Article

A new species of pencil smelt *Nansenia boreacrassicauda* (Microstomatidae, Argentiniformes) from the North Atlantic Ocean

JAN YDE POULSEN[1,2]

[1]*Department of Fish and Shellfish, Greenland Institute of Natural Resources, Kivioq 2, PB 570, 3900 Nuuk, Greenland.*
E-mail: JaPo@natur.gl
[2]*Fish Section, Australian Museum, 6 College Street, Sydney NSW 2010, Australia*

Abstract

A new microstomatid oceanic species, *Nansenia boreacrassicauda* spec. nov., is described from the temperate and sub-arctic Atlantic Ocean. The new species is part of the "stubby caudal peduncle" group and includes the northernmost record of any *Nansenia* species close to the Arctic Circle. The new species is putatively most similar to the Mediterranean *Nansenia iberica*, distinguished by a smaller caudal peduncle length/depth ratio, a smaller predorsal distance, more gill rakers, a different lateral line scale type and distribution. Extended *Nansenia* species distributions and specimens that show extralimital characters in relation to previous works are presented, addressing the current problematic taxonomic issues prevalent in pencil smelts and closely related genera. The new species is described due to increased collecting and taxonomic efforts off Greenland and is not necessarily related to ocean temperature changes.

Key words: oceanic, coastal, subarctic, North Atlantic, taxonomy, mitogenome, climate change

Introduction

Sixteen species prior to this study are currently included in the pencil-smelt genus *Nansenia* (Jordan & Evermann 1896) of the family Microstomatidae (Kobyliansky 1992). They are all small-mouthed elongated fishes separated primarily on continuous characters and usually found in the mesopelagic realm between 200 and 1000 m. Some species of *Nansenia* were separated into a new genus *Bathylagichthys* by Kobyliansky (1986), based on the presence of a system of dermal trunk channels, multicusped dentary teeth, a mesocoracoid, tripartite postcleithrum and a urodermal bone all present in the latter genus. However, *Bathylagichthys* is currently a genus within the family Bathylagidae and relationships of groups within these families are unclear at present (Kobyliansky 1985; 1986; 1990a; 1990b). In fact, Bathylagidae and Microstomatidae have no characters defining the two families, a testament to the taxonomic and phylogenetic problems with these fishes at present (Kawaguchi & Butler 1984). Certainly, *Nansenia* and *Bathylagichthys* show many similar traits, such as general body form, presence of an adipose fin, opercular bones, and small mouths with dentition on the dentary and vomer (Lloris & Rucabado 1985). The classification separating the two genera, also into different families, by Kobyliansky (1986) was controversial; later Kobyliansky (1990b), Johnson & Patterson (1996) and Nelson (2006) included bathylagids within the Microstomatidae. However, the classification presented by the latter studies showing Bathylaginae as a subfamily within the Microstomatidae has not generally been adopted in later literature. Regardless, the classification of *Bathylagichthys* within the Bathylaginae, a genus that shows many similarities to *Nansenia* in the Microstomatinae, remains problematic concerning taxonomy of bathylagid and microstomatid fishes.

Species of *Nansenia* can be divided into subgroups based on several different morphological characters and distributions. However, the value of these divisions is questionable concerning phylogenetic relationships, as several trends related to continuous characters seem to cross the different subgroups. Unfortunately, almost no molecular data (associated with voucher specimen data) are present at this time, characters likely to shed some light on problematic species delimitations. Recent materials are few, as many species of *Nansenia* are rare and not commonly caught from an exclusively pelagic and often oceanic distribution. The revision of *Nansenia* by

Kawaguchi & Butler (1984) is the most important contribution to date, although as they noted, it is preliminary and new species are to be described. The best diagnostic characters for species within the genus *Nansenia* were noted by Matallanas (1986a) as pertaining to the opercular bones, the lateral line scales and the crumenal organ, the latter previously considered a synapomorphy for the argentiniform and alepocephaliform fishes (Greenwood & Rosen 1971). However, that result is not supported from both early developmental characters (Ahlstrom *et al.* 1984) and extensive molecular data (Poulsen *et al.* 2009; Betancur-R *et al.* 2013). Despite the problematic status of the crumenal organ in designating otocephalan and euteleostean relationships, Matallanas (1986a) noted two types of crumenal organs within *Nansenia*, a feature largely unstudied at present.

The distributions of *Nansenia* species are generally wide, although they are based on few specimens for most species. Microstomatid fishes are few and far between in the subarctic province north of the sub-polar front (SPF) between 48° and 54°N, an important species barrier from both topographic and water currents in the Atlantic Ocean (Vecchione *et al.* 2010; Sutton *et al.* 2013). However, wide ranging meso- or epi-pelagic oceanic taxa such as *Nansenia* are not necessarily affected by such barriers. The few species found in subarctic Atlantic Ocean waters, *Nansenia groenlandica* (Reinhardt 1840), *Nansenia oblita* (Facciolà 1887), and *Nansenia tenera* (Kawaguchi & Butler 1984), have also been observed in the temperate Atlantic but show patchy distributions, and misidentifications are present. There are massive gaps in our knowledge concerning species diversity in subarctic north Atlantic waters, from both taxonomic and sampling difficulties, and it is often difficult to establish the cause of new species records (Poulsen 2015).

Material and methods

Materials. The holotype of *Nansenia boreacrassicauda* **sp. n.** was caught by *R/V Pâmiut*, Greenland Institute of Natural Resources (GINR), September 3, 2008, leg 5, haul 15, during a standard Greenland halibut survey, with a non-closing Alfredo III bottom trawl with a mesh size of 140 mm and cod-end mesh-liner of 30 mm. It was deposited at the Zoological Museum University of Copenhagen (ZMUC) as P192172 from an original tissue/field number #8086. Catch locality between Greenland and Iceland (Denmark Strait) was 65°32'N, 30°57'W. Coll./ID by J.Y. Poulsen. The bottom and fishing depth was 382–400 m with a bottom temperature of 3.19°C. The five paratypes of *N. boreacrassicauda* **sp. n.** were provided from the Zoological Museum in Hamburg (ZMH). Additional comparative materials were provided also by the ZMH, section Unidad de Zoología at the Universitat Autònoma de Barcelona (UAB), Museum of Comparative Zoology (MCZ), Department of Biology, Faculty of Science Kochi University (BSKU) and the Australian Museum (AMS) fish collection. All specimens were digitally x-rayed at the AMS, examined under a stereomicroscope, and morphological measurements done with a digital caliper to the nearest 0.1 mm or 0.01 mm for CPL and CPD. Vertebral counts include the posterior urostyle and the most anterior "half-vertebra" connecting the vertebral column to the cranium. Other methods of counts and measurements, terminology, and abbreviations follow Kawaguchi & Butler (1984) or are explained in Table 1. Number of gill rakers often varies on the cerato- and epibranchial bones from one side to the other although the total number is mostly identical.

Several specimens examined during the course of this study show characters outside the ranges previously reported (e.g. Kawaguchi & Butler 1984). The extralimital characters are taxonomically important compared to ranges previously described, precluding simple expansions of the morphometric ranges for the taxa involved (specimens discussed below). I have noted these specimens in the following section as "cf." including the extralimital characters in parentheses. Specimens included as comparative materials cover all species in the North Atlantic as well as all species in the "stubby caudal peduncle" subgroup (1.0–1.5 CPL/CPD ratio), with the exception of the Pacific distributed *Nansenia ahlstromi* (Kawaguchi & Butler 1984).

Nansenia boreacrassicauda Poulsen, new species
Figs. 1A–D; Table 1

Type materials. *Holotype.* ZMUC P192172, 232.0 mm SL (65°32'N, 30°57'W).
Paratypes. ZMH 122532 (ISH 174-1986), 197.2 mm SL (57°46'N, 18°5'W); ZMH 120802 (ISH 968-1982),

265.2 mm SL (49°48'N, 25°54'W); ZMH 122530 (ISH 264-1986), 226.0 mm SL (57°34'N, 18°12'W); ZMH 122553 (ISH 201-1986), 230.8 mm SL (57°43'N, 17°40'W); ZMH 120833 (ISH 967-1982), 268.0 mm SL (43°42'N, 28°27'W).

Comparative materials. *Nansenia ardesiaca*. AMS I.22817-025, 129.3 mm SL (Indian Ocean, off the Australian Northwest Shelf); BSKU 28403, 134.5 mm SL (Okinawa Through, Okinawa, Japan).

Nansenia cf. *ardesiaca* (adipose fin not pigmented). AMS I.22817-025, 124.2 mm SL (Indian Ocean, off the Australian Northwest Shelf); BSKU 13127, 155.0 mm SL (Northwestern Pacific Ocean, off Kochi, Japan); MCZ 159274, 82.6 mm SL (31°26'N, 16°28'W).

Nansenia atlantica. ZMH 103928 (ISH 335-1966), 90.8 mm SL (10°46'N, 23°54'W); ZMH 105441 (ISH 457-1968), 110.8 mm SL (16°14'N, 22°24'E); ZMH 105453 (ISH 686-1968), 152.0 mm SL (08°21'N, 24°10'W); ZMH 105485 (ISH 1311-1968), 169.0 mm SL (16°08'N, 22°22'W); AMS I.20066-072, 81.1 mm SL (off Brush Island, New South Wales, Australia).

Nansenia iberica (paratype). UAB 1985.6.14, 237.0 mm SL (Northwestern Mediterranean Ocean, off Blanes, Spain).

Nansenia oblita. MCZ 66132(2), 43.6 and 77.3 mm SL (37°01'N, 00°05'W); MCZ 66134, 87.8 mm SL (39°57'N, 06°43'E).

Nansenia cf. *oblita* (adipose base pigmented). MCZ 66133, 59.3 mm SL (14°30'N, 21°47'W).

Nansenia cf. *pelagica* (vertebrae 46). ZMH 120958 (ISH 465-1982), 106.5 mm SL (45°24'N, 27°41'W).

Nansenia tenera. MCZ 66016, 96.4 mm SL (49°53'N, 39°18'W).

The complete mitochondrial DNA sequences (mitogenomes), except a part of the control region, were determined for the holotype of *N. boreacrassicauda* **sp. n.** as well as a southeast Greenland specimen (64°57'N, 34°27'W) of *Argentina silus* (ZMUC P192172 and P192171, respectively). They were determined using conventional lab-methods employing DNA extraction (Qiagen Puregene kit), long-amplification (LA) PCR of the entire mitochondrial genome (Cheng *et al.* 1994), nested short PCR using the LA PCR product as template, direct cycle-sequencing with dye-labeled terminators and Sanger Sequencing on automated DNA sequencers (Applied Biosystems). Lab-work and sequencing were carried out at the Ocean Research Institute (ORI), University of Tokyo, and at the Biodiversity Laboratory and Sequencing Facility at the University of Bergen (UIB). Universal fish primers covering a range of teleost fishes were employed (e.g. Miya & Nishida 1999; Byrkjedal *et al.* 2011).

Results

Diagnosis (Table 1). *Nansenia boreacrassicauda*: a "stubby caudal species" with PCL/PCD ratio 1.20–1.31; predorsal length less than 50% SL; dentition extensive, falling into high-number teeth group, often noted for the dentary resembling a closely-spaced picket fence; vomerine teeth curved; eye large, approximately 40% of HL; large crescent of white tissue on posterior half of eye; large circumorbitals present; concave indentation in posterior margin of operculum present (opercular tube), somewhat variable between type materials (Figs. 2A–B); large ventral strip of bioluminescent tissue associated with large scales, running from isthmus to vent, appearing dark in preservative; large patches of distinct whitish, fatty tissue present on anterior and posterior parts of preorbital bone, elongated patch bordering all opercular bones, long strip dorsally separating cranial bones from nape, all patches fading in preservative; lateral-line scales large and modified, showing two pointed projections at posterolateral margins below adipose fin (Fig. 2C), extending several scales onto caudal fin rays; crumenal organ with relatively small accessory cartilage between fifth cerato- and epibranchial, fourth epibranchial with uncinate process (Fig. 2D), gill rakers on accessory cartilage 6–7, on fifth ceratobranchial 9–10 (total 16), epibranchial-5 + ceratobranchial-4 with 16 gill rakers in total; adipose fin large, proximal part heavily pigmented; large pineal window present between eyes; aphakic gap present, acorn- or oval shaped; pseudobranch filaments 15–21; otoliths lanceolate, approximately 7.0 mm (3.0% SL) assembled (each broken into two), rostrum long, ventral margin denticles broad and deep, appearing highly convoluted; body color golden-brownish, scales strongly iridescent when freshly caught, dull brown after preservation in alcohol/formaldehyde (Fig. 1). The new species was LSID registered in ZooBank, the online registrat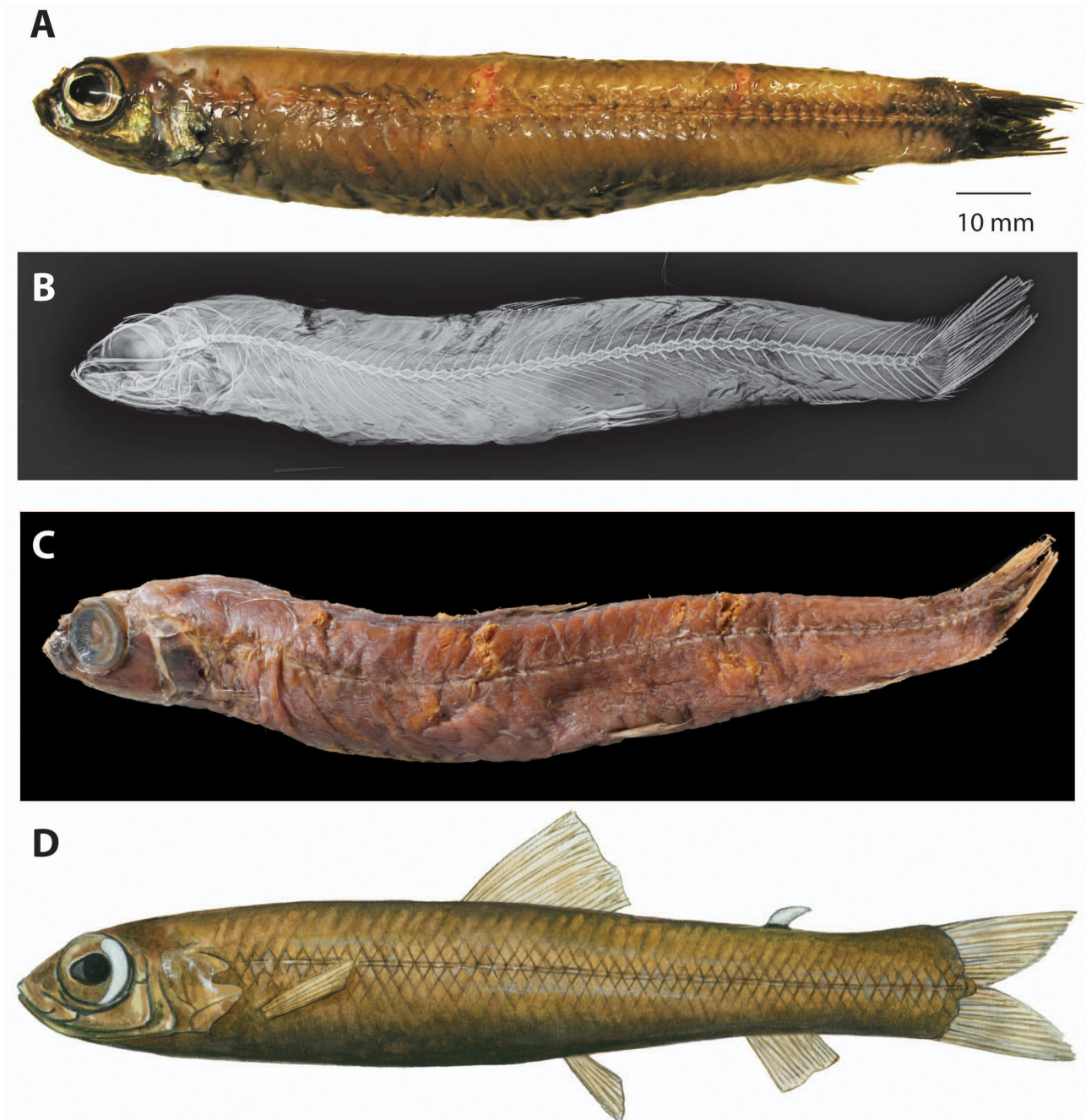ion system for the ICZN, and can be located at: http://zoobank.org/urn:lsid:zoobank.org:act:C71E330B-D48A-4665-9D09-C9A03F83E1C3

FIGURE 1. *Nansenia boreacrassicauda* **sp. n.** Holotype (ZMUC P192172). (A) newly caught off southeast Greenland 2008. (B) radiograph image. (C) formalin-fixed and alcohol preserved specimen (D) illustration of holotype.

Etymology. *Nansenia boreacrassicauda*. Species derivative originating from Latin "boreas" (Subarctic or to the north) referring to distribution of type materials, from Latin "crassus" (fat, stout) and Latin "cauda" (tail) referring to the stubby caudal peduncle. Suggested vernacular name: northern fat-tail (pencil smelt).

Distribution. *Nansenia boreacrassicauda* is a temperate and Subarctic Atlantic species found across the SPF (Fig. 3). The latitudinal range from this study is between 43°42'N and 65°32'N, within a narrow longitudinal band at present ranging from 17°40'W to 30°57'W. It is oceanic although possibly associated with topographic structures such as the Mid-Atlantic Ridge system.

Morphometrics of comparative materials examined in the present study are presented in Table 2. Morphological character ranges and distributions are presented for all 17 species of *Nansenia* in Table 3 with data compiled from Kawaguchi & Butler (1984), Matallanas (1986b), Kobyliansky (1992), Merella *et al.* (1997), and this study (Table 1–2).

TABLE 1. Morphometrics and meristics of *Nansenia boreacrassicauda* sp.n type specimens.

Specimen	ZMUC P192172	ZMH 122532	ZMH 122530	ZMH 122553	ZMH 120802	ZMH 120833
Status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype
Locality	65°32'N, 30°57'W	57°46'N, 18°5'W	57°34'N, 18°12'W	57°43'N, 17°40'W	49°48'N, 25°54'W	43°42'N, 28°27'W
TL	249.0	228.2	245.3	250.0	288.5	285.1
SL (mm)	232.0	197.2	226.0	230.8	265.2	268.0
% SL						
HL	21.2	21.9	20.9	21.2	20.2	20.0
Predorsal	47.3	46.3	45.6	46.1	47.1	47.0
Preanal	79.0	81.6	81.0	80.2	81.1	79.1
Prepelvic	56.7	57.3	56.2	57.6	55.8	57.1
Snout length	3.8	4.7	4.6	4.4	4.1	3.9
Eye diameter	7.4	8.6	8.2	8.6	7.9	7.9
Dorsal base length	9.5	12.7	11.9	11.4	13.3	11.5
Anal base length	7.2	-	6.9	7.3	6.8	6.9
Width at eye	9.0	8.3	9.1	9.4	9.8	9.4
Depth at eye	11.1	12.1	11.7	13.7	13.5	14.2
Depth dorsal fin	15.4	15.4	15.6	14.6	15.8	15.6
Width at pectoral	10.3	10.0	10.6	10.2	10.5	10.8
Caudal depth (CPD)	9.2	8.7	8.8	8.1	8.5	8.1
Caudal length (CPL)	11.6	11.0	11.0	10.3	11.1	10.1
Eye (% HL)	38.3	39.4	39.1	40.6	39.3	39.4
CPL	26.7	21.7	24.9	23.7	29.4	27.1
CPD	21.5	17.2	20.0	18.7	22.5	22.6
CPL/CPD	1.26	1.26	1.25	1.27	1.31	1.20
Pre-caudal vertebrae	25	26	26	27	25	26
Caudal vertebrae	22	21	21	21	21	21
Total vertebrae	47	47	47	48	46	47
Dorsal rays	11	11	12	11	12	-
Anal rays	9	-	10	9	10	-
Pectoral rays	12	-	11	12	11	-
Pelvic rays	12	11	11	11	12	-
Branchiostegal rays	4	4	4	4	-	-
Lateral line scales	51	-	50	49	50	51
Gill rakers	12+1+24 = 37	13+1+26 = 40	11+1+25 = 37	13+1+26 = 40	13+1+24 = 38	12+1+24 = 37
Pseudobranch filaments	20	16	17	18	21	15
Teeth vomer	34	40	36	32	38	44
Teeth dentary	138	152	122	116	140	122

TABLE 2. Morphometrics and meristics of newly examined *Nansenia* comparative materials used for this study.

Specimen	AMS I.20066-072	ZMH 103928	ZMH 105441	ZMH 105453	ZMH 105485	UAB 1985.6.14	AMS I.22817-025	AMS I.22817-025	BSKU 28403
Species	*N. atlantica*	*N. atlantica*	*N. atlantica*	*N. atlantica*	*N. atlantica*	*N. iberica*	*N. ardesiaca*	*N. ardesiaca*	*N. ardesiaca*
Locality	Southeast Australia	10°46'N, 23°54'W	16°14'N, 22°24'E	08°21'N, 24°10'W	16°08'N, 22°22'W	Northwest Mediterranean	Northwest Australia	Northwest Australia	Okinawa Through
TL	90.6	101.1	117.8	164.8	180.4	263.2	135.9	142.0	144.5
SL (mm)	81.5	90.8	110.8	152.0	169.0	237.0	124.2	129.3	134.5
% SL									
HL	29.3	24.6	24.4	23.2	21.4	20.7	20.0	20.2	21.0
Predorsal	54.4	54.1	52.7	48.1	49.3	48.1	46.2	46.0	46.1
Preanal	82.5	82.2	81.8	78.9	79.2	81.0	80.8	79.0	80.3
Prepelvic	59.6	59.9	62.0	58.0	57.8	57.2	56.0	54.1	55.0
Snout length	4.8	5.6	5.1	3.8	4.1	4.3	3.3	3.1	2.8
Eye diameter	12.5	8.0	8.9	9.2	8.2	8.0	8.5	9.6	9.1
Dorsal base length	13.9	9.6	10.4	9.3	10.6	12.7	8.9	11.1	9.3
Anal base length	7.5	8.6	7.4	8.1	9.1	6.5	7.1	7.1	6.3
Width at eye	10.7	8.7	9.3	8.5	7.9	8.1	7.2	7.3	7.9
Depth at eye	15.0	11.7	12.5	12.4	12.3	10.8	12.1	10.3	10.5
Depth dorsal fin	15.6	14.0	13.0	14.8	12.5	11.7	12.9	14.1	13.0
Width at pectoral	12.5	13.7	10.9	10.3	8.6	10.4	10.2	11.5	9.4
Caudal depth (CPD)	9.9	8.0	8.6	9.7	8.4	7.9	7.2	7.0	6.7
Caudal length (CPL)	11.7	11.2	11.5	13.1	12.5	14.0	12.2	12.4	13.0
Eye (% HL)	42.4	35.4	37.4	39.1	37.6	39.2	41.8	47.5	42.6
CPL	9.5	10.2	12.7	19.9	21.2	33.2	15.2	16.0	17.4
CPD	8.1	7.3	9.5	14.8	14.2	18.8	8.9	9.1	9.0
CPL/CPD	1.17	1.40	1.34	1.34	1.49	1.77	1.71	1.76	1.93
Pre-caudal vertebrae	23	22	23	22	23	26	27	29	29
Caudal vertebrae	19	21	21	21	21	21	20	19	19
Total vertebrae	42	43	44	43	44	47	47	48	48
Dorsal rays	11	9	10	10	10	10	10	10	11
Anal rays	9	9	9	9	9	9	9	9	10
Pectoral rays	10	-	-	-	11	-	11	12	11
Pelvic rays	11	10	10	10	10	12	12	12	12
Branchiostegal rays	4	4	-	4	4	4	4	4	
Lateral line scales	45	-	49	44	49	48	53	-	-
Gill rakers	11+1+23 = 35	11+1+23 = 35	11+1+23 = 35	11+1+21 = 33	12+1+20 = 33	12+1+24 = 37	10+1+21 = 32	10+1+19 = 30	10+1+23 = 34
Pseudobranch filaments	16	15	19	17	16	20	16	-	17
Teeth vomer	26	28	30	30	40	40	26	26	30
Teeth dentary	80	82	108	132	148	120	60	70	70^c

TABLE 2. (continued)

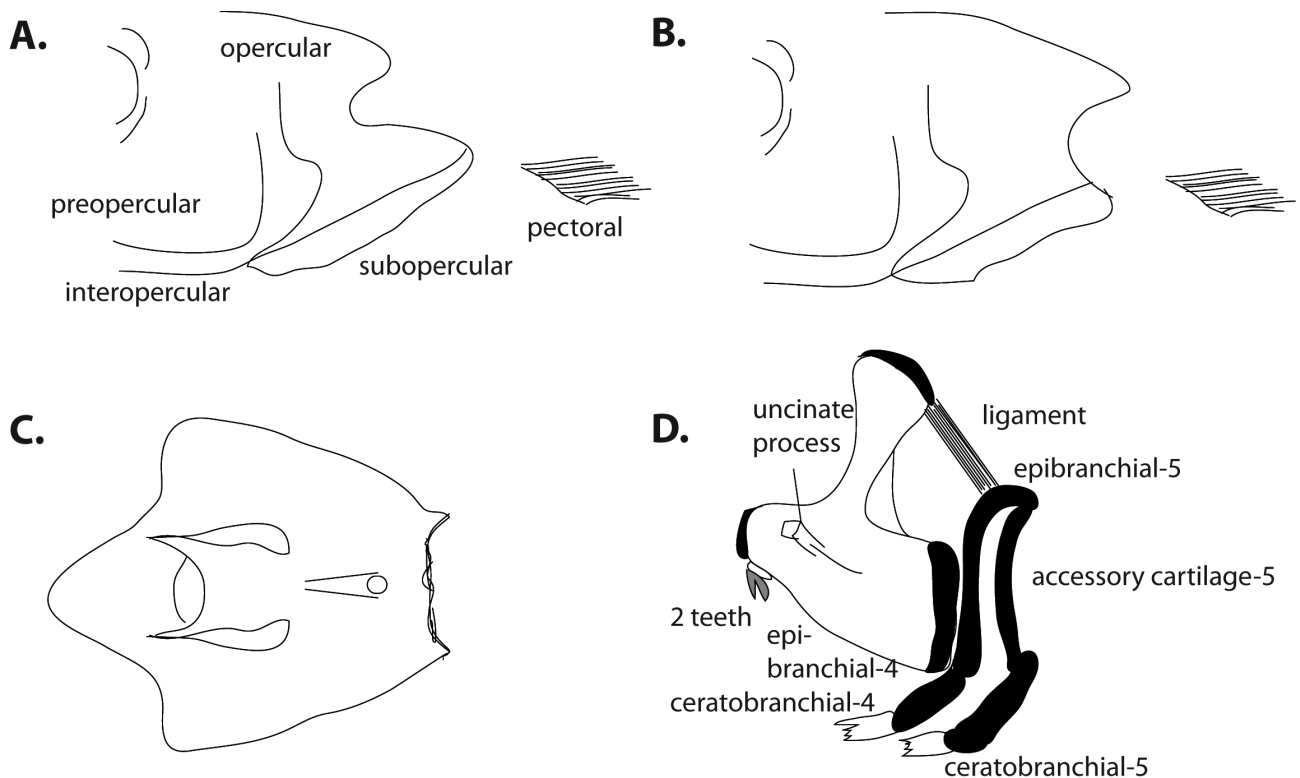| Specimen	BSKU 13127	ZMH 120958	MCZ 159274	MCZ 66016	MCZ 66134	MCZ 66132	MCZ 66132	MCZ 66133
Species	*N. ardesiaca*	*Nansenia.* cf. *pelagica*	*Nansenia.* cf. *ardesiaca*	*N. tenera*	*N. oblita*	*N. oblita*	*N. oblita*	*Nansenia* cf. *oblita*
Locality	Off Kochi, Japan	45°24N, 27°41'W	31°26'N, 16°28'W	49°53'N, 39°18'W	39°57'N, 06°43'E	37°01'N, 00°05'W	37°01'N, 00°05'W	14°30'N, 21°47'W
TL	178.0	119.0	91.7	109.3	100.9	90.3	47.2	64.7
SL (mm)	155.0	106.5	82.6	96.4	87.8	77.3	43.6	59.3
% SL								
HL	19.4	22.8	25.8	24.9	24.8	25.0	26.8	27.8
Predorsal	43.9	48.1	45.5	44.7	52.2	53.3	53.4	55.8
Preanal	80.0	82.9	74.8	82.8	81.8	82.4	85.8	83.3
Prepelvic	53.5	57.7	52.3	53.1	59.0	57.8	61.5	60.7
Snout length	2.9	5.2	5.6	5.8	4.8	5.6	5.7	5.9
Eye diameter	8.3	8.2	9.6	9.3	9.5	8.9	9.6	9.6
Dorsal base length	9.2	10.5	13.7	9.6	11.3	12.7	13.1	10.8
Anal base length	5.7	7.5	12.1	5.8	8.0	7.2	9.2	8.8
Width at eye	7.4	7.3	10.5	7.7	9.3	9.6	9.4	9.4
Depth at eye	9.7	10.7	12.5	10.5	11.8	11.3	14.4	14.3
Depth dorsal fin	13.1	14.7	14.4	14.3	15.7	14.9	13.8	15.9
Width at pectoral	9.9	8.9	10.8	10.8	11.2	11.5	10.6	12.5
Caudal depth (CPD)	6.6	8.4	8.4	7.2	8.8	8.2	8.0	9.8
Caudal length (CPL)	14.1	10.0	13.1	12.7	9.8	10.0	8.9	11.1
Eye (% HL)	42.9	36.9	38.2	37.5	37.9	35.8	38.5	34.7
CPL	21.9	10.6	10.8	12.2	8.6	7.7	3.5	6.6
CPD	10.2	8.9	6.9	6.9	7.7	6.3	3.9	5.8
CPL/CPD	2.15	1.19	1.57	1.77	1.12	1.22	1.11	1.14
Pre-caudal vertebrae	28	25	24	23	26	25	25	24
Caudal vertebrae	20	22	23	21	20	20	20	19
Total vertebrae	48	47	47	44	47	45	45	43
Dorsal rays	11	11	14	11	11	8	8	10
Anal rays	12	-	12	8	9	10	9	9
Pectoral rays	11	-	12	10	11	11	12	-
Pelvic rays	11	9	10	12	12	11	10	-
Branchiostegal rays	4	-	-	-	-	4	4	4
Lateral line scales	62	-	50	45	-	54	-	-
Gill rakers	10+1+19 = 30	13+1+26 = 40	9+1+16 = 26	13+1+29 = 43	12+1+25 = 38	11+1+22 = 34	11+1+22 = 34	10+1+22 = 33
Pseudobranch filaments	18	18	20	17	-	16	-	-
Teeth vomer	40	28	26	20	20	24	18	22
Teeth dentary	86[c]	60	84	60	64	62	50	50

FIGURE 2. Morphological characters of *Nansenia boreacrassicauda* **sp. n.** (A) opercular tube of the holotype. (B) opercular tube of the paratype (ZMH 122530). Note the less concave, differently angled and wider indentation in the opercular bone as compared to the holotype. (C) lateral line scales below adipose fin of the holotype and one paratype (ZMH 122532). (D) crumenal organ of the holotype. Black denotes cartilage.

The mitochondrial (mt) genome of *Nansenia boreacrassicauda* shows the canonical mt gene order found in most vertebrates (Poulsen *et al.* 2013). This gene order was also found in the argentinid taxon *Argentina silus*, determined in this study*,* as well as in other argentiniform fishes (Ishiguro *et al.* 2003). The mitogenomic DNA sequences were deposited in DDBJ, EMBL and GenBank, holotype labeled according to GenSeq (Chakrabarty *et al.* 2013), and included as part of the Greenland Fishes barcoding project as GLF242 and GLF021 (www.barcodinglife.org, Ratnasingham & Hebert 2007) for *N. boreacrassicauda* and *A. silus*, respectively.

Nansenia boreacrassicauda. GenBank/GenSeq: AP012955/genseq-1 mitogenome.

Argentina silus. GenBank: AP012952.

Discussion

Taxonomic relationships and characters. *Nansenia boreacrassicauda* is putatively closely related to the Mediterranean *N. iberica*, separated from it by a much more stubby caudal peduncle, shorter predorsal length, more gill rakers (overlap at 37), a modified lateral line scale, and a North Atlantic distribution in colder waters (Table 1–2). Both species are "robust", although whether this body morph has any value concerning delimitation of species groups within *Nansenia* is unknown. Both otoliths from the holotype of *N. boreacrassicauda* were broken into two, although the general outline of the otolith appears similar to *N. iberica* (Matallana, 1986b). However, deep convolutions of especially the ventral margin are present and the rostrum is strongly elongated. The latter study figured a large ventral indent in the otolith of *N. iberica*, corresponding to the position of breakage in both otoliths in the holotype of *N. boreacrassicauda*.

The lateral line scales below the adipose fin in *N. boreacrassicauda* are reminiscent of *N. iberica* in overall shape (Matallanas 1986a), although the posterior margin is somewhat irregular, with the posterolateral margins elongated and sharply pointed (Fig. 2C). This is a unique lateral line scale configuration, found in the holotype and

in one paratype (ZMH 122532). The lateral line scales below the adipose fin have been lost in the remaining type materials. Structure of the scales supports a close relationship to *N. iberica*, and shows this character taxonomic informative, similar to for example species rich genera within the rattail family Macrouridae (Cohen *et al.* 1990).

The opercular tube and crumenal organ in *N. boreacrassicauda* both show a different configuration as compared to *N. iberica*, although these structures are not uniform across specimens and variation is present within species (Fig. 2; Matallanas 1986a).
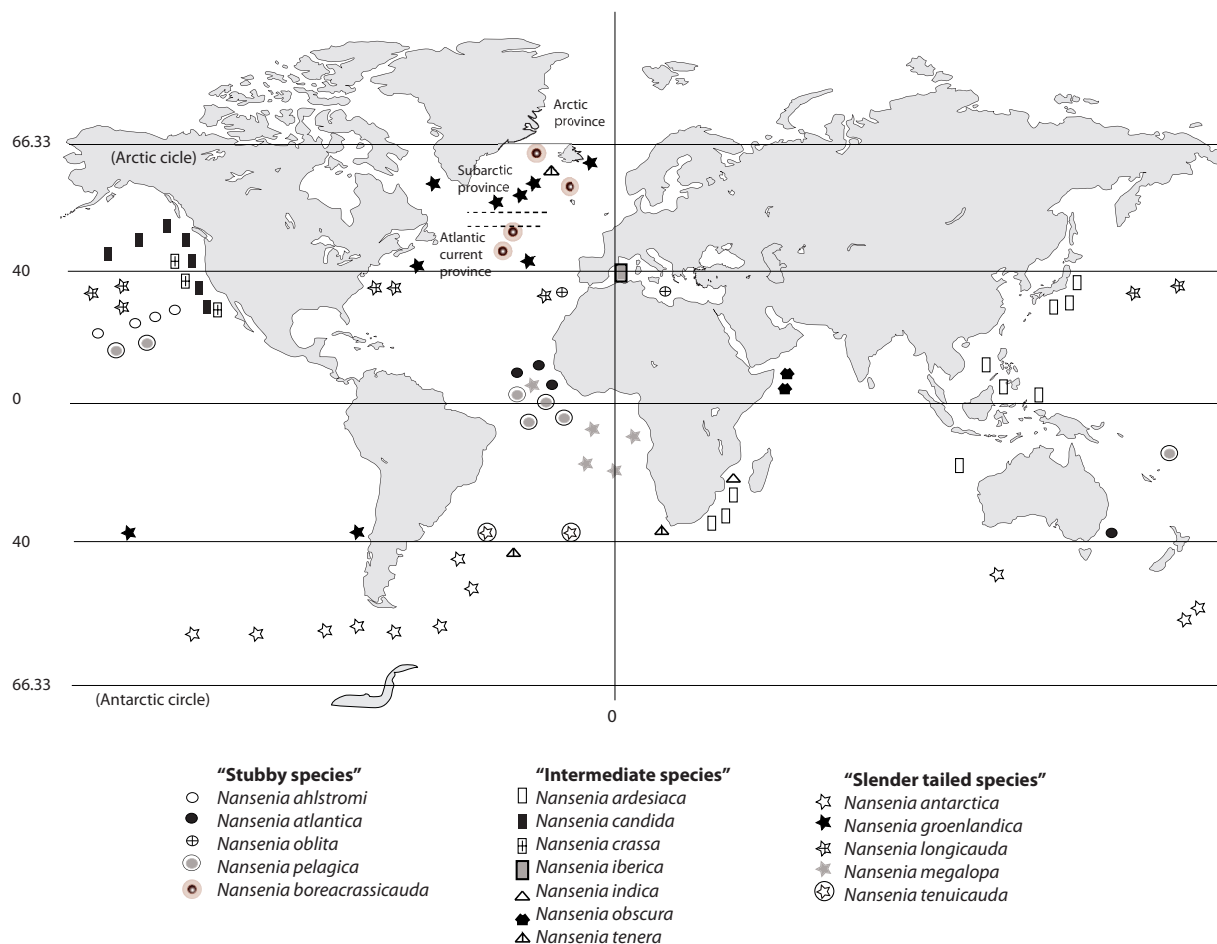
FIGURE 3. Distributions of the 17 valid species listed according to CPL/CPD subgroups of *Nansenia*. Dashed lines denote the Sub-Polar Front (SPF) ranging between approximately 48°N and 54°N, usually an important transition zone and faunal barrier in the North Atlantic concerning species distributions. Map modified from free vector maps (http://freevectormaps.com).

The concave indent in the posterior margin of the operculum (opercular tube) is large and deep in the holotype of *N. boreacrassicauda* and is situated above the pectoral base, i.e., no overlap is present in the vertical plane (Figs. 1D, 2A). A similar configuration seems to be present in one paratype (ZMH 122532), although the specimen is somewhat damaged in this region. The other four paratypes show clear overlaps, and the indent is somewhat less deep although wider (Fig. 2B). This opercular tube is distinct and present in all species of *Nansenia* though apparently showing intraspecific variability. Matallanas (1986a) and Merella *et al*. (1997) showed its variability between taxa, possibly showing some taxonomic information. However, the indent is in fact tube-shaped, with a convex arch visible in the opercular bone in front of the indent, connecting the gill chamber with the external environment at all times. This is likely an adaptation to a continuous swimming behavior allowing a small outflow of water during moderate active swimming. Similar outlets are found in the genus *Bathylagichthys* (pers. obs.) and seem intuitively functional more than taxonomical. However, differences in shape and position relative to the pectoral fin are present between taxa, although in the type materials of *N. boreacrassicauda,* the configurations of the opercular tube are reminiscent of several species examined during this study as well as illustrations by Matallanas (1986a). Considering the variation observed in the type materials of *N. boreacrassicauda* from this

study, I am reluctant to include this character at present in designating North Atlantic species. However, the opercular tube is a distinct feature of microstomatid fishes, although its significance as a taxonomic character is possibly not intraspecific. Comparisons of the opercular tube of *N. iberica* and most paratypes of *N. boreacrassicauda* show virtually no differences present.

The crumenal organ, a structure involving the fourth and fifth gill arches in combination with the anterior part of the esophagus (Nelson 1967; Greenwood & Rosen 1971), was previously considered an argentiniform and alepocephaliform synaphomorphic character, although the association of the two lineages has subsequently been shown artificial based on developmental and molecular characters. An accessory cartilage is present between the ceratobranchial and epibranchial bones on the fifth gill arch, the latter connecting with the epibranchial on the fourth gill arch. All the bones possess tooth-less gill rakers. The structure is distinct, not to be confused with the epibranchial organ present in other otocephalans (Nelson 1967), and shows variation between taxa in both lineages of fishes. It is most certainly involved in the processing of prey, as various food items are occasionally found retained by the gill rakers involved (pers. obs.). However, it is presently not possible to establish the amount of taxonomic information related to this structure, although the accessory cartilage and the connection of the two epibranchials clearly vary between these fishes (Greenwood & Rosen 1971). Two types of crumenal organs were noted by Matallanas (1986a) within six species of *Nansenia* examined; *N. oblita* and *N. crassa* (Lavenberg 1965) show a configuration presented by Greenwood & Rosen (1971), lacking an uncinate process on the fourth epibranchial, whereas the uncinate process is present in *N. iberica*, *N. atlantica* (Blache & Rossignol 1962), *N. ardesiaca* (Jordan & Thompson 1914) and *N. tenera*. Of the two species lacking the uncinate process, *N. crassa* shows an accessory cartilage bigger than in *N. oblita*, although more crumenal gill rakers are present in the latter. *Nansenia boreacrassicauda* shows the uncinate process present and quite distinct, although the configuration of this process is most similar to *N. atlantica* for this character. The accessory cartilage is relatively small compared to *N. iberica* (Fig. 2D), a configuration reminiscent of *N. ardesiaca* (Matallanas 1986a). The epibranchial overlap of the accessory cartilage is large and is somewhat less arching compared to the dorsal part of the epibranchial in *N. iberica*. The ligament connecting the two epibranchials is large. I have found no clear taxonomic information within *Nansenia* concerning the crumenal organ, or in the number of gill rakers present on the bones or cartilages that makes up this structure. This is supported by *N. oblita* and *N. crassa*, both species lacking the uncinate process, having no other characters present that supports a close relationship. In fact, the two species clearly belongs within different *Nansenia* subgroups based on for example dentition and the latter appearing robust (Table 3).

Nansenia boreacrassicauda is likely a North Atlantic endemic whereas *N. iberica* is a Mediterranean endemic. The two species differ based on several continuous characters, such as the CPL/CPD ratio and the predorsal length – both of these features are symptomatic and important in species separation of *Nansenia* taxa - and one of several reasons why taxonomy continues to present problems with these fishes. Matallanas (1986b) noted a CPL/CPD ratio of 1.7 for the holotype and 1.9 for the paratype of *N. iberica*. Merella *et al.* (1997) noted 1.80 and 1.81 for two additional Mediterranean specimens. Considerable shrinkage has occurred (250 vs. 237 mm SL) in the newly examined paratype (UAB 1985.6.14) compared to the species description by Matallanas (1986b), although measurements of % SL and ratios remain highly similar (Table 2). The close relationship suggested of *N. boreacrassicauda* and *N. iberica* is, however, tentative, and is mostly based on the robust body shape and the lateral line scales, despite the CPL/CPD ratio being much bigger for similar sized adult *N. iberica* specimens. The CPL/CPD ratio was noted as the most important morphological feature in distinguishing species groups by Kawaguchi & Butler (1984), although they do not necessarily represent natural groups. Comparisons of similar-sized specimens are extremely important for *Nansenia* taxonomy. *Nansenia iberica* shows many characters close to or within the ranges observed in *N. crassa*, a Northeast Pacific endemic species. *Nansenia boreacrassicauda* appears "robust", or somewhat compact, compared to *N. atlantica*; this is a trait also found in other *Nansenia* taxa: *N. ardesiaca*, *N. iberica*, *N. candida* and *N. crassa*. Whether robustness constitutes a natural species group character remains unknown, although it is presently not supported by the usual employed characters such as for example the CPL/CPD ratio (Table 3).

The crescent of white tissue on the posterior half of the eye is large in *N. boreacrassicauda*, similar to any other species of *Nansenia*, although it is apparently absent in *N. candida* (Cohen, 1958). It fades with preservation, and I have found no taxonomic information in this character for the purpose of this study. Species of *Nansenia* have many pseudobranch filaments present, ranging from 15–21 in type materials of *N. boreacrassicauda*, although clearly no taxonomic information is present across species for this character (Table 1–2).

TABLE 3. Range of characters in all 17 *Nansenia* species. Parenthesis designates unique holotype. O = Putatively Oceanic, C = Putatively Coastal, A = Atlantic Ocean, I = Indian, P = Pacific, M = Mediterranean, S = Southern Seas.

Character	CPL/CPD ratio	Predorsal length	Vertebrae	Gill rakers	Dentary	Vomer	Br. rays	Max. SL	Adipose pigmentation	Latitudinal range	Habitat	Distribution
N. ahlstromi	1.0–1.3	50.5–55.8	35–36	40	100	30	3	95.0	Prox.	20°N–35°N	O	P
N. atlantica	1.2–1.5	48.1–56.9	41–44	30–36	80–148	35	4	167.5	Prox.	20°N–10°S	C	A/P
N. boreacrassicauda	1.2–1.3	45.6–47.3	46–47	37–40	116–152	32–40	4	268.0	Prox.	40°N–65°N	O	A
N. oblita	1.1–1.2	55.0–56.1	42–45	30–36	30	18	4	180.0	None/Prox.	50°N–30°N	C	M/A
N. pelagica	1.1–1.5	50.4–57.8	38–39	36–41	60	35	4	107.5	Prox.	30°N–20°S	O	A/P
N. ardesiaca	1.7–2.3	45.7–48.6	46–48	27–35	60–75	25–35	4	200.0	Dist./None	40°N–40°S	C	P/I
N. candida	1.8–2.2	49.4–57.6	44–47	26–31	80–100	12–21	3	179.2	Prox.	30°N–55°N	C/O	P
N. crassa	1.7–2.2	49.0–60.2	43–46	35–37	150–180	20–35	4	266.0	Prox.	40°N–20°N	C	P
N. iberica	1.7–1.9	48.0–49.3	46–47	35–37	130	30	4	250.0	Prox.	35°N–45°N	C	M
N. indica	2.0	46.4	47	29	-	-	4	(107.0)	Dist.	20°S–30°S	C	I
N. obscura	2.2–2.6	48.4–51.7	42–44	30–37	-	-	4	154.4	Prox.	10°S–20°S	C	I
N. tenera	1.9–2.4	43.4–45.8	42–44	43–46	60	16	4	129.0	None	40°S–60°N	C/O	A
N. antarctica	2.5–3.0	45.9–47.7	49–50	37–45	75	27	3	207.5	Prox.	40°S–60°S	O	S
N. groenlandica	2.8–4.0	43.7–45.6	42–45	37–45	50–65	20–22	3	132.0	Prox.	40°N–70°N	O	A
N. longicauda	3.0–4.1	41.8–46.0	47–50	23–27	50	24	4	133.0	None	20°N–40°N	O	A/P
N. megalopa	2.8–3.2	42.1–44.2	44–45	21–23	35–50	-	4	139.5	Prox.	10°N–20°S	O	A
N. tenuicauda	2.7–3.1	44.0–45.8	46	38–42	26	8	4	84.0	None	35°S–45°S	O	A

Nansenia boreacrassicauda shows similarities also to *N. atlantica*, with which it shares a stubby caudal peduncle with a CPL/CPD ratio less than 1.5, although separated from it by a shorter predorsal length, more vertebrae, more gill rakers and a much more robust body (Tables 1–3).

Some confusion existed prior to this study concerning *N. atlantica,* caused by Kawaguchi & Butler (1984), as they noted that the origin of the dorsal fin base was in front of the center of the body, contrary to their own measurements showing the predorsal length extending posterior to the middle of the body, i.e., more than 50% SL. *Nansenia atlantica* was described by Blache & Rossignol (1962) who noted the dorsal fin *"elle est insérée un peu en avant du milieu du corps"*, although based on only two juveniles 15 and 16 mm SL, syntypes now lost (Eschmeyer 2014). Kawaguchi & Butler (1984) noted predorsal lengths of 51.9–56.9% SL in their examined materials consisting of tropical Atlantic adults. These measurements have been used in all three subsequent valid species descriptions without re-examination (Matallanas 1986b; Kobyliansky 1992; Usachev & Kobyliansky 1992). The specimens of *N. atlantica* examined in this study show a predorsal length ranging from 48.1–54.1% SL, and the range for this character is hereby extended for this taxon (Table 2). However, clear allometric growth changes are present in this species, as smaller specimens show greater predorsal lengths (above 50% SL) and larger specimens show considerably shorter predorsal lengths (below 50% SL). Disregarding the allometric growth changes found in juveniles, predorsal length in adults remains an important trait within the genus *Nansenia*, as adults of all species show distinct predorsal ranges (Table 3). The predorsal length is likely correlated with other continuous characters, such as the CPL/CPD ratio and other measurements related to elongation of the body.

One 81.5 mm SL specimen (AMS I. 20066-072) off southeastern Australia is here identified as *N. atlantica* (Table 2), extending the distribution of this species considerably, as it was previously considered a tropical Atlantic Ocean endemic as mentioned above (Fig. 3). However, a large amount of variation is present within specimens identified as *N. atlantica* at present (pers. obs.), including considerable allometric growth, and a taxonomic study for this issue is needed. The Australian specimen shows an uncharacteristic stubby caudal peduncle (CPL/CPD ratio 1.17) compared to other *N. atlantica* (Table 2), and is likely representing a Pacific population or even a distinct species as compared to the tropical Atlantic *N. atlantica*.

Nansenia boreacrassicauda shows many similarities with *N. ardesiaca* (Jordan & Thompson 1914), although separated from it by a smaller PCL/PCD ratio and in having many more dentary and vomerine teeth (Table 1–3). Mitogenomic data of *N. ardesiaca* by Ishiguro *et al.* (2003), the only other species of *Nansenia* with the mitogenome determined (AP004106), show an average distance of 5% sequence variation compared to *N. boreacrassicauda* depending on gene sequences compared (data not shown). Re-examination for confirmation of identification of this specimen was not possible. However, indications are that mitogenomic data are useful for species delimitation within closely related species of *Nansenia*, although rarity of specimens precludes a thorough molecular comparison at present.

Another 106.5 mm SL specimen (ZMH 120958) noted here as *Nansenia* cf. *pelagica*, caught at 45°24'N, 27°41'W, shows a combination of characters that is not congruent with any other species (Table 2). More materials from the temperate Atlantic are needed for comparisons with this specimen.

Additional materials for various taxa would improve the present study. However, the differences observed in a number of newly examined specimens are far outside ranges previously reported for several species, and inclusion of materials covering all ambiguous species identifications is beyond this study. I have chosen a conservative approach: describing one new species only and including data for several other specimens showing characters that do not fit into existing work. In addition, molecular data (mitogenome) adequate for clade delimitation on multiple taxonomic levels (Avise *et al.* 1987) are included for future comparisons with the holotype of *N. boreacrassicauda*.

Multiple taxonomic issues are present for *Nansenia* at present not necessarily related to gradients of continuous characters or distributional gaps. For example, Kobyliansky (1992) described two new species from the Indian Ocean, *N. indica* and *N. obscura*, without considering the previously described species *Nansenia macrolepis* (Gilchrist 1922) distributed in the same area. The latter species was synonymized with *N. ardesiaca* by Kawaguchi & Butler (1984) and characters separating *N. indica* from *N. ardesiaca* are not present (Table 3). *Nansenia ardesiaca* was noted by Kobyliansky (1992) to have the adipose fin base pigmented (proximal pigmentation), although Kawaguchi & Butler (1984) stated that the tip (distal part) was pigmented for this species. The matter is unresolved at present as specimens of *N. ardesiaca* newly examined in this study, e.g., AMS I.22817-025 materials from the Indian Ocean, show the adipose fin distally pigmented in some specimens with no pigmentation in others. Lack of adipose fin pigmentation is the most common for *N. ardesiaca* (pers. obs.). However, this contradicts the

description by Kawaguchi & Butler (1984) and change due to preservation is a possibility. The specimen described as *N. macrolepis* by Gilchrist (1922) was distinctly figured without adipose fin pigmentation although not discussed. Indications are that variation of pigmentation in the adipose fin is present for *N. ardesiaca*, slightly worrying concerning the wide use of this character in *Nansenia* taxonomy (Table 3). Alternatively, sympatric *N. ardesiaca* forms are present, separated by the adipose fin pigmentation, although no other characters support this at present (Table 2–3). Therefore, the observation of *N. ardesiaca* with a distally pigmented adipose fin, as also noted by Kawaguchi & Butler (1984) as designating this species, shows the species *Nansenia indica* (Kobyliansky 1992) a synonym of *Nansenia ardesiaca* (Jordan & Thompson, 1914).

The best characters for discriminating between adult species of *Nansenia* are: predorsal length, CPL/CPD ratio, number of vertebrae, number of gill rakers, number of teeth, morphology of lateral-line scales (below adipose fin), adipose fin pigmentation and possibly a "robust" vs. non-robust body form. Morphology of the opercular tube and crumenal organ varies between and within taxa and is taxonomically ambiguous at this point. Except for a unique low number of vertebrae in *Nansenia ahlstromi*, all characters employed for species discrimination in *Nansenia* must be used in combination for accurate species identification (Table 3). Juveniles remain problematic for identification and allometric growth is to be expected for most species.

Identification of *Nansenia* taxa can be initiated using a variety of characters, although the taxonomic information denoting natural clades concerning these characters are not clear at present. Identification of valid species is done via a combination of characters, although specimens showing extralimital characters (Table 2) are making the identification of some species trivial at present (Table 3). The taxonomy of *Nansenia* is in need of 1) recognition of extralimital characters in specimens available, 2) molecular data and 3) new materials as many oceanic species are represented by very few specimens. Traditionally, branchiostegal rays have been used to separate two species groups. However, these plate-like rays are often damaged and quite difficult to distinguish in some specimens, and not included in the following key. This is in line with Kawaguchi & Butler (1984) who noted that natural groups could not be defined by branchiostegal rays.

Identification key to species of *Nansenia* with a "stubby caudal peduncle" (CPL/CPD ratio 1.0–1.5)

1a. Dentary teeth 80 or more. 2
1b. Dentary teeth 60 or less. 4
2a. Predorsal length less than 48% SL; vertebrae 46–48 . . . . *Nansenia boreacrassicauda* sp.n
2b. Predorsal length more than 48% SL; vertebrae 35–44 3
3a. Gill rakers 40; vertebrae 35–36. . . . . *Nansenia ahlstromi*
3b. Gill rakers 30–36; vertebrae 41–44. . . . . *Nansenia atlantica*
4a. Dentary teeth approx. 30; adipose fin w/o pigmentation; vertebrae 42–45 . . . . *Nansenia oblita*
4b. Dentary teeth approx. 60; adipose fin proximally pigmented; vertebrae 38–39 . . . . *Nansenia pelagica*

Distribution and ecology. *Nansenia boreacrassicauda* is the fourth species in the genus *Nansenia* from Subarctic Atlantic waters, although specimens are rare and likely non-abundant on any measure along its entire longitudinal range. The catch locality between southeastern Greenland and Iceland in the Denmark Strait of the holotype in 2008, close to the Arctic Circle at 66°33'N, shows it to be the most northern record of any *Nansenia* species to date. It is likely oceanic along many other rare *Nansenia* taxa (Table 3). No additional specimens of *N. boreacrassicauda* have been observed since 2008 despite extensive yearly surveys off Greenland (pers. obs.). Although the holotype was caught on the border between the Arctic and Subarctic provinces in 2008, being the most northern record of all the type materials, the existence of the paratypes in Subarctic and temperate waters, caught in 1982 and 1986, indicates this species present for many years. The new species described is therefore based on an increased taxonomical effort and not necessarily associated with possible changing ocean temperatures, a very important notion concerning faunal changes in the Subarctic and Arctic provinces, as cold-water chemistry (including acidification) is relative strongly affected by temperature (IGBP, IOC, SCOR 2013). This must, however, always be considered in the context of the pelagic realm at Subarctic latitudes being poorly explored or showing taxonomic issues present (Møller *et al.* 2010; Poulsen 2015). The distributions of surface-associated taxa in Subarctic latitudes are further complicated by recent years of increased temperatures in boreal summers (Donlon *et al.* 2010), bringing for example valuable Bluefin tuna into southeastern Greenland waters (MacKenzie *et al.* 2014). However, it is currently not possible to evaluate whether new species distributions

observed in the Subarctic Atlantic are true range expansions, or they are common examples of increased interest and more resolved taxonomy for commercial important species (Byrkjedal *et al.* 2004). Kawaguchi & Butler (1984) noted a cold-water group including *N. groenlandica* and *N. tenera*, and now also including *N. boreacrassicauda*. Cohen (1984) noted *N. oblita* off western Ireland, expanding its distribution outside the Mediterranean, although no specimen information was given and confirmation of identity not possible. *Nansenia oblita* was recently included in the Subarctic fauna by Jónsson & Pálsson (2013) although specimens could not be verified. The specimen recorded by Møller *et al.* (2010) as *N. oblita* (ZMUC P191778), in an annotated checklist of Greenland fishes, is a misidentification being a species within the genus *Bathylagichthys* as currently recognized by Kobyliansky (1986; 1990a) (pers. obs., ongoing works).

Since most *Nansenia* taxa have been caught in upper meso- or epipelagic layers, temperature is clearly an important parameter for these fishes, corroborated by relative distinct distribution patterns (Fig. 3). The holotype of *N. boreacrassicauda* was caught over a bottom depth of 382–400 m at a temperature of 3.19°C close to the Arctic Circle in boreal summer. Considering the temperate and Subarctic distribution of type materials of *N. boreacrassicauda* (Fig. 3), indications are that North Atlantic cold surface water temperatures are the important parameter concerning the presence of this oceanic species. This is corroborated by the findings of all paratypes along a narrow longitudinal band along the mid-Atlantic ridge (Fig. 3). No temperature data are available for the few specimens present of *N. iberica* from the western Mediterranean or the North Atlantic paratypes of *N. boreacrassicauda*. However, the mesopelagic layers of the Mediterranean are temperature homogenous and never drop below 13°C in the western parts (Lejeusne *et al.* 2010), and the presence of *N. boreacrassicauda* in southern temperate Atlantic waters could possibly occur more frequently in boreal winters. The complicated vicarious events that have formed the present day Mediterranean Ocean, including the Messinian Salinity Crisis 5–7 million years ago and the subsequent Pliocene opening to the Atlantic (Bianchi & Morri, 2000), could possibly be involved in the separation of warm-water endemics, such as *N. iberica*. However, shallow-, slope- and deep-water benthic and demersal gadiforms have recently been shown highly similar to Atlantic populations previously considered separate species (Bañón *et al.* 2013; Francisco *et al.* 2014). Fish species distributions are to be evaluated individually in the context of the Mediterranean being a distinct Atlantic Province, although an oceanic mesopelagic habitat as found in *N. boreacrassicauda* seems to restrict expansion into coastal areas.

The new species shows large and numerous gill rakers adapt for retaining smaller pelagic crustaceans, and is likely hunting by vision in well-lit surface waters, corroborated by the large eye being approximately 40% HL (Table 1). This is similar to other *Nansenia* species believed to congregate in high productivity upper pelagic areas (Kawaguchi & Butler 1984). It is currently difficult to assess whether species such as *N. boreacrassicauda* and *N. iberica* are truly rare occurrences, or are simply rarely caught due to their fast swimming abilities and exclusively pelagic habitats being infrequently sampled.

Acknowledgements

References

Ahlstrom, E.H., Moser, H.G. & Cohen, D.M. (1984) Argentinoidei: development and relationships. *In*: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.D., Kendall, A.W. & Richardson, S.C. (Eds.), *Ontogeny and Systematics of Fishes.* American Society of Ichthyologists and Herpetologists, Allen Press Inc., Lawrence, 760 pp.

Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb. & Saunders, N.C. (1987) Intraspecific

Phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, 18, 489–522.
http://dx.doi.org/10.1146/annurev.es.18.110187.002421

Bañón, R., Arronte, J.C., Vázquez-Dorado, S., Río, J.L.D. & Carlos, A.D. (2013) DNA barcoding of the genus *Lepidion* (Gadiformes: Moridae) with recognition of *Lepidion eques* as a junior synonym of *Lepidion lepidion*. *Molecular Ecology Resources,* 13, 189–199.
http://dx.doi.org/10.1111/1755-0998.12045

Betancur-R, R., Broughton, R.E., Wiley, E.O., Carpenter, K., López J.A., Li, C., Holcroft, N.I., Arcila, D., Sanciangco, M., Cureton II, J.C., Zhang, F., Buser, T., Campbell, M.A., Ballesteros, J.A., Roa-Varon, A., Willis, S., Borden, W.C., Rowley, T., Reneau, P.C., Hough, D.J., Lu, G., Grande, T., Arratia, G. & Ortí, G. (2013)The Tree of Life and a New Classification of Bony Fishes. *PLOS Currents Tree of Life*, 2013, 1–45.
http://dx.doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288

Bianchi, C.N. & Morri, C. (2000) Marine biodiversity of the Mediterranean Sea: Situation, problems and prospects for future research. *Marine Pollution Bulletin*, 40, 367–376.
http://dx.doi.org/10.1016/S0025-326X(00)00027-8

Blache, J. & Rossignol, M. (1962) *Nansenia atlantica* nov. sp. (Teleostei, Clupeiformes, Opisthoproctoidei, Microstomidae). Poisson bathypelagique nouveau du Golfe de Guinée (diagnose provisoire). *Cahiers O. R. S. T. O. M. (Office de la Recherche Scientifique et Technique Outre-Mer) Série Océanographie*, 2, 103–106.

Byrkjedal, I., Godø, O.R. & Heino, M. (2004). Northward range extensions of some mesopelagic fishes in the Northeastern Atlantic. *Sarsia*, 89, 484–489.
http://dx.doi.org/10.1080/00364820410009265

Byrkjedal, I., Poulsen, J.Y. & Galbraith, J. (2011) *Leptoderma macrophthalmum* n.sp., a new species of smooth-head (Otocephala: Alepocephalidae) from the Mid Atlantic Ridge. *Zootaxa*, 2876, 49–56.

Chakrabarty, P., Warren, M., Page, L.M. & Baldwin, C.C. (2013) GenSeq: an updated nomenclature and ranking for genetic sequences from type and non-type sources. *Zookeys*, 346, 29–41.
http://dx.doi.org/10.3897/zookeys.346.5753

Cheng, S., Higuchi, R. & Stoneking, M. (1994) Complete mitochondrial genome amplification. *Nature Genetics*, 7, 350–351.
http://dx.doi.org/10.1038/ng0794-350

Cohen, D.M. (1958) *Nansenia candida*, a new species of argentinid fish from the North Pacific, with notes on other species of *Nansenia*. *Stanford Ichthyological Bulletin*, 7, 52–57.

Cohen, D.M. (1984) Argentinidae. *In*: Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J. & Tortonese, E. (Eds.), *Fishes of the North-eastern Atlantic and the Mediterranean. Vol. 1.* UNESCO, Paris, pp. 386–391.

Cohen, D.M., Inada, T., Iwamoto, T. & Scialabba, N. (1990) FAO species catalogue. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. *FAO Fisheries Synopsis*, 125, 1–442.

Donlon, C.J., Martin, M., Stark, J., Roberts-Jones, J., Fiedler, E. & Wimmer, W. (2012) The Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) system. *Remote Sensing of Environment,* 116, 140–158.
http://dx.doi.org/10.1016/j.rse.2010.10.017

Eschmeyer, W.N. (2014) Catalog of Fishes: GENERA, SPECIES, REFERENCES. Electronic version. Available from: http://www.research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 1 March 2015)

Facciolà, L. (1887) Sull'esistenza di due forme diverse di *Microstoma* nel Mar di Messina. *Naturalista Siciliano*, 6, 193–197.

Francisco, S.M., Robalo, J.I., Stefanni, S., Levy, A. & Almada, V.C. (2014) *Gaidropsarus* (Gadidae, Teleostei) of the North Atlantic Ocean: a brief phylogenetic review. *Journal of Fish Biology*, 85, 473–487.
http://dx.doi.org/10.1111/jfb.12437

Free Vector Maps (2015) Available from http://freevectormaps.com (accessed 31 March 2015)

Gilchrist, J.D.F. (1922) Deep-sea fishes procured by the S.S. "Pickle" (Part 1). *Report Fisheries and Marine Biological Survey. Union of South Africa*, 2, 41–79.

Greenwood, P.H. & Rosen, D.E. (1971). Notes on the structure and relationships of the alepocephaloid fishes. *American Museum Novitates*, 2373, 1–41.

IGBP, IOC, SCOR (2013) *Ocean acidification summary for policymakers - Third symposium on the ocean in a high-CO_2 World.* International Geosphere-Biosphere Programme, Stockholm, 22 pp.

Ishiguro, N.B., Miya, M. & Nishida, M. (2003) Basal euteleostean relationships: a mitogenomic perspective on the phylogenetic reality of the "Protacanthopterygii". *Molecular Phylogenetics and Evolution*, 27, 476–488.
http://dx.doi.org/10.1016/S1055-7903(02)00418-9

Jónsson, G. & Pálsson, J. (2013) *Islenskir Fiskar (Icelandic fishes)*. Mál og menning, Reykjavík, 493 pp.

Johnson, D.G & Patterson, C. (1996) Relationships of Lower Euteleostean Fishes. *In*: Stiassny, M.L.J., Parenti, L.R. & Johnson, D.G. (Eds.), *Interrelationships of Fishes*, Academic Press Limited, San Diego, pp. 251–332.

Jordan, D.S. & Evermann, B.W. (1896) The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. *Bulletin of the United States National Museum*, 47, 1–1240.

Jordan, D.S. & Thompson, W.F. (1914) Record of the fishes obtained in Japan in 1911. *Memoirs of the Carnegie Museum*, 6, 205–313.

Kawaguchi, K. & Butler, J.L. (1984) Fishes of the genus *Nansenia* (Microstomatidae) with descriptions of seven new species.

Contributions in Science, Natural History Museum of Los Angeles County, 352, 1–22.

Kobyliansky, S.G. (1985) Material for the revision of the genus *Bathylagus* Günther (Bathylagidae): the group of "light" deepsea smelts. *Voprosy Ikhtiologii*, 25(1), 51–67. [in Russian, English translation in *Journal of Ichthyology*, 25(2), 1–17]

Kobyliansky, S.G. (1986) Materials for a revision of the family Bathylagidae (Teleostei, Salmoniformes). *Transactions of the P.P. Shirshov Institute of Oceanology*, 121, 6–50. [in Russian, English summary]

Kobyliansky, S.G. (1990a) Two new species of the genus *Bathylagichthys* Kobyliansky (Bathylagidae, Salmoniformes) from Southern Hemisphere subpolar waters. *Voprosy Ikhtiologii*, 30(4), 537–542. [in Russian, English translation in *Journal of Ichthyology*, 30 (5), 21–27]

Kobyliansky, S.G. (1990b) Taxonomic status of microstomatid fishes and problems of classification of suborder Argentinoidei (Salmoniformes, Teleostei). *Trudy Instituta Okeanologii Akademiya Nauk SSSR*, 125, 148–177. [in Russian, English summary]

Kobyliansky, S.G. (1992) Two new species of the genus *Nansenia* (Microstomatidae, Salmoniformes) from the western Indian Ocean. *Voprosy ikhtiologii*, 32 (2), 3–9. [in Russian, English translation in *Journal of Ichthyology*, 32 (7), 30–36]

Lavenberg, R.J. (1965) A new species of microstomatid fish (*Nansenia*) from California waters. *Copeia*, 3, 281–285. http://dx.doi.org/10.2307/1440788

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F. & Pérez, T. (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology and Evolution*, 25, 250–260. http://dx.doi.org/10.1016/j.tree.2009.10.009

Lloris, D. & Rucabado, J.A. (1985) A new species of *Nansenia* (*N. problematica*) (Salmoniformes: Bathylagidae) from the southeast Atlantic. *Copeia*, 1, 141–145.

MacKenzie, B.R., Payne, M.R., Boje, J., Høyer, J.L. & Siegstad, H. (2014) A cascade of warming impacts brings bluefin tuna to Greenland waters. *Global Change Biology*, 20 (8), 2484–2491. http://dx.doi.org/10.1111/gcb.12597

Matallanas, J. (1986a) Descriptión de algunas estructuras de interés taxonómico en *Nansenia* (Pisces, Microstomatidae). *Miscellània Zoològica*, 10, 233–238.

Matallanas, J. (1986b) *Nansenia iberica*, a new species of Microstomatidae (Pisces, Salmoniformes). *Cybium*, 10, 193–198.

Merella, P., Alemany, F., Carbonell, A. & Quetglas, A. (1997) New record of *Nansenia iberica* (Salmoniformes: Microstomatidae) in western Mediterranean. *Cybium*, 21, 211–215.

Miya, M. & Nishida, M. (1999) Organization of the mitochondrial genome of a deep-sea fish, *Gonostoma gracile* (Teleostei: Stomiiformes): First example of transfer RNA gene rearrangements in bony fishes. *Marine Biotechnology*, 1, 416–426. http://dx.doi.org/10.1007/PL00011798

Møller, P.R., Nielsen, J.G., Knudsen, S.W., Poulsen, J.Y., Sünksen, K. & Jørgensen, O.A. (2010) A checklist of the fish fauna of Greenland waters. *Zootaxa*, 2378, 1–84.

Nelson, G.J. (1967) Epibranchial organs in lower teleostean fishes. *Journal of Zoology London*, 153, 71–89. http://dx.doi.org/10.1111/j.1469-7998.1967.tb05031.x

Nelson, J.S. (2006) *Fishes of the World. 4th Edition.* John Wiley & Sons (Inc.), Hoboken, New Jersey, 601 pp.

Poulsen, J.Y. (2015) Fifth confirmed record and North Atlantic range expansion of the rare pelagic bobtail snipe eel genus *Neocyema* (Cyematidae, Elopomorpha). *Marine Biodiversity Records*, 8 (e53), 1–5. http://dx.doi.org/10.1017/S175526721500024X

Poulsen, J.Y., Byrkjedal, I., Willassen, E., Rees, D., Takeshima, H., Satoh, T.P., Shinohara, G., Nishida, M. & Miya, M. (2013) Mitogenomic sequences and evidence from unique gene rearrangements corroborate evolutionary relationships of Myctophiformes (Neoteleostei). *BMC Evolutionary Biology*, 13 (111), 1–21. http://dx.doi.org/10.1186/1471-2148-13-111

Poulsen, J.Y., Møller, P.R., Lavoué, S., Knudsen, S.W., Nishida, M. & Miya, M. (2009) Higher and lower-level relationships of the deep-sea fish order Alepocephaliformes (Teleostei: Otocephala) inferred from whole mitogenome sequences. *Biological Journal of the Linnean Society*, 98, 923–936. http://dx.doi.org/10.1111/j.1095-8312.2009.01323.x

Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes*, 7, 355–364. http://dx.doi.org/10.1111/j.1471-8286.2007.01678.x

Reinhardt, J.C.H. (1840) Om nye Grönlandske fiske. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 7, 8–10. [1839]

Sutton, T.T., Letessier, T.B. & Bardarson, B. (2013) Midwater fishes collected in the vicinity of the Sub-Polar Front, Mid-North Atlantic Ocean, during ECOMAR pelagic sampling. *Deep-Sea Research II,* 98, 292–300. http://dx.doi.org/10.1016/j.dsr2.2013.08.001

Usachev, S.G. & Kobyliansky, S.G. (1992) *In*: Kobyliansky, S.G. (1992) Two new species of the genus *Nansenia* (Microstomatidae, Salmoniformes) from the western Indian Ocean. *Voprosy ikhtiologii*, 32 (2), 3–9. [in Russian, English translation in *Journal of Ichthyology*, 32 (7), 30–36]

Vecchione, M., Bergstad, O.A., Byrkjedal, I., Falkenhaug, T., Gebruk, A.V., Godø, O.R., Gislason, A., Heino, M., Høines, Å.S., Menezes, G.M.M., Piatkowski, U., Priede, I.G., Skov, H., Søiland, H., Sutton, T. & Wenneck, T.L. (2010) Biodiversity Patterns and Processes on the Mid-Atlantic Ridge. *In*: McIntyre, A.D. (Ed.), *Life in the World´s Oceans: Diversity, Distribution, and Abundance*. Wiley-Blackwell Publishing Ltd, West Sussex, pp. 103–121.