucker count	55.2–80.7 (71.5 ± 2.2)	65.3–88.4 (78.5 ± 4.2)	69.0–89.0	79.7–93.7 ^e	51.0–63.7 (58.0 ± 1.7)	91.1–123.4 (102.6 ± 7.2)
Ligula length, % hectocotylized arm length	46–56 (52.0 ± 1.1)	67–71 (68.3 ± 0.6)	47–61	56–66 ^e	61–72 (65.8 ± 1.3)	60–64 (62.7 ± 1.3)
Ligula width, % ligula length	8.0–14.1 (10.3 ± 0.5)	3.9–10.6 (6.3 ± 1.0)	11.0–18.0	4.6–6.5 ^e	6.3–11.1 (8.6 ± 0.4)	9.0–13.4 (11.5 ± 0.9)
Calamus length, % ligula length	45.0–63.3 (55.4 ± 2.1)	48.0–57.1 ^e	No data	55.6–62.5 ^e	No data	20.0–24.1 ^e
Number of spermatophores	27.5–43.3 (36.8 ± 1.4)	28.0–43.5 (36.9 ± 2.8)	12.0–20.0	37.5–66.7 ^e	26.7–60.0 (42.3 ± 2.9)	14.3–17.2 (15.6 ± 0.9)
Spermatophore length	5–22 (12.5 ± 2.4)	4–19 ^e	No data	No data	3–25 (13.1 ± 2.3)	49–52 ^e
Fecundity of females	27.9–48.0 (39.8 ± 0.5)	104.0–120.0 ^e	No data	No data	75.0–119.0 (92.8 ± 4.4)	46.3–63.5 (57.9 ± 1.1)
Ripe oocyte length	78.0–135.9 (108.1 ± 1.8)	92.0–114.3 ^e	No data	No data	97.5–142.2 (121.0 ± 5.9)	118.7–167.1 (150.6 ± 3.3)
	65–168 (99.5 ± 6.8)	227–300 (259.0 ± 21.5)	No data	No data	70–342 (218.9 ± 34.2)	136
	12.5–13.0 ^e	No data; large vitellogenic oocytes are 17.0–22.0 (mean 20.0) mm	14.0–17.0	No data	15.0–22.0 (18.0 ± 0.7)	No data
	52.1–54.2 ^e	No data; large vitellogenic oocytes 19.1–24.7 (mean 22.5)	No data	No data	21.1–40.7 (27.8 ± 2.3)	No data

^a data for individual USNM 574859 provided by A. L. Allcock (A. L. Allcock, unpubl. data) included; ^bHoyle 1886 [34], Appelloff 1893 [36], Russell 1909 [41], 1922 [42], Grieg 1933 [44], Nesis 2001 [51], Taite et al. 2023 [57]; ^cCollins et al. 2001 [22], Allcock et al. 2006 [26], Strugnell et al. 2009 [56], Gleadall 2013 [32], Luna et al. 2021 [55], Pratt et al. 2021 [57]; ^dKondakov 1941 [65], Akimushkin 1965 [66], Nesis 1987 [49], Hochberg 1998 [67]; ^en = 2; ^fCollins et al. 2001 [22], Allcock et al. 2006 [26], Strugnell et al. 2009 [56], Gleadall 2013 [32], Taite et al. 2023 [57]; ^gLeyning 1930 [62], MacGinitie GE 1955 [70], MacGinitie N 1959 [71], Kondakov et al. 1981 [63], Nesis 2001 [51], Bluhm et al. 2004, Furuya 2010 [72]

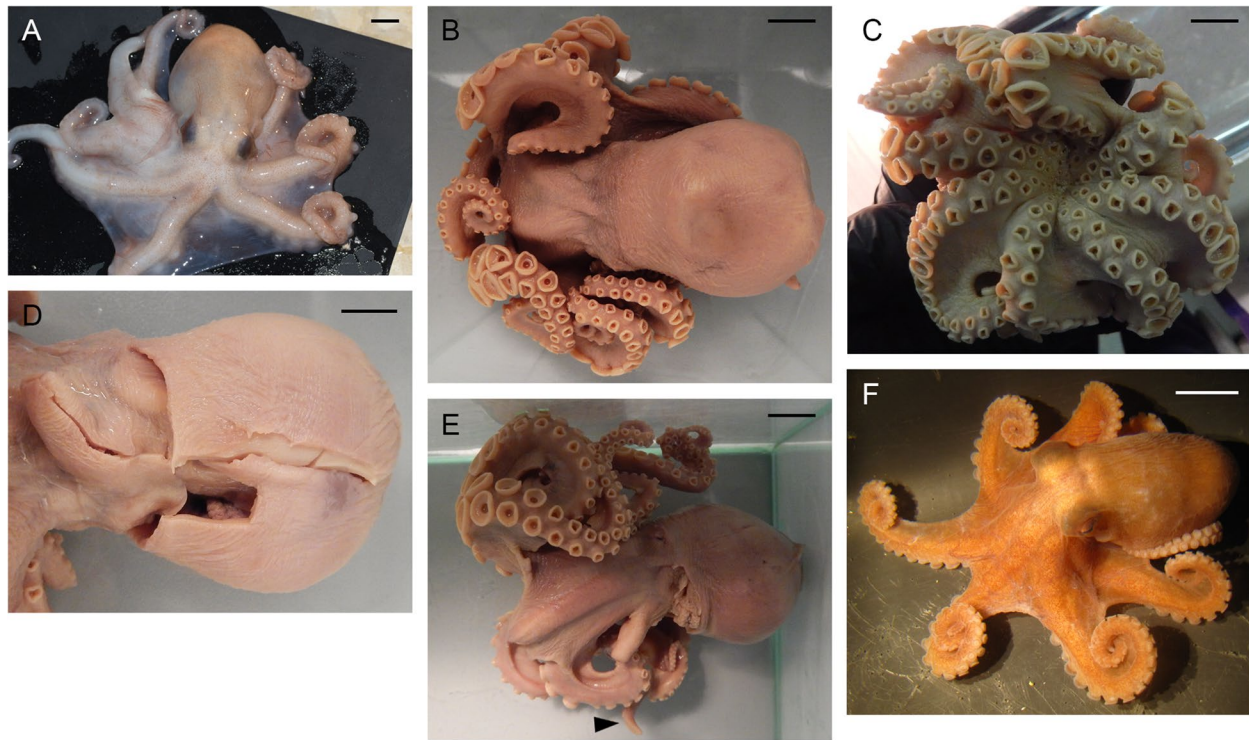


Fig. 14 *Muusoctopus sibiricus* (Løyning, 1930) [62]. External view. **a–d**, LS-L-3 (pre-spent male, mantle length (ML) 38 mm, Laptev Sea, live) and fixed (**b–d**): dorsal (**a, b**) and ventral (**c, d**) view, mantle cut and piece taken for molecular analysis in **d**; **e**, ESS-A-19 (mature male, ML 39 mm, the East-Siberian Sea, fixed): lateral view; **f**, LS-O-22 (not analyzed; Laptev Sea, live): dorsal view. Arrowhead indicates the hectocotylus in male. Scale bars = 10 mm

Remarks Reports of *M. sibiricus* by Bizikov [94] from the Bering Sea continental slope are in fact referable to another Pacific *Muusoctopus* species, but not to *M. sibiricus*: these individuals are larger than *M. sibiricus* and *M. leioderma* (Table 9) [63, 65–67, 92] [this study]; and their stylets differ from those of *M. sibiricus* in shape [94] [this study]. The stylets of *M. sibiricus* in this study are considered vestigial following Bizikov [94] [p. 39], because they are very small, and the left and right stylets are highly variable within the same individual and among the individuals.

A diagnosis of *M. sibiricus* was absent in the literature prior to this study. *Muusoctopus sibiricus* differs from other Arctic and North Atlantic *Muusoctopus* species, excepting *M. leioderma*, in having skin folds in live animals, and otherwise in: 1) funnel organ morphology; 2) a presence of enlarged suckers, and generally larger suckers than other regional species; 3) proportionally longer gills (values are overlapping with *M. aegir* and *Muusoctopus* sp. 1) with 10 or 11 (mode 10) outer and 10 inner lamellae per demibranch; 4) vestigial stylets; 5) occasionally having a bicuspid second lateral and rachidian with 3–4 cusps; 6) proportionally the longest hectocotylized arm

relative to ML and opposite arm, with a very long and narrow ligula and short calamus; and 6) more and larger spermatophores (although data are lacking on spermatophore number in *M. leioderma* and *Muusoctopus* sp. 1), of different proportions to those of *M. aegir* (Table 9) [26, 32, 62, 63, 65–67, 92] [this study].

DNA barcoding

There were no sequences of *M. sibiricus* in either GenBank (<https://www.ncbi.nlm.nih.gov/genbank>) or BOLD (<https://www.boldsystems.org/>) databases prior to this study. The analyses of available sequences of *Muusoctopus*, *Benthoctopus* and *Vulcanoctopus* González & Guerra, 1998 (in González et al. 1998) [96] from these databases vs. our sequence of *M. sibiricus* support recognizing it as a distinct species (SM.01 Fig. S1).

Discussion

Species identification

The main characters used to identify the Arctic and northern North Atlantic species of *Muusoctopus* are provided in Table 9, with the differences among species reported in the Remarks sections for each species. The most frequently cited characters in species descriptions

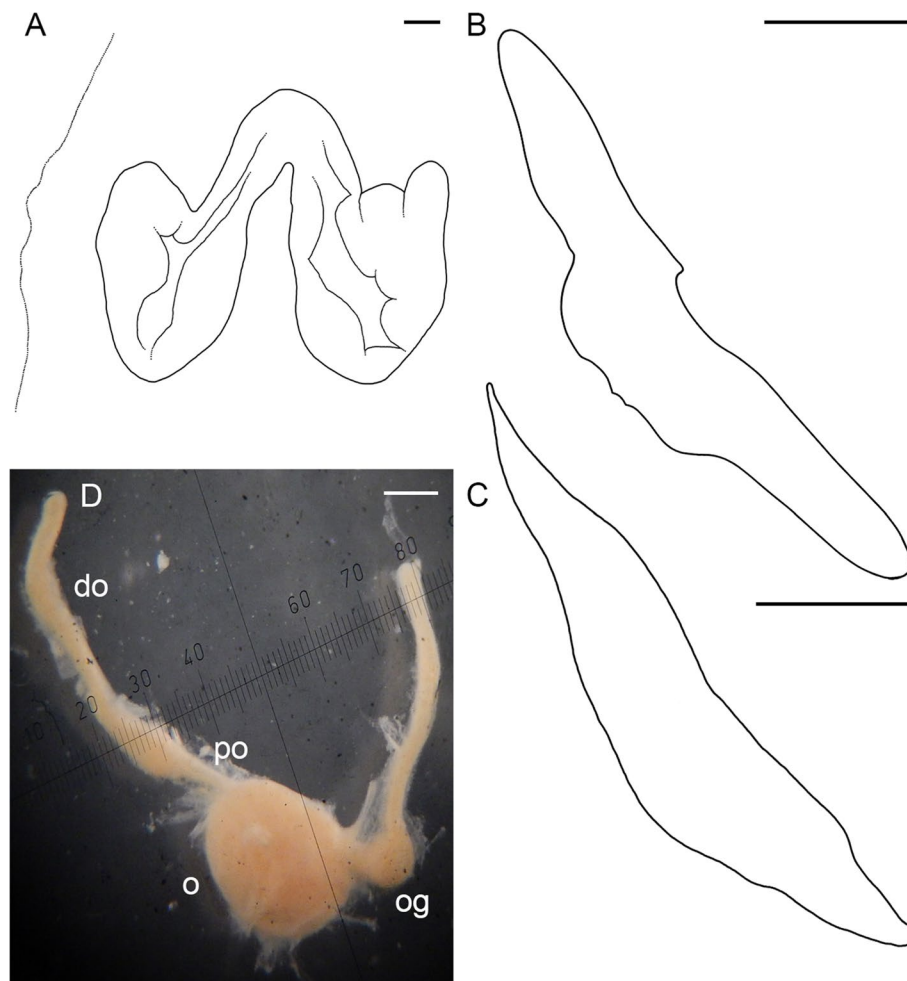


Fig. 15 *Muusoctopus sibiricus* (Løyning, 1930) [62]. General anatomy and female reproductive anatomy. **a**, LS-L-3 (pre-spent male, mantle length (ML) 38 mm, the Laptev Sea): funnel organ (**a**) and stylet (**b**); **c**, ESS-A-19 (mature male, ML 39 mm, the East-Siberian Sea): stylet; **d**, ESS-A-51 (early immature female, ML 14 mm, the East-Siberian Sea): female reproductive tract. Scale bars = 1 mm. Abbreviations: do, distal oviduct; o, ovary; og, oviducal gland; po, proximal oviduct

are relative mantle width; sucker diameter; arm, hectocotylied arm, opposite arm, gill, ligula and calamus lengths; funnel organ morphology; sucker (normal and hectocotylied arms) and gill lamellae counts; and stylet morphology (present/vestigial/absent). *COI* sequences may differentiate species, and these are currently available for *M. aegir* (as *Muusoctopus* sp. [57]; see Remarks section for this species for explanation of why we think it is *M. aegir*), *M. johnsonianus* [26, 57, 97], *M. normani* [26, 57] and *M. sibiricus* [this study].

Biogeography and phylogeography

Eleven species of cephalopods complete their entire life-cycle in the Arctic: the squid *Gonatus fabricii* (Lichtenstein, 1818) [98], sepiolids *Rossia palpebrosa* Owen, 1835 [99], *R. moelleri* Steenstrup, 1856 [100] and *R. megaptera* Verrill, 1881 [87], and octopods *Cirrotheuthis muelleri*

Eschricht, 1836 [101], *B. arcticus*, *B. bairdii*, *B. pugniger*, *M. sibiricus*, *M. leioderma* and *Muusoctopus* sp., which is described here as *M. aegir* [75, 86, 93, 102]. Here, we also report *Muusoctopus* sp. 1, apparently new species from the Canadian Arctic Archipelago and Baffin Bay. Of these species, *R. moelleri* and *M. sibiricus* are the most shallow and cold-water species among their respective genera [50, 51, 86, 93]. Little is known of the depth distribution of *Muusoctopus* sp. 1, but *M. aegir* ascends from deeper to shallower depths towards the pole, frequenting mean depths of 951 m in Icelandic waters, 518 m in the Barents Sea, and 403 m in the Kara Sea (polar emergence). Both *B. arcticus* and *C. muelleri* also manifest such polar emergence [23, 50, 51, 103].

Of the 12-now recognized Arctic cephalopod taxa, seven are incirrates, and four of them of *Muusoctopus* taxa; only polar emergence is present [23, 50, 51, 86, 93,

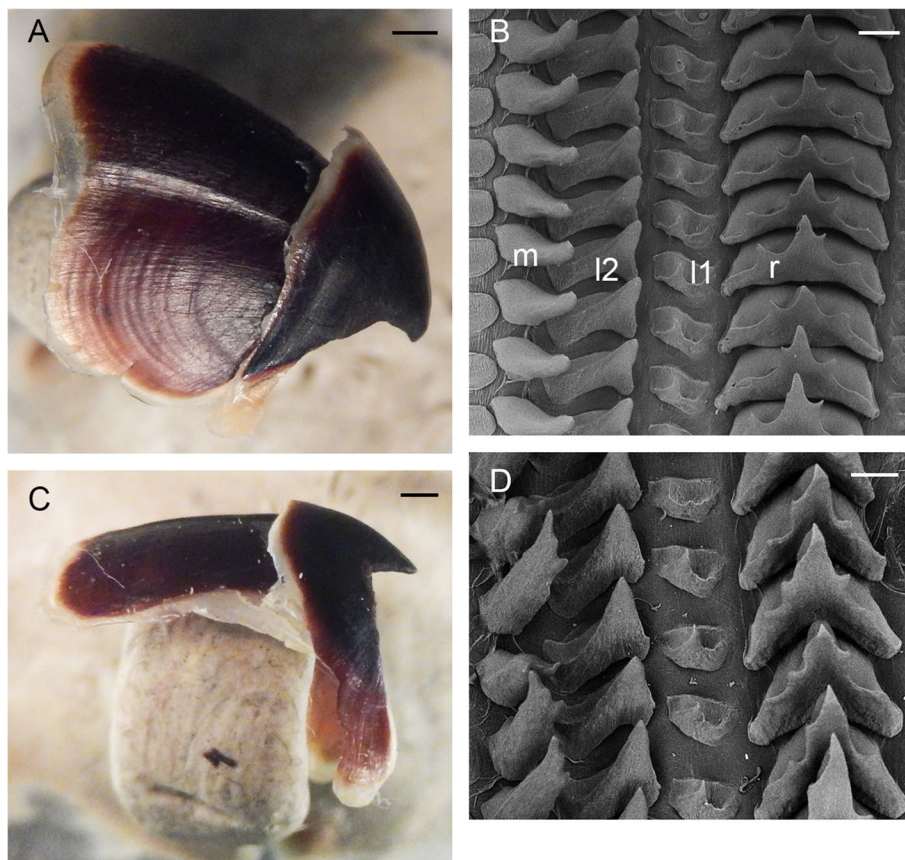


Fig. 16 *Muusoctopus sibiricus* (Løyning, 1930) [62]. Beak and radula. **a–c**, LS-L-3 (pre-spent male, mantle length (ML) 38 mm, Laptev Sea): upper (**a**) and lower (**b**) beak, and unworn section of radula (**c**); **d**, ESS-A-19 (mature male, ML 39 mm, East-Siberian Sea): unworn section of radula. Scale bars: **a, c** = 1 mm, **b, d** = 100 μ m. Abbreviations: l1, first lateral tooth; l2, second lateral tooth; m, marginal tooth; r, rachidian tooth

103]. In contrast, of the 54 cephalopod taxa reported from Antarctic waters, 27 are incirrates, of which 17 manifest either polar emergence or submergence (the opposite trend) [86, 97, 104]. *Muusoctopus* manifest polar emergence at both poles [51, 97] [this study].

Results from non-molecular biogeography methods suggest that *M. sibiricus* originated in the North Pacific, and *M. aegir* (at the time as *Be. piscatorum*) in the North Atlantic [50–52]. These indicate that *Muusoctopus* entered the Arctic independently from the Atlantic and Pacific. Molecular methods suggest that the origins of the *Muusoctopus* is either from the North Pacific [32, 97] or North Atlantic [92], with different dispersal

thereafter. No molecular study has included Arctic material. However, independent appearances of *Muusoctopus* species from the Atlantic and Pacific Arctic are congruent with molecular genetics results [32, 92, 97].

It is known that the ink sac was lost independently within deep-sea Incirrata [15]. In *Sasakiopus salebrosus* (Jorgensen et al., 2010) [105], there is both a vestigial functional ink sac and ink duct [105]. In Arctic *M. sibiricus*, Arctic and northern North Pacific *M. leioderma*, North Atlantic *M. johnsonianus* and *M. normani*, and South Atlantic *M. bizikovi* Gleadall, Guerrero-Komrutz, Hochberg & Laptikhovskiy, 2010 [31], there is no ink sac, but a non-functional vestige of the ink duct

(See figure on next page.)

Fig. 17 *Muusoctopus sibiricus* (Løyning, 1930) [62]. Hectocotylus and male reproductive anatomy. **a**, ESS-A-19 (mature male, mantle length (ML) 39 mm, the East-Siberian Sea): hectocotylus; **b–d**, LS-L-3 (pre-spent male, ML 38 mm, the Laptev Sea): hectocotylus (**b**), spermatophoric complex (**c**), dissected, ventral view, and spermatophore (**d**). Scale bars: **a, b, d** = 1 mm, **c** = 5 mm. Abbreviations: ag, accessory gland; ca, calamus; cb, cement body, di, diverticulum; ea, ejaculatory apparatus; he, head; sd, sperm duct; sg, spermatophoric glands; sr, seminal reservoir; ss, spermatophoric sac; te, testis; th, thread; to, terminal organ



Fig. 17 (See legend on previous page.)

is present [31, 32, 67] [this study]. Stylets have seldom been reported in *Muusoctopus* species descriptions [29, 43, 77, 106], however, vestigial stylets in East Arctic *M. sibiricus* and North Pacific *Muusoctopus* sp., and the absence of stylets in the West Arctic *M. aegir* and the well-developed stylets in several of the Atlantic and Pacific species [26, 31, 94, 107] [this study] suggest an independent reduction of stylets in ancestral *Muusoctopus* taxa. Shared common vestigial absences of a particular character among many closely related species are more likely explanation than multiple losses [108], which is supposed to be the case for ink sac, but not stylets, in *Muusoctopus*.

Reproductive biology and ecology

The spermatophore morphology of *Muusoctopus* [26, 29, 31, 107] [this study] differs from that of *Bathypolypus* [23]. In some species of *Muusoctopus*, the ejaculatory apparatus is the longest part of the spermatophore, and in others it is the seminal reservoir [26, 29, 31, 107] [this study]. An ontogenetic increase in the spermatophore size (with spermatophores produced later during ontogenesis being larger than those produced earlier), and production of the tentative spermatophores prior to the onset of normal spermatophorogenesis are known for squids and sepiolids [80, 109–117], and for cirrate octopods [118]. Herein we report an ontogenetic increase in the spermatophore size for incirrate octopods (in *M. aegir* and *M. sibiricus*), in addition to production of the tentative spermatophores prior to the onset of normal spermatophorogenesis (in *M. aegir*).

The spermatophore number in *Muusoctopus* (typically to 20–25) is greater than in *Bathypolypus* (to 6) [23, 26, 32] [this study]. In *M. sibiricus*, we report up to 52 spermatophores, which are relatively longer than in other species of *Muusoctopus* [26, 32] [this study], surpassed in length only by some *Enteroctopus* Rochebrune & Mabile, 1889 [119] [120].

Although sperm in the oviducal glands is considered the typical mechanism of incirrate fertilization [121], it has not been recorded in *Muusoctopus*. Here, it is reported for the first time in this genus (in *M. aegir*). Synchronous maturation of the oocytes with their further division into two portions, of which only one undergoes consecutive development, supposedly occurs for the most of deep-sea and Antarctic incirrates, with realized fecundity ranging ~40–100% in these species [122–124]. We regard the latter value to be an overestimation because of sample conditions, rendering post-ovulatory follicles similar to resorbed oocytes and vice versa: the realized fecundity is ~24–90% in deep-sea and polar squids [125]. Still, low fecundity and large ripe oocytes in deep-sea North Atlantic and Arctic *Muusoctopus* species

[26, 90] [this study] conform with known data on the reproductive biology of deep-sea and Antarctic octopods, as does the realized fecundity of *M. aegir* [122–124].

Conclusions

Two new species of deep-sea octopods of the genus *Muusoctopus* are reported, and a diagnosis for *M. sibiricus* is provided. The key characters and metrics are given in a table to identify these octopods in the northern North Atlantic and Arctic. This resolves a long-standing issue with Arctic non-*Bathypolypus* deep-sea octopods erroneously reported as '*Be. piscatorum*' and otherwise ignored. The unusually large sample size for a deep-sea species ($n=37$) spanning the area off Iceland to the Kara Sea enabled analysis of biology and ecology of the new species, *M. aegir*. Reproductive biology of *Muusoctopus* octopods is reported, including the original data on realized fecundity and fertilization. Equations for estimating octopod size from beak measurements are provided, which are an invaluable tool in analyses of predator diets.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40851-023-00220-x>.

Additional file 1.

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Authors' contributions

A.V.G., G.G. and R.M.S. conceptualized and designed the work, collected, and analyzed morphological data, acquired images, prepared figures, interpreted results, and drafted the work. M.E.B., L.L.J., S.H.O., D.V.Z. and O.L.Z. provided the samples and contextual information, and participated in interpretation of results. E.I.K., E.I.S. and L.H.S. analyzed molecular data, acquired respective images, and prepared respective figures. All authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article [and its supplementary information files]. New species nomenclatural acts are registered in ZooBank. Genetic data are deposited in GenBank, NCBI. This article has been registered at Zoobank (urn:lsid:zoobank.org:pub:18E04F52-1AFB-452D-8FD4-936CECF228E6F).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

- Grimpe G. *Chunioteuthis* eine neue Cephalopodengattung. *Zool Anz*. 1916;46:349–59.
- Ushakov PV. Study of deep-sea fauna. *Priroda*. 1952;6:100–2.
- Voss GL. The biogeography of the deep-sea Octopoda. *Malacologia*. 1988;29:295–307.
- Orbigny A d'. Mollusques, Echinodermes, Foraminifères et Polypiers, recueillis aux Iles Canaries par MM. Webb et Berthelot. Mollusques. In: Webb PB, Berthelot S, editors. *Histoire Naturelle des Iles Canaries Tome II Partie 2 Zoologie*. Paris: Baillière; 1836. p. 45:73–104, 46:105–117 (1840).
- Norman MD, Finn JK, Hochberg FG. Family Octopodidae. In: Jereb P, Roper CFE, Norman MD, Finn JK, editors. *Cephalopods of the world An annotated and illustrated catalogue of cephalopod species known to date No 4, Vol 3: Octopods and Vampire Squids*. Rome: FAO; 2013. p. 36–215.
- Norman MD, Hochberg FG, Huffard C, Mangold KM (1922–2003). *Octopodoidea Orbigny, 1839. Octopods, octopuses, devilfishes*. Version 16 November 2016 (under construction). [Internet]. The Tree of Life Web Project. 2016 [cited 2022 Feb 3]. Available from: <http://tolweb.org/Octopodoidea/20194/2016.11.16>.
- Robson GC. A monograph of the Recent Cephalopoda. Part I. Octopodinae. London: British Museum (Natural History); 1929.
- Rochebrune AT d'. Étude monographique de la famille des Eledonidae. *Bull Soc Philomath Paris*. 1884;8:152–63.
- Strugnell JM, Norman MD, Vecchione M, Guzik M, Allcock AL. The ink sac clouds octopod evolutionary history. *Hydrobiologia*. 2014;725:215–35.
- Taki I. On two new eledonid octopods from the Antarctic Sea. *J Fac Appl Biol Sci Hiroshima Univ*. 1961;3:297–316.
- Sauer WHH, Gleadall IG, Downey-Breedt N, Doubleday Z, Gillespie G, Haimovici M, et al. World Octopus Fisheries. *Rev Fish Sci Aquac*. 2021;29:279–429.
- Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C, et al. Recent pace of change in human impact on the world's ocean. *Sci Rep*. 2019;9:11609.
- Jørgensen LL, Arvanitidis C, Birchenough SNR, Clark MR, Cruz ICS, Cunha M, et al. Marine invertebrates. The Second World Ocean Assessment, Vol 1. New York: United Nations; 2021. p. 141–60.
- Engel MS, Ceriaco LMP, Daniel GM, Dellapé PM, Löbl I, Marinov M, et al. The taxonomic impediment: a shortage of taxonomists, not the lack of technical approaches. *Zool J Linn Soc*. 2021;193:381–7.
- Voss GL. Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). In: Clarke MR, Trueman ER, editors. *The Mollusca, Vol 12, Paleontology and neontology of cephalopods*. New York: Academic Press; 1988. p. 253–76.
- Purser A, Marcon Y, Hoving HJT, Vecchione M, Piatkowski U, Eason D, et al. Association of deep-sea incirrate octopods with manganese crusts and nodule fields in the Pacific Ocean. *Curr Biol*. 2016;26:R1268–9.
- Hartwell AM, Voight JR, Wheat CG. Clusters of deep-sea egg-brooding octopods associated with warm fluid discharge: an ill-fated fragment of a larger, discrete population? *Deep Sea Res*. 2018;(135):1–8.
- Hoving HJT, Perez JAA, Bolstad KSR, Braid HE, Evans AB, Fuchs D, et al. Chapter 3. The study of deep-sea cephalopods. In: Vidal EAG, editor. *Advances in marine biology: advances in cephalopod science biology, ecology, cultivation and fisheries 67*. London: Elsevier; 2014. p. 235–359.
- Grimpe G. Teuthologische Mitteilungen. VII. Systematische Übersicht der Nordsee-cephalopoden. *Zool Anz*. 1921;52:297–305.
- Gleadall IG. Some old and new genera of octopus. *IIS*. 2004;10:99–112.
- Verrill AE. Report on the cephalopods, and on some additional species dredged by the U.S. fish commission steamer 'Fish Hawk', during the season of 1880. *Bull Mus Comp Zool*. 1881;8:99–116.
- Collins MA, Yau C, Allcock L, Thurston MH. Distribution of deep-water benthic and benthic-pelagic cephalopods from the north-east Atlantic. *J Mar Biol Assoc UK*. 2001;81:105–17.
- Muus BJ. The *Bathypolypus-Benthoctopus* problem of the North Atlantic (Octopodidae, Cephalopoda). *Malacologia*. 2002;44:175–222.
- Vecchione M, Young RE, Piatkowski U. Cephalopods of the northern Mid-Atlantic Ridge. *Mar Biol Res*. 2010;6:25–52.
- Pratt A, France SC, Vecchione M. Survey of bathyal incirrate octopods in the western North Atlantic. *Mar Biodivers*. 2021;51:49.
- Allcock AL, Strugnell JM, Ruggiero H, Collins MA. Redescription of the deep-sea octopod *Benthoctopus normani* (Massy 1907) and a description of a new species from the Northeast Atlantic. *Mar Biol Res*. 2006;2:372–87.
- Prosch V. Nogle nye Cephalopoder, beskrevne og anatomisk under sogte. *K Dansk Vidensk Selsk Skr*. 1847;1:53–72.
- Verrill AE. Results of recent dredging expeditions on the coast of New England. *Am J Sci Arts*. 1873;3:5–15.
- Voss GL, Pearcy WG. Deep-water octopods (Mollusca: Cephalopoda) of the northeastern Pacific. *Proc Calif Acad Sci*. 1990;47:47–94.
- Verrill AE. Notice of recent additions to the marine fauna of the eastern coast of North America, No. 7. *Am J Sci Arts*. 1879;18:468–70.
- Gleadall IG, Guerrero-Kommritz J, Hochberg FG, Laptikhovskiy VV. The inkless octopuses (Cephalopoda: Octopodidae) of the southwest Atlantic. *Zool Sci*. 2010;27:528–53.
- Gleadall IG. A molecular sequence proxy for *Muusoctopus januarii* and calibration of recent divergence among a group of mesobenthic octopuses. *J Exp Mar Biol Ecol*. 2013;447:106–22.
- MolluscaBase eds. MolluscaBase. *Muusoctopus* Gleadall, 2004. [Internet]. World Register of Marine Species. 2022 [cited 2022 Feb 3]. Available from: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=527126>.
- Hoyle WE. Report on the Cephalopoda collected by H.M.S. 'Challenger' during the years 1873–1876. HMS 'Challenger' Reports: Zoology. 1886;XVI:1–246.
- Lønning E. Öfversigt öfver Sveriges Cephalopoder. Bihang till K Svenska vet akad handlingar. 1892;17:1–12.
- Appelløf A. Teuthologische Beiträge. III. Bemerkungen über die auf der norwegischen Nordmeer-Expedition (1876–78) gesammelten Cephalopoden. *Bergens Mus Aarbog*. 1893;1:7–13.
- Massy AL. Preliminary notice of new and remarkable cephalopods from the south-west coast of Ireland. *Ann Mag Nat Hist*. 1907;20:377–84.

38. Massy AL. The Cephalopoda Dibranchiata of the coasts of Ireland. *SI*. 1909;i:1–39.
39. Massy AL. Cephalopoda of the Irish Coast. *Proc Roy Irish Acad, B*. 1928;38:1–25.
40. Pfeffer G. Die Cephalopoden Nordisches Plankton. 1908;2:9–116.
41. Russell ES. Preliminary notices of the Cephalopoda collected by the F.C. 'Goldseeker'. *Ann Mag Nat Hist*. 1909;3:446–55.
42. Russell ES. Report on the Cephalopoda collected by the research steamer 'Goldseeker' during the years 1903–1908. *Fish Board Scotl*. 1922;3:1–45.
43. Robson GC. A monograph of the Recent Cephalopoda. Part II. The Octopoda (excluding the Octopodinae). London: British Museum (Natural History); 1932.
44. Grieg JA. The cephalopod fauna of Svalbard. *Tromsø Mus Aars, Nat Avd*. 1933;53:1–19.
45. Grimpe G. Die cephalopoden des arktischen gebietes. *Fauna Arctica*. 1933;6:489–514.
46. Stephen AGIX. – The Cephalopoda of Scottish and adjacent waters. *Earth Environ Sci Trans R Soc Edinb*. 1944;61:247–70.
47. Muus BJ. Skallus, sotaender, blaecksprutter. *Dan Fauna*. 1959;65:1–239.
48. Aldrich FA, Lu CC. On an octopod from Placentia Bay. *Newfoundland Veliger*. 1968;11:70–1.
49. Nesis KN. *Cephalopods of the World*. Neptune City: Tropical Fish Hobby-est Publications; 1987.
50. Nesis KN. Cephalopod molluscs of the Arctic Ocean and its seas. In: Kafanov AI, editor. *Fauna and distribution of molluscs: North Pacific and Arctic Basin*. Vladivostok: USSR Academy of Sciences; 1987. p. 115–36.
51. Nesis KN. West-Arctic and East-Arctic distributional ranges of cephalopods. *Sarsia*. 2001;86:1–11.
52. Nesis KN. Distribution of Recent cephalopoda and implications for Pliocene events. *Berliner Paläobiol Abh*. 2003;3:199–224.
53. Nixon M. A note on the eggs of *Benthoctopus piscatorum* (Cephalopoda: Octopoda). *J Zool*. 1991;223:499–500.
54. Nixon M, Young JZ. *The brains and lives of cephalopods*. Oxford: Oxford University Press; 2003.
55. Luna A, Rocha F, Perales-Raya C. A review of cephalopods (Phylum: Mollusca) of the Canary Current Large Marine Ecosystem (Central-East Atlantic, African coast). *J Mar Biol Assoc UK*. 2021;101:1–25.
56. Strugnell J, Voight JR, Collins PC, Allcock AL. Molecular phylogenetic analysis of a known and a new hydrothermal vent octopod: their relationships with the genus *Benthoctopus* (Cephalopoda: Octopodidae). *Zootaxa*. 2009;2096:442–59.
57. Taitte M, Dillon L, Strugnell JM, Drewery J, Allcock AL. DNA barcoding reveals unexpected diversity of deep-sea octopuses in the North-East Atlantic. *Biol Environ*. 2023;123:1–12.
58. Hoyle WE. Diagnoses of new species of Cephalopoda collected during the cruise of H.M.S. 'Challenger'. Part I: The Octopoda. *Ann Mag Nat Hist*. 1885;15:222–36.
59. Toll RB. *Benthoctopus oregonae*, a new species of octopod (Mollusca, Cephalopoda) from the southern Caribbean with a redescription of *Benthoctopus januarii* (Hoyle, 1885). *Bull Mar Sci*. 1981;31:83–95.
60. Zezina ON. Biogeography of the bathyal zone. *Adv Mar Biol*. 1997;32:389–426.
61. Watling L, Guinotte J, Clark MR, Smith CR. A proposed biogeography of the deep ocean floor. *Prog Oceanogr*. 2013;111:91–112.
62. Løyning P. *Benthoctopus sibiricus*, a supposed new species of the Cephalopoda from the Siberian Arctic Ocean. *Maud' Sci Res*. 1930;5:1–11.
63. Kondakov NN, Moskalev LI, Nesis KN. *Benthoctopus sibiricus* Løyning, an octopod endemic of the eastern Arctic. In: Kuznetsov AP, editor. *Ecological investigations of the shelf*. Moscow: Institute of Oceanology, USSR Academy of Sciences; 1981. p. 42–56.
64. Berry SS. Preliminary notices of some new Pacific cephalopods. *Proc US Natl Mus*. 1911;40:589–92.
65. Kondakov NN. Cephalopods of the far eastern seas. *Res Far East Seas*. 1941;1:216–55.
66. Akimushkin II. Cephalopods of the seas of the USSR. Jerusalem: Israel Program for Scientific Translations; 1965.
67. Hochberg FG. Class Cephalopoda. In: Valentich-Scott P, Blake JA, editors. *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel Volume 8 The Mollusca Part 1, The Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda*. Santa Barbara: Santa Barbara Museum of Natural History; 1998. p. 175–236.
68. Kondakov NN. Class Cephalopoda. In: Gaevskaia NS, editor. *A manual of the fauna and flora of the northern seas of the USSR*. Moscow: Soviet Science; 1948. p. 447–50.
69. Berry SS. Notes on some Japanese cephalopods. A review of Sasaki's 'Albatross' Report. *Ann Mag Nat Hist*. 1921;8:351–2.
70. MacGinitie GE. Distribution and ecology of the marine invertebrates of Point Barrow. *Alaska Smith Misc Coll*. 1955;128:1–201.
71. MacGinitie N. Marine Mollusca of Point Barrow, Alaska. *Proc US Natl Mus*. 1959;59–208.
72. Bluhm B, Iken K, Mincks Hardy S, Sirenko B, Holladay B. Community structure of epibenthic megafauna in the Chukchi Sea. *Aquat Biol*. 2009;7:269–93.
73. Feder HM, Foster NR, Jewett SC, Weingarter TJ, Baxter R. Mollusks in the Northeastern Chukchi Sea. *Arctic*. 1994;47:145–63.
74. Furuya H. A new dicyemid from *Benthoctopus sibiricus* (Mollusca: Cephalopoda: Octopoda). *J Parasitol*. 2010;96:1123–7.
75. Golikov AV, Sabirov RM, Gudmundsson G. Cephalopoda (Smokkdýr), *Muusoctopus* sp. [Internet]. 2018 [cited 2022 Feb 3]. Available from: <http://www.ni.is/biota/animalia/mollusca/cephalopoda/muusoctopus-sp>.
76. Roper CFE, Voss GL. Guidelines for taxonomic descriptions of cephalopod species. *Mem Mus Vic*. 1983;44:48–63.
77. O'Shea S. The marine fauna of New Zealand: Octopoda (Mollusca:Cephalopoda). Wellington: National Institute of Water and Atmospheric Research; 1999.
78. Clarke MR. The identification of cephalopod 'beaks' and the relationship between beak size and total body weight. *Bull Br Mus Nat Hist, Zool*. 1962;8:419–80.
79. Sauer WH, Lipiński MR. Histological validation of morphological stages of sexual maturity in chokker squid *Loligo vulgaris reynaudii* D'Orb (Cephalopoda: Loliginidae). *S Afr J Mar Sci*. 1990;9:189–200.
80. Nigmatullin CM, Zalygalin VP, Sabirov RM. Ontogenetic aspects of morphology, size, structure and production of spermatophores in ommasphrephid squids: an overview. *Berliner Paläobiol Abh*. 2003;3:225–40.
81. Zar JH. *Biostatistical analysis*. Upper Saddle River: Prentice Hall; 2010.
82. Hammer Ø, Harper DAT, Ryan PD. *PAST: paleontological statistics software package for education and data analysis*. *Paleontol Electron*. 2001;4:1–9.
83. Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol Mar Biol Biotechnol*. 1994;3:294–9.
84. Tamura K, Stecher G, Kumar S. MEGA11: Molecular evolutionary genetics analysis version 11. *Mol Biol Evol*. 2021;38:3022–7.
85. Gontcharov AA, Marin B, Melkonian M. Are combined analyses better than single gene phylogenies? A case study using SSU rDNA and *rbcl* sequence comparisons in the Zygnematophyceae (Streptophyta). *Mol Biol Evol*. 2004;21:612–24.
86. Xavier JC, Cherey Y, Allcock L, Rosa R, Sabirov RM, Blicher ME, et al. A review on the biodiversity, distribution and trophic role of cephalopods in the Arctic and Antarctic marine ecosystems under a changing ocean. *Mar Biol*. 2018;165:93.
87. Verrill AE. The cephalopods of the north-eastern coast of America. Part II. The smaller cephalopods, including the "squids" and the octopi, with other allied forms. *Trans Conn Acad Sci*. 1881;5:259–446.
88. Verrill AE. Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others recently recorded. *Trans Conn Acad*. 1884;VI:139–294.
89. Verrill AE. Third catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others recently recorded. *Trans Conn Acad*. 1885;VI:395–452.
90. Barratt IM, Johnson MP, Allcock AL. Fecundity and reproductive strategies in deep-sea incirrate octopuses (Cephalopoda: Octopoda). *Mar Biol*. 2007;150:387–98.
91. Faulkes A. *Edda*. Snorri Sturluson. London: Charles E. Tuttle; 1995.
92. Ibáñez CM, Pardo-Gandarillas MC, Peña F, Gleadall IG, Poulin E, Sellanes J. Phylogeny and biogeography of *Muusoctopus* (Cephalopoda: Enterocotopodidae). *Zool Scr*. 2016;45:494–503.

93. Golikov AV, Sabirov RM, Lubin PA, Jørgensen LL. Changes in distribution and range structure of Arctic cephalopods due to climatic changes of the last decades. *Biodiversity*. 2013;14:28–35.
94. Bizikov VA. The shell in Vampyropoda (Cephalopoda): morphology, functional role and evolution. *Ruthenica*. 2004;Supplement 3:1–88.
95. Reinhardt JCH. Om Grönlands fiske. In: Ørsted HC, editor. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandling og dets Medlemmers Arbejder, pt 30. København: A. F. Høst; 1830. p. 1–17.
96. González AF, Guerra A, Pascual S, Briand P. *Vulcanoctopus hydrothermalis* gen. et sp. nov. (Mollusca, Cephalopoda): an octopus from a deep-sea hydrothermal vent site. *Cah Biol Mar*. 1998;39:169–84.
97. Strugnell JM, Cherey Y, Cooke IR, Gleadall IG, Hochberg FG, Ibáñez CM, et al. The Southern Ocean: source and sink? *Deep-Sea Res*. 2011;58:196–204.
98. Lichtenstein HC. *Onychoteuthis*, Sepien mit Krallen. *Isis* (Oken). 1818;9:1591–2.
99. Owen R. Mollusca – Cephalopoda. nov. gen. – *Rossia* (Owen). In: Ross JC, editor. Account of the objects in the several departments of natural history, seen and discovered during the present expedition. London: A. W. Webster; 1835. p. 92–9.
100. Steenstrup J. Hectocotyldannelsen hos Octopodslægterne *Argonauta* og *Tremoctopus*, oplyst ved lagttagelse af lignende Dannelse hos Blaksprutterne i Almindelighed. *K Dansk Vidensk Selsk Skr*. 1856;4:185–216.
101. Eschricht DF. *Cirrotheuthis mulleri*, eine neue Gattung der Cephalopoden bildend. *Nova Acta physico-med*. 1836;18:625–34.
102. Golikov AV, Ceia FR, Sabirov RM, Batalin GA, Blicher ME, Gareev BI, et al. Diet and life history reduce interspecific and intraspecific competition among three sympatric Arctic cephalopods. *Sci Rep*. 2020;10:21506.
103. Golikov AV, Artemev GM, Blicher ME, Gudmundsson G, Jørgensen LL, Olafsdottir SH, et al. Deep and cold: are Boreal and Arctic finned octopods, *Stauroteuthis syrtensis* and *Cirrotheuthis muelleri* (Cephalopoda, Octopoda, Cirrata), ecological analogues? *Deep-Sea Res I*. 2022;181:103706.
104. Strugnell JM, Rogers AD, Prodöhl PA, Collins MA, Allcock AL. The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics*. 2008;24:853–60.
105. Jørgensen EM, Strugnell JM, Allcock AL. Description and phylogenetic relationships of a new genus of octopus, *Sasakiopus* (Cephalopoda: Octopodidae), from the Bering Sea, with a redescription of *Sasakiopus salebrosus* (Sasaki, 1920). *J Mollus Stud*. 2010;76:57–66.
106. Vecchione M, Allcock L, Piatkowski U, Strugnell J. *Benthooctopus rigbyae*, n. sp., a new species of cephalopod (Octopoda; Incirrata) from near the Antarctic Peninsula. *Malacologia*. 2009;51:13–28.
107. Norman MD, Hochberg FG, Lu CC. Mid-depth octopuses (200–1000 m) of the Banda and Arafura seas (Cephalopoda: Octopodidae and Alloposidae). In: Crosnier A, Bouchet P, editors. *Resultats des Campagnes MUSORSTOM, Volume 16 Paris: Mémoires Museum National d'Histoire Naturelle* 172. Paris: Museum National d'Histoire Naturelle; 1997. p. 357–83.
108. Sereno PC. Logical basis for morphological characters in phylogenetics. *Cladistics*. 2007;23:565–87.
109. Drew GA. Sexual activities of the squid *Loligo pealii* (Les.). II. The spermatophore; its structure, ejaculation and formation. *J Morphol*. 1919;32:379–435.
110. Sabirov RM. Spermatophorogenesis and reproductive strategy in males of ommastrephid squids (Oegopsida: Ommastrephidae) [PhD Thesis]. Moscow: Institute of Evolutionary Morphology; 1995.
111. Nigmatullin CM, Laptikhovskiy VV, Sabirov RM. Reproductive biology of the commander squid. In: Elizarov AA, editor. *Fisheries biology of the commander squid and fishes in the slope communities of the western Bering Sea*. Moscow: All-Russian Institute of Fisheries and Oceanography; 1996. p. 101–24.
112. Hoving HJT, Lipiński MR, Dam L. The male reproductive strategy of a deep-sea squid: sperm allocation, continuous production, and long-term storage of spermatophores in *Histioteuthis miranda*. *ICES J Mar Sci*. 2010;67:1478–86.
113. Sabirov RM, Golikov AV, Nigmatullin ChM, Lubin PA. Structure of the reproductive system and hectocotylus in males of lesser flying squid *Todaropsis eblanae* (Cephalopoda: Ommastrephidae). *J Nat Hist*. 2012;46:1761–78.
114. Golikov AV, Morov AR, Sabirov RM, Lubin PA, Jørgensen LL. Functional morphology of reproductive system of *Rossia palpebrosa* (Cephalopoda, Sepiolida) in Barents Sea. *Proc Kazan Uni, Nat Sci Ser*. 2013;155:116–29.
115. Golikov AV, Blicher ME, Jørgensen LL, Walkusz W, Zakharov DV, Zimina OL, et al. Reproductive biology and ecology of the boreoatlantic armhook squid *Gonatus fabricii* (Cephalopoda: Gonatidae). *J Moll Stud*. 2019;85:287–99.
116. Cuccu D, Mereu M, Agus B, Cau A, Culurgioni J, Sabatini A, et al. Male reproductive system and spermatophores production and storage in *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae): A look into deep-sea squids' reproductive strategy. *Deep-Sea Res*. 2014;91:86–93.
117. Golikov AV. Distribution and reproductive biology of decabrachian cephalopods (Sepiolida, Teuthida) in the Barents Sea and adjacent areas [PhD Thesis]. Moscow: Moscow State University; 2015.
118. Golikov AV, Blicher ME, Gudmundsson G, Manushin IE, Poulsen JY, Zakharov DV, et al. Flapjack devilfish in the northern North Atlantic: morphology, biology and ecology of *Opisthoteuthis borealis* (Cephalopoda, Octopoda, Cirrata). *Mar Biodivers*. 2020;50:108.
119. Rochebrune AT d', Mabile J. *Mollusques. Mission scientifiques du Cap Horn, 1882–83*. 1889;6:1–129.
120. Voight JR. Differences in spermatophore availability among octopodid species (Cephalopoda: Octopoda). *Malacologia*. 2009;51:143–53.
121. Mangold K. *Organes genitiaux-reproduction, croissance et duree de vie. Cephalopodes Traite de Zoologie, volume 5(4)*. Paris: Masson; 1989. p. 459–552.
122. Nigmatullin CM. Ovary development, potential and actual fecundity and oocyte resorption in coleoid cephalopods: a review. *Berliner Paläo-biol Abh*. 2002;1:82–4.
123. Nigmatullin CM. About reproductive biology of females in some species of Antarctic cephalopods. *Proc All-Rus Inst Fish Oceanogr*. 2007;147:307–19.
124. Laptikhovskiy V. Reproductive strategy of deep-sea and Antarctic octopods of the genera *Graneledone*, *Adelieledone* and *Muusoctopus* (Mollusca: Cephalopoda). *Aquat Biol*. 2013;18:21–9.
125. Golikov AV, Blicher ME, Hoving H-JT, Zakharov DV, Sabirov RM. Actual fecundity of the Arctic squid *Gonatus fabricii* (Cephalopoda) based on the examination of a rarely encountered spent female. *Moll Res*. 2021;41:83–6.

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