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ORIGINAL PAPER

First complete description of the dark-mouth skate *Raja arctowskii* Dollo, 1904 from Antarctic waters, assigned to the genus *Bathyraja* (Elasmobranchii, Rajiformes, Arhynchobatidae)

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Abstract

The dark-mouth skate, *Raja arctowskii* Dollo, 1904 from Antarctic waters is an extraordinary case in skate taxonomy. For more than 100 years, this species has been known only from three empty egg capsules and the species as such has remained undescribed due to the lack of specimens that could be assigned to Dollo's small capsules. Since trawled egg capsules and an egg capsule containing a near-term embryo became available, it finally was possible to connect specimens with the empty egg capsules and completely describe Dollo's *R. arctowskii* with detailed external morphology, skeletal features, clasper morphology, and clasper skeleton and assign it to the genus *Bathyraja* Ishiyama, 1958a. *Bathyraja arctowskii* is one of the smallest known species of *Bathyraja*, attaining only a 61 cm total length (TL). It is characterized by an at least partly, usually completely medium to dark grayish pigmented mouth cavity, as well as the often dark underside of the nasal curtain from very small juvenile stages onwards. It further differs from most congeners in Antarctic and Subantarctic waters in the absence of thorns on the dorsal disc. It appears to be a wide-ranging, circumantarctic species found in the Atlantic, Pacific, and Indian Ocean sectors of the Southern Ocean. The species seems to be locally common at least in the Atlantic sector, with up to 94 juvenile to subadult specimens caught in one single haul.

Keywords Systematics · Taxonomy · Morphology · DNA analysis · Egg capsules · Southern Ocean

Introduction

Raja arctowskii Dollo, 1904 is an extraordinary case in skate taxonomy, because it was named based only on three empty egg capsules of very small size from off the Antarctic Peninsula, but the species as such remained undescribed due to lack of specimens which could be assigned to Dollo's small egg capsules.

In "Fishes of the Southern Ocean", Stehmann and Bürkel (1990: 88, 94) mentioned, keyed out and commented on a *Bathyraja* sp., which appeared to be the most abundant skate species in the Atlantic sector of Antarctic waters, primarily in the Weddell Sea. A specific account was not given by Stehmann and Bürkel (1990) due to its unresolved nomenclatorial status. Stehmann (1985: 209) had briefly commented on a few external characteristics of this species as *Bathyraja* sp. 2 and underlined its small size of 60 cm maximum total length, as compared with other Southern Ocean skate species.

The first reference to the species after Dollo (1904) was by Bigelow and Schroeder (1965) describing a mature male of 490 mm TL from northeast off the South Shetland Islands at

Matthias F. W. Stehmann and Simon Weigmann contributed equally to this work.

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220–240 m depth, and a female of 258 mm TL from northeast off Clarence Island at 585–595 m depth as *Breviraja griseocauda* (Norman, 1937); both specimens were captured by USNS "Eltanin." The second reference was by Springer (1971) describing a mature male of 485 mm TL as *B. griseocauda* captured by RV "Hero" in 1969 off Brabant Island north of the Antarctic Peninsula in a 94 m depth. Authors of both papers did not recognize the very small size of their mature males, as compared with the much larger *B. griseocauda* in the SW Atlantic, of which, however, they compared only with Norman's (1937) holotype female of 460 mm TL plus five males of 250–332 mm TL at BMNH London and apparently overlooked their immature juvenile stage. Springer (1971: 7), however, commented on *Raja arctowskii* Dollo, 1904 and its original only 60 mm long egg capsules but failed to relate this small capsule size to the small size of Bigelow and Schroeder's (1965) and his small mature males of his *B. griseocauda* and considered *R. arctowskii* a *nomen dubium*.

Since the 1970s, many specimens of a very small *Bathyraja*-like skate were captured and preserved by German Antarctic expeditions primarily in the Weddell Sea and off Atlantic Antarctic islands north of Antarctic Peninsula, e.g., South Shetlands. The small size of mature males sampled focused our attention on *Raja arctowskii* and its small egg capsules, but to prove the identity required a mature female containing egg capsules. Although such a female became available, it was not found for the present study and other evidence was needed, which was found in an egg capsule containing a male near-term embryo. Based on this evidence, we could finally prove the identity with Dollo's *R. arctowskii*, as briefly indicated by Weigmann (2016).

We are presenting here the so far lacking complete description and new generic assignment of *Bathyraja arctowskii* (Dollo, 1904) with detailed external morphology, skeletal features, clasper morphology and clasper skeleton. Finally, the valid status of this small Antarctic skate species could be confirmed.

Material and methods

Institutional acronyms follow Sabaj (2019). External morphometric measurements were taken by vernier caliper to one-tenth of a millimeter (mm) from the specimens preserved in 70% ethanol. Measurements were taken between perpendicular lines where relevant and largely following Bigelow and Schroeder (1953). Exceptions: prenasal snout length from snout tip to transverse line through anterior edge of nostrils, and orbit plus spiracle length after Clark (1926); ventral head length from snout tip to transverse line through fifth gill slits, clasper length, and eyeball horizontal diameter after Ishiyama (1958a); dorsal head length medially from snout tip to occipital joint, as well as tail and nasal curtain measurements after Hubbs and Ishiyama (1968); spiracle length measured diagonally as depression and as aperture proper; length of pelvic lobes measured from point of articulation of anterior lobe according to Stehmann (1985); width across pelvic-fin base between anterior points of articulation, anterior pelvic lobe base width, width across posterior pelvic lobe as maximum width across expanded lobe, head width at anterior margin of orbits, as well as disc and preorbital snout length direct (point-to-point) after Last and Séret (2008). Measurements of egg capsules were taken after Treloar et al. (2006), Ebert and Davis (2007), and Concha et al. (2009, 2012). The following measurements are newly introduced in this paper: central body length excluding aprons (CBL), central body width excluding lateral keels (CBW), as well as anterior and posterior horn lengths measured horizontally between perpendicular lines. Terminology of clasper glans components and skeleton cartilages follows Hulley (1970, 1972) and Stehmann (1970). Skeletal morphometric measurements of cranium and scapulocoracoid were made after McEachran and Compagno (1979), with postoccipital length of jugal arches measured from level posterior edge of cranium to posterior end of jugal arches, and of pelvic girdle after Stehmann et al. (2008); vertebral counts follow Springer and Garrick (1964) and Krefft (1968a). Skeletal morphometric measurements and meristics were taken and counted from radiographs except for measurements of scapulocoracoid taken from dissected elements. Subantarctic and Antarctic waters are treated as Southern Ocean herein following common practice and a draft for amending the ocean limits by the International Hydrographic Organization (IHO). Nevertheless, the IHO officially still recognizes only four oceans, i.e., the Indian, Pacific, Atlantic, and Arctic oceans and any drafts that have been circulated have no authority as a reference source (see Weigmann 2016 for further details). The cartographic base used for the location map is from the Quantarctica package (Matsuoka et al. 2018).

Molecular data

Tissue samples stored in 95% alcohol associated with voucher specimens held at the Te Papa Tongarewa Museum of New Zealand were sent to GJPN. DNA was extracted using the E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Inc. Norcross, GA). Total DNA was then subjected to PCR amplification of the mitochondrial NADH2 using primers described in Naylor et al. (2005). Amplified fragments were cleaned and sent out to Retrogen (6645 Nancy Ridge Drive, San Diego, Ca 9212) for bi-directional sequencing. Resulting DNA sequences were edited using Geneious® Pro v. 6.1.7 (Biomatters Ltd. Auckland, New Zealand, available at http://www.geneious.com). The edited sequences were translated to amino acids and aligned with corresponding NADH2 sequences from representatives of available closely related species occurring in the region using the MAFFT module within the Geneious Package (Biomatters Ltd. Auckland, New Zealand). The aligned amino acid sequences were translated back, in frame, to their original nucleotide sequences, to yield a nucleotide alignment. The alignment was subjected to a maximum likelihood analysis using the General Time Reversible model with rate categories optimized to fit the data and additional parameters to accommodate among site rate heterogeneity the proportion of invariant sites (GTR+I+G). Phylogenetic analyses were conducted using the software package PAUP*4.0a build 168).

Results

Systematic account

Bathyraja arctowskii Dollo, 1904

(Antarctic dark-mouth skate)

(Figs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 1, 17, 18, 19, 20, 21, 22, 23, 24, 25, and 26, Tables 1, 2, 3, 4, 5, 6, and 7)

Raja arctowskii Dollo, 1904—Poissons in: Expédition Antarctique Belge 1897–99 Zoologie, Antwerpen 1904: 11, 51, 52, plate IX, Fig. 10. Types: three empty egg capsules IRSNB 25 [orig. 3005], IRSNB 26 [orig. 3006], IRSNB 27 [orig. 3007]; Weigmann (2016: 953).

Breviraja griseocauda (not Norman, 1937)—Bigelow & Schroeder (1965: R43–R46, Fig. 4).

Bathyraja griseocauda (not Norman, 1937)—Springer (1971: 5–7, Figs. 2 and 4B).

Bathyraja n. sp. (dwarf)—Hanchet et al. (2013: 621, 631).

Bathyraja sp. 2—Stehmann (1985: 209); Jones et al. (2009: 53, 54, 63 [erroneously as *Bathydraco* sp. 2], 64); Kalisz (2013: 4–24).

Bathyraja sp.—Stehmann & Bürkel (1990: 88, 94).

Bathyraja sp. (dwarf)—Smith et al. (2008: 1170–73, 1175–78).

Primary material examined in detail (11 specimens): ZMH 120216 (ex ISH 489-1981), 1 adult male, 533 mm TL, 60° 51′ S, 55° 34′ W, 18.03.81, 280–294 m depth (taken together with 1 female and 1 juvenile male listed under additional material); **ZMH 123230** (ex ISH 210-1987), 1 adult female, 535 mm TL, 61° 07′ S, 55° 53′ W, 30.10.87, 126–149 m depth (taken together with 3 further females listed under additional material); **ZMH 114702** (ex ISH 753-1976), 1 subadult female, 427 mm TL, 61° 53′ S, 58° 53′ W, 29.01.76, 200 m depth; **ZMH 121822** (ex ISH 37-1984), 1 subadult male, 424 mm TL, 2 juvenile males 246 mm TL and 181 mm TL, 4 juvenile females 333 mm TL, 236 mm TL, 163 mm TL, and 135 mm TL, 61° 11′ S, 56° 12′ W, 13.11.83, 375 m depth (taken together with 87 further specimens listed under additional material); **ZMH 9014**, 1 near-term male embryo taken from egg capsule, 120 mm TL, 61° 13.9′ S, 56° 25.4′ W, 21.11.96, 403–415 m depth.

Additional material, only partially examined (267 specimens): MNHN 1987-0232, adult male, 591 mm TL, Prydz Bay, 66° 59′ 24″ S, 73° 52′ 52″ E, 26.01.85, 475 m depth (morphometrics, meristics and description notes kindly provided for this specimen by Bernard Séret, photographs and radiographs by Jonathan Pfliger, Guy Duhamel and Zouhaira Gabsi); USNM 204703, late subadult male, 477 mm TL, 64° 12.1S, 62° 40′ W, 09.02.1969, 94 m depth; ZMH 114623 (ex ISH 1025-1976), 1 female, 421 mm TL, 62° 39′ S, 59° 51′ W, 30.01.76, 200–238 m depth; ZMH 114650 (ex ISH 1027-1976), 1 female, 358 mm TL, 61° 39′ S, 57° 36′ W, 28.01.76, 400 m depth; ZMH 114695 (ex ISH 771-1976), 1 female, 394 mm TL, 61° 39′ S, 57° 36′ W, 28.01.76, 400 m depth; ZMH 114696 (ex ISH 767-1976), 1 juvenile male, 342 mm TL, 60° 49′ S, 55° 37′ W, 27.01.76, 300–350 m depth; ZMH 114701 (ex ISH 754-1976), 1 juvenile female, 234 mm TL, 62° 05′ S, 60° 16′ W, 29.01.76, 306 m depth; ZMH 115002 (ex ISH 1026-1976), 1 juvenile female, 139 mm TL, 60° 49′ S, 55° 42′ W, 24.02.76, 345–405 m depth; ZMH 115009 (ex ISH 1028-1976), 5 juvenile females, 250, 263, 291, 197, and 309mm TL, 4 juvenile males 303, 304, 308, and 355 mm TL, 60° 24′ S, 45° 40′ W, 15.02.76, 400 m depth; ZMH 115022 (ex ISH 757-1976), 1 female, 355 mm TL, 60° 50′ S, 55° 42′ W, 17.02.76, 363 m depth; ZMH 115023 (ex ISH 756-1976), 1 male postembryo, 141 mm TL, 60° 50′ S, 55° 35′ W, 16.02.76, 400 m depth; ZMH 115024 (ex ISH 755-1976), 1 juvenile male, 353 mm TL, 65° 28′ S, 67° 42′ W, 05.02.76, 300 m depth; ZMH 115188 (ex ISH 299-1977), 1 female, 465 mm TL, 1 adult male, 589 mm TL, 62° 23.5′ S, 61° 12′ W, 28.11.77, 235 m depth; ZMH 115191 (ex ISH 687-1978), 1 subadult male, 392 mm TL, 1 female, 463 mm TL, 61° 13.7′ S, 56° 09.9′ W, 21.11.77, 288–300 m depth; ZMH 115195 (ex ISH 693-1978), 1 juvenile male, 248 mm TL, 60° 52′ S, 55° 29.7′ W, 21.11.77, 235–240 m depth; ZMH 115241 (ex ISH 685-1978), 1 juvenile female, 339 mm TL, 2 juvenile males, 156 and 328 mm TL, 60° 25′ S, 46° 39′ W, 16.01.78, 300–360 m depth; ZMH 115243 (ex ISH 689-1978), 2 juvenile males, 299 and 346 mm TL, 2 adult males, 502 and 520 mm TL, 3 adult females, 492, 510, and 535 mm TL (all damaged), 60° 53′ S, 55°19′ W, 24.01.78, 345–400 m depth; ZMH 115253 (ex ISH 684-1978), 1 juvenile female, 252 mm TL, 4 juvenile males, 220+ (severely damaged), 315, 371, and 376 mm TL, 60° 49′ S, 55° 44′ W, 25.01.78, 478–490 m depth; ZMH 115334 (ex ISH 698-1978), 1 subadult male, 365 mm TL, 62° 01′ S, 59° 58′ W, 04.03.78, 225–227 m depth; ZMH 115447 (ex ISH 688-1978), 1 juvenile male, 256 mm TL, 1 adult female, 510 mm TL, 60° 50′ S, 55° 36′ W, 25.02.78, 211–315 m depth; ZMH 120216 (ex ISH 489-1981), 1 female, 347 mm TL, 1 juvenile male, 327 mm TL, 60° 51′ S, 55° 34′ W, 18.03.81, 280–294 m depth (taken together with 1

Table 1 *Bathyraja arctowskii*, mophometrics and meristics. Individual values for primary adult male, primary adult female, primary subadult male, primary subadult female, and adult male MNHN 1987-0232*, as well as ranges for juveniles and embryo ($n = 7$) and means for all 12 specimens. Proportional individual values are expressed as percentages of total length (TL) 70% ethanol preserved; minimum, maximum, and mean of TL are given in millimeters

	Primary adult male, ZMH 120216		Primary adult female with extreme tail tip missing, ZMH 123230		Primary subadult male, ZMH 121822		Primary subadult female, ZMH 114702		Adult male, MNHN 1987–0232		Minimum juveniles and embryo ($n = 7$)	Maximum juveniles and embryo ($n = 7$)	Mean all specimens ($n = 12$)
	mm	% TL	mm	% TL	mm	% TL	mm	% TL	mm	% TL	% TL	% TL	% TL
TL, mm	533.0	100.0	535.0	100.0	424.0	100.0	427.0	100.0	591.0	100.0	120.0	333.0	327.0
Disc, width	352.0	66.0	330.0	61.7	261.0	61.6	282.0	66.0	384.0	65.0	51.7	64.6	62.4
Disc, length	296.0	55.5	273.0	51.0	212.0	50.0	238.0	55.7	320.0	54.1	44.2	50.8	50.0
Snout length, preorbital	72.5	13.6	61.0	11.4	48.5	11.4	69.0	16.2	74.0	12.5	8.1	11.6	11.4
Snout length, preoral	67.0	12.6	61.0	11.4	47.0	11.1	64.7	15.2	75.0	12.7	8.8	11.3	11.3
Snout length, prenasal	55.5	10.4	50.5	9.4	38.7	9.1	55.0	12.9	56.0	9.5	7.4	9.4	9.2
Orbit, horizontal diameter	25.0	4.7	24.6	4.6	20.5	4.8	17.7	4.1	24.0	4.1	4.6	5.8	4.9
Eyeball, horiz. diameter	18.0	3.4	20.0	3.7	15.5	3.7	15.5	3.6	19.6	3.3	3.9	4.6	4.0
Interorbital width	19.0	3.6	16.0	3.0	13.0	3.1	13.0	3.0	21.0	3.6	3.2	3.8	3.4
Spiracle length	16.5	3.1	14.0	2.6	12.7	3.0	12.0	2.8	16.0	2.7	2.7	3.8	2.9
Interspiracular width	42.2	7.9	39.3	7.3	31.0	7.3	30.0	7.0	43.0	7.3	7.9	8.8	8.1
Orbit + spiracle length	28.5	5.3	26.0	4.9	22.0	5.2	21.0	4.9	30.5	5.2	4.9	5.9	5.2
D1, height	19.3	3.6	8.7	1.6	12.1	2.9	9.5	2.2	17.4	2.9	1.6	3.1	2.3
D1, base length	22.0	4.1	24.5	4.6	16.6	3.9	12.2	2.9	27.6	4.7	2.1	4.2	3.7
D2, height	14.5	2.7	10.0	1.9	10.5	2.5	10.0	2.3	13.5	2.3	1.6	2.3	2.0
D2, base length	13.8	2.6	21.0	3.9	14.6	3.4	12.5	2.9	19.8	3.4	2.8	4.0	3.4
Interdorsal space	0.0	0.0	1.5	0.3	3.4	0.8	3.3	0.8	2.5	0.4	0.0	1.4	0.5
C, base length	9.0	1.7	12.0	2.2	7.0	1.7	15.0	3.5	Nm	Nm	1.9	5.2	2.9
C, height epichordal lobe	2.1	0.4	1.0	0.2	1.9	0.4	1.5	0.4	Nm	Nm	0.2	0.5	0.3
C, height hypochordal lobe	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tail, postdorsal length	9.0	1.7	12.0	2.2	7.0	1.7	15.0	3.5	8.0	1.4	1.9	5.2	2.7
Tail, height at V-tips	11.5	2.2	11.0	2.1	9.5	2.2	8.5	2.0	17.3	2.9	2.3	4.3	2.6
Tail, width at V-tips	17.2	3.2	20.0	3.7	15.5	3.7	15.5	3.6	24.7	4.2	3.3	4.5	3.7
Tail, height at D1-origin	4.5	0.8	4.0	0.7	3.7	0.9	4.0	0.9	5.7	1.0	0.9	1.3	1.0
Tail, width at D1-origin	11.5	2.2	10.0	1.9	7.9	1.9	6.8	1.6	11.7	2.0	1.1	2.0	1.7
Tail, lateral fold length	250.0	46.9	255.0	47.7	198.8	46.9	189.0	44.3	278.0	47.0	32.8	47.6	42.3
Head length, ventrally	149.5	28.0	133.5	25.0	109.0	25.7	119.0	27.9	165.0	27.9	21.5	25.9	25.0
Head length, dorsally	106.0	19.9	95.0	17.8	74.5	17.6	92.3	21.6	Nm	Nm	14.2	18.7	17.9
Mouth width	41.0	7.7	34.5	6.4	29.0	6.8	27.3	6.4	42.0	7.1	6.5	8.4	7.3
Internarial width	35.5	6.7	34.1	6.4	25.5	6.0	28.0	6.6	41.0	6.9	6.0	7.2	6.5
Nasal curtain, length	22.0	4.1	20.0	3.7	14.5	3.4	15.5	3.6	29.0	4.9	2.4	3.4	3.5
Nasal curtain, width each lobe	12.0	2.3	12.0	2.2	9.5	2.2	9.0	2.1	16.7	2.8	2.0	2.7	2.3
Nasal curtain, space between lobes	28.0	5.3	23.0	4.3	19.5	4.6	17.0	4.0	20.8	3.5	2.8	4.0	3.8
Gill slit length, 1st	7.2	1.4	6.5	1.2	4.3	1.0	3.2	0.7	6.3	1.1	0.7	1.4	1.1
Gill slit length, 3rd	9.2	1.7	7.5	1.4	4.9	1.2	3.8	0.9	8.3	1.4	1.1	1.6	1.3
Gill slit length, 5th	5.8	1.1	4.9	0.9	3.3	0.8	3.6	0.8	3.8	0.6	0.8	1.4	0.9
Interspace first gill slits	77.0	14.4	77.0	14.4	62.3	14.7	65.3	15.3	82.8	14.0	14.2	15.9	14.9
Interspace fifth gill slits	48.5	9.1	56.0	10.5	41.0	9.7	53.5	12.5	48.9	8.3	9.3	11.1	10.0
V-length, ant. Lobe	63.5	11.9	59.0	11.0	53.5	12.6	46.5	10.9	79.0	13.4	10.3	13.1	12.1
V-length, post. Lobe	103.0	19.3	73.5	13.7	75.0	17.7	69.0	16.2	127.0	21.5	11.1	18.7	16.7
Clasper, postcloaca length	137.0	25.7	–	–	86.5	20.4	–	–	142.0	24.0	6.7	10.4	16.0
Clasper length	118.0	22.1	–	–	73.0	17.2	–	–	120.0	20.3	3.8	6.2	12.4
Snout tip to mid-cloaca	259.0	48.6	254.5	47.6	193.5	45.6	212.0	49.6	281.0	47.5	41.3	45.6	45.2
Snout tip to 1st hemal spine	269.5	50.6	267.0	49.9	203.5	48.0	220.0	51.5	Nm	Nm	43.8	48.2	47.4
Snout tip to axis max. disc width	160.0	30.0	150.0	28.0	122.0	28.8	136.0	31.9	185.0	31.3	24.2	30.9	28.7
Mid-cloaca to D1	225.0	42.2	221.0	41.3	181.5	42.8	164.0	38.4	254.0	43.0	44.1	46.7	43.9
Mid-cloaca to D2	252.0	47.3	240.5	45.0	201.0	47.4	181.5	42.5	285.5	48.3	48.2	52.3	48.1
Mid-cloaca to tail tip	271.0	50.8	280.0	52.3	223.5	52.7	211.0	49.4	314.0	53.1	53.2	60.2	54.5
Snout angle, °	110		112		120		112		105		125	140	123.1
Tooth rows, upper jaw	24		29		25		27		24		22	27	25.5
Tooth rows, lower jaw	24		28		27		25		25		21	29	25.7
Trunk vert., Vtr	31		32		33		37		31		30	33	32.0
Predorsal tail vert., Vprd	76		70		74		74		76		66	80	73.8

Table 1 (continued)

	Primary adult male, ZMH 120216	Primary adult female with extreme tail tip missing, ZMH 123230	Primary subadult male, ZMH 121822	Primary subadult female, ZMH 114702	Adult male, MNHN 1987–0232	Minimum juveniles and embryo (*n* = 7)	Maximum juveniles and embryo (*n* = 7)	Mean all specimens (*n* = 12)
	mm % TL	mm % TL	mm % TL	mm % TL	mm % TL	% TL	% TL	% TL
Terminal vert., Vterm (approximately)	29	29	25	40	28	23	30	27.6
Total vert., Vtotal (approximately)	136	131	132	151	135	120	138	133.5
Pectoral rays l./r.	76/75	73/74	73/74	89/90	79/78	~ 70/~ 70	76/77	74.9/75.1
Pelvic rays l./r.	5 + 16/ 5 + 17	4 + 16/ 4 + 17	4+~18/ 4+~18	5 + 20/ 5 + 19	5 + 17/5 + 18	4 + 20/4 + ~ 18	5 + 19/5 + 19	4.7 + 17/4.7 + 17

Nm not measured

*Measurements for adult male MNHN 1987-0232 were kindly provided by Bernard Séret (ICHTHYO CONSULT)

adult male listed under primary material); ZMH 120217 (ex ISH 491-1981), 5 juvenile females, 143, 160, 184, 205, and 212 mm TL, 4 juvenile males, 146, 159, 204, and 260 mm TL, 60° 50′ S, 55° 39′ W, 19.03.81, 450–470 m depth; ZMH 120223 (ex ISH 492-1981), 2 juvenile females, 243 and 245 mm TL, 2 juvenile males, 162 and 172 mm TL, 1 juvenile male, 343 mm TL, 1 adult male, 532 mm TL, 62° 12′ S, 57° 00′ W, 16.03.81, 0–140 m depth; ZMH 121820 (ex ISH 41-1984), 3 females, 385, 391, and 475 mm TL, 1 juvenile male, 267 mm TL, 1 subadult male, 416 mm TL, 61° 07′ S, 56° 05′ W, 15.11.83, 235 m depth; ZMH 121821 (ex ISH 39-1984), 1 juvenile female, 232 mm TL, 1 juvenile male, 271 mm TL, 1 subadult male, 361 mm TL, 61° 06′ S, 55° 59′ W, 15.11.83, 177 m depth; ZMH 121822 (ex ISH 37-1984), 87 specimens, males 141–432 mm TL, females 149–475 mm TL, 61° 11′ S, 56° 12′ W, 13.11.83, 375 m depth (taken together with 7 specimens listed under primary material); ZMH 122009 (ex ISH 33-1985), 1 female, 460 mm TL, 61° 20′ S, 54° 42.3′ W, 10.01.85, 292 m depth; ZMH 122065 (ex ISH 172-1985), 1 subadult male, 421 mm TL, 61° 20′ S, 54° 44′ W, 21.02.85, 311–364 m depth; ZMH 122072 (ex ISH 176-1985), 1 female, 483 mm TL, 61° 17′ S, 56° 04′ W, 23.02.85, 279–288 m depth; ZMH 122075 (ex ISH 114-1985), 1 juvenile male, 285 mm TL, 1 female, 464 mm TL, 72° 53.1′ S, 19° 29.3′ W, 20.02.85, 423 m depth; ZMH 122079 (ex ISH 178-1985), 1 female, 368 mm TL, 61° 06′ S, 56° 04′ W, 24.02.85, 238–274 m depth; ZMH 122084 (ex ISH 175-1985), 1 juvenile female, 301 mm TL, 61° 12′ S, 56° 09′ W, 22.02.85, 301–318 m depth; ZMH 122097 (ex ISH 167-1985), 1 juvenile male, 352 mm TL, 60° 52′ S, 55° 30′ W, 27.02.85, 306–310 m depth; ZMH 122107 (ex ISH 104-1985), 1 juvenile female, 311 mm TL, 73° 23.4′ S, 21° 30.5′ W, 18.02.85, 475 m depth; ZMH 122299 (ex ISH 953-1986), 1 female, 213 mm TL, 4 juvenile males, 249, 304, 305 and 317 mm TL, 60° 51′ S, 55° 34′ W, 11.05.86, 319–320 m depth; ZMH 122301 (ex ISH 955-1986), 3 juvenile males, 245, 290 and 331 mm TL, 1 1 juvenile female, 308 mm TL, 1 female, 332 mm TL, 61° 20′ S, 55° 48′ W, 13.05.86, 249–259 m depth; ZMH 122328 (ex ISH 956-1986), 2 juvenile males, 265 and 347 mm TL, 1 subadult male, 363 mm TL, 1 female, 370 mm TL, 61° 18′ S, 55° 06′ W, 13.05.86, 261–309 m depth; ZMH 122333 (ex ISH 954-1986), 1 juvenile female, 237 mm TL, 60° 51′ S, 55° 35′ W, 11.05.86, 319–320 m depth; ZMH 122498 (ex ISH 959-1986), 2 subadult males, 435 and 440 mm TL, 1 late subadult male, 470 mm TL, 1 adult male, 520 mm TL, 60° 57′ S, 55° 19′ W, 10.06.86, 220–246 m depth; ZMH 122499 (ex ISH 960-1986), 1 juvenile male, 304 mm TL, 2 subadult males, 362 and 374 mm TL, 1 late subadult male, 461 mm TL, 1 juvenile female, 313 mm TL, 2 females, 351 and 445 mm TL, 60° 57′ S, 55° 07′ W, 10.06.86, 377–383 m depth; ZMH 122500 (ex ISH 962-1986), 1 juvenile female, 253 mm TL, 61° 06′ S, 55° 57′ W, 11.06.86, 143 m depth; ZMH 122510 (ex ISH 969-1986), 3 females, 243, 273 and 273 mm TL, 2 males, 223 and 275 mm TL, 61° 02′ S, 55° 00′ W, 13.06.86, 319–337 m depth; ZMH 122516 (ex ISH 958-1986), 1 subadult male, 450 mm TL, 60° 51′ S, 55° 45′ W, 09.06.86, 284–291 m depth; ZMH 122545 (ex ISH 964-1986), 1 juvenile female, 300 mm TL, 60° 51′ S, 55° 29′ W, 12.06.86, 466–493 m depth; ZMH 122546 (ex ISH 963-1986), 1 juvenile male, 297 mm TL, 60° 51′ S, 55° 27′ W, 12.06.86, 334–343 m depth; ZMH 122574 (ex ISH 967-1986), 1 juvenile female, 247 mm TL, 61° 07′ S, 56° 08′ W, 13.06.86, 283–307 m depth; ZMH 122575 (ex ISH 965-1986), 4 juvenile females, 187, 233, 267, and 327 mm TL, 60° 50′ S, 55° 42′ W, 12.06.86, 359–401 m depth; ZMH 122576 (ex ISH 968-1986), 2 juvenile males, 139 and 255 mm TL, 61° 04′ S, 56°

Table 2 *Bathyraja arctowskii*, morphometrics of cranium based on radiographs. Proportional values are expressed as percentages of nasobasal length (NBL)

	Primary adult male, ZMH 120216, 533 mm TL		Primary adult female with extreme tail tip missing, ZMH 123230, 535 mm TL		Primary subadult male, ZMH 121822, 424 mm TL		Primary subadult female, ZMH 114702, 427 mm TL	
	mm	% NBL	mm	% NBL	mm	% NBL	mm	% NBL
Cranium TL	117.5	192.7	99.4	187.0	71.4	181.7	85.0	216.7
Nasobasal length (NBL)	61.0	100.0	53.2	100.0	39.3	100.0	39.2	100.0
Max. ethmoidal width	58.5	95.8	55.1	103.7	40.6	103.3	38.3	97.7
Min. dorsal interorb. width	19.0	31.1	16.0	30.1	13.0	33.1	13.0	33.2
Min. internasal width	8.6	14.1	8.9	16.7	5.9	15.1	9.0	22.8
Max. width nasal apertures	24.7	40.5	20.9	39.3	14.3	36.4	13.0	33.1
Min. ventral interorb. width/basal plate width	16.4	27.0	14.3	26.9	10.7	27.3	10.4	26.5
Max. width otic region	32.4	53.2	30.4	57.1	23.6	60.0	20.3	51.7
Max. width jugular	36.4	59.7	33.7	63.3	24.8	63.2	25.3	64.6
Rostral shaft length	56.2	92.2	45.7	86.0	31.8	80.9	45.7	116.5
Rostrum base width	14.1	23.1	14.9	28.0	10.6	27.0	9.0	22.8
Postnasal length orbit region	20.9	34.2	19.2	36.2	12.6	32.0	10.9	27.9
Length otic region	17.9	29.4	14.8	27.8	11.7	29.8	15.6	39.7
Postoccipital length jugal arches	1.0	1.6	0.6	1.1	0.0	0.0	0.0	0.0
Tip rostrum to tip ant. fontanelle	51.6	84.7	41.0	77.2	28.7	73.1	44.5	113.6
Tip rostrum to end ant. fontanelle	72.4	118.6	59.6	112.1	40.2	102.2	52.9	135.0
Tip rostrum to level ant. propterygia	12.7	20.9	7.5	14.1	7.7	19.5	7.4	18.8
Tip rostrum to level max. ethmoidal width	61.9	101.5	52.9	99.5	36.3	92.3	50.4	128.5
Tip rostrum to symphysis upper jaw	68.0	111.4	61.0	114.7	41.3	105.1	55.6	141.8
Ant. fontanelle length	20.3	33.2	17.8	33.5	11.5	29.3	8.6	21.8
Ant. fontanelle max. width	11.1	18.2	13.1	24.7	8.3	21.1	9.2	23.4
Angle post. edge nasal capsules, °	54		75		74		66	

01′ W, 13.06.86, 350–369 m depth; ZMH 123066 (ex ISH 163-1987), 1 adult male, 525 mm TL, 60° 03′ S, 55° 58′ W, 29.10.86, 170–280 m depth; ZMH 123074 (ex ISH 166-1987), 1 adult male, 505 mm TL, 61° 00′ S, 56° 02′ W, 15.11.86, 176–767 m depth; ZMH 123075 (ex ISH 167-1987), 1 female, 394 mm TL, 60° 52′ S, 55° 35′ W, 16.11.86, 214–461 m depth; ZMH 123078 (ex ISH 168-1987), 1 female, 375 mm TL, 62° 14′ S, 58° 18′ W, 18.11.86, 470–500 m depth; ZMH 123080 (ex ISH 165-1987), 1 juvenile male, 195 mm TL, 62° 23′ S, 55° 10′ W, 14.11.86, 263–314 m depth; ZMH 123085 (ex ISH 169-1987), 2 females, 363 and 424 mm TL, 61° 46′ S, 58° 53′ W, 18.02.87, 271–282 m depth; ZMH 123089 (ex ISH 171-1987), 2 adult males, 527 and 586 mm TL, 61° 44′ S, 58° 37′ W, 18.02.87, 267–280 m depth; ZMH 123201 (ex ISH 213-1987), 2 females, 385 and 450 mm TL, 1 late subadult male, 495 mm TL, 61° 01′ S, 55° 58′ W, 31.10.87, 316–359 m depth; ZMH 123202 (ex ISH 209-1987), 4 juvenile females, 270, 272, 277 and 298 mm TL, 1 female, 372 mm TL, 1 adult female, 529 mm TL, 61° 06′ S, 56° 07′ W, 30.10.87, 260–297 m depth; ZMH 123230 (ex ISH 210-1987), 1 juvenile female, 262 mm TL, 1 female, 395 mm TL, 1 adult female, 531 mm TL, 61° 07′ S, 55° 53′ W, 30.10.87, 126–149 m depth (taken together with 1 adult female listed under primary material); ZMH 123232 (ex ISH 212-1987), 2 juvenile females, 314 and 334 mm TL, 2 females, 435 and 452 mm TL, 6 juvenile males, 309, 310, 315, 330, 330 and 335 mm TL, 1 late subadult male, 470 mm TL, 1 adult male, 495 mm TL, 61° 01′ S, 56° 24′ W, 30.10.87, 342–359 m depth; ZMH 123243 (ex ISH 218-1987), 1 female, 410 mm TL, 1 adult female, 608 mm TL, 60° 55′ S, 55° 24′ W, 01.11.87, 238–270 m depth; ZMH 123251 (ex ISH 216-1987), 1 juvenile male, 356 mm TL, 1 adult male, 560 mm TL, 60° 51′ S, 55° 34′ W, 01.11.87, 300–336 m depth; ZMH 123253 (ex ISH 215-1987), 3 juvenile males, 232, 280 and 350 mm TL, 60° 50′ S, 55° 38′ W, 01.11.87, 384 m depth; ZMH 123399 (ex ISH 54-1989), 4

Table 3 *Bathyraja arctowskii*, morphometrics of pelvic girdle based on radiographs, plus interorbital width dorsally and shoulder girdle maximum width as reference values. Proportional values are expressed as percentages of pelvic girdle maximum width (PGW)

	Primary adult male, ZMH 120216, 533 mm TL		Primary adult female with extreme tail tip missing, ZMH 123230, 535 mm TL		Primary subadult male, ZMH 121822, 424 mm TL		Primary subadult female, ZMH 114702, 427 mm TL	
	mm	% PGW	mm	% PGW	mm	% PGW	mm	% PGW
Interorbital width dorsally	19.0	36.1	16.0	27.8	13.0	34.6	13.0	33.8
Shoulder girdle max. width	76.1	144.7	Damaged	Damaged	58.2	154.6	69.8	181.4
Pelvic girdle max. width (PGW)	52.6	100.0	57.6	100.0	37.6	100.0	38.5	100.0
Median transverse thickness	6.6	12.5	7.8	13.5	4.4	11.6	5.0	13.0
Length prepelvic process (from level PGW)	21.1	40.2	25.8	44.8	19.1	50.7	18.1	47.0
Length prepelvic proc. (from level ant. edge pelvic girdle)	16.4	31.2	18.7	32.4	14.1	37.6	10.7	27.8
Depth posterior arc (from level PGW)	11.1	21.0	9.3	16.1	6.9	18.4	4.7	12.2
Depth post. arc (from level post. edge pelvic girdle)	8.9	16.9	8.6	15.0	7.3	19.4	6.8	17.7
Iliac foramina number	2		2		2		2	

juvenile males, 148, 151, 220 and 294 mm TL, 2 juvenile females, 187 and 250 mm TL, 1 female postembryo, 143 mm TL (all specimens ex MNHN), 74° 37′ S, 29° 36′ W, 10.02.89, 798–810 m depth; ZMH 123415 (ex ISH 25-1989), 2 juvenile males, 326 and 371 mm TL, 2 early subadult males, 395 and 396 mm TL, 1 juvenile female, 337 mm TL, 1 female, 487 mm TL, 74° 40′ S, 29° 31′ W, 03.02.89, 593–602 m depth; ZMH 123419 (ex ISH 60-1989), 1 juvenile male, 72° 55′ S, 19° 49′ W, 12.02.89, 602–617 m depth; ZMH 123420 (ex ISH 20-1989), 2 late juvenile males, 368 and 384 mm TL, 1 subadult male, 412 mm TL, 4 females, 330, 351, 382, and 420 mm TL, 74° 37′ S, 29° 38′ W, 04.02.89, 701–708 m depth.

Specimens with only collection data, few photographs and notes, kindly provided by Andrew Stewart (*n* = 61; asterisk denotes specimens used for molecular analyses): NMNZ P.036116, 1 adult specimen, 500 mm TL, 71° 43.0000′ S, 177° 7.8000′ E, 08 Feb 1999, 870–940 m depth; NMNZ P.036132, 1 male postembryo, 165 mm TL, 72° 23.1000′ S, 175° 58.1000′ E, 09 Feb 1999, 772–986 m depth; NMNZ P.036182, 1 adult specimen, 570 mm TL, 72° 12.3000′ S, 178° 36.0500′ W, 06 Feb 1999, 773–801 m depth; NMNZ P.036184, 2 adult specimens, 531 and 582 mm TL, 71° 30.000′ S, 177° 0.000′ E, 1999; NMNZ P.037551, 1 adult female, 610 mm TL, 71° 56.900′ S, 176° 34.0000′ W, 01 Feb 2000, 809–848 m depth; NMNZ P.037552, 1 adult male, 565 mm TL, 71° 54.650′ S, 178° 4.0000′ W, 08 Feb 2000, 770–809 m depth; NMNZ P.037554, 1 adult male, 551 mm TL, 71° 53.200′ S, 178° 9.0000′ W, 06 Feb 2000, 799–851 m depth; NMNZ P.037786, 1 adult male, 571 mm TL, 71° 3.00000′ S, 179° 39.00000′ E, 12 Mar 2001, 1178–1374 m depth; NMNZ P.037794, 1 adult female, 604 mm TL, 71° 28.000′ S, 176° 46.000′ E, 17 Feb 2001, 1200 m depth; NMNZ P.038600, 1 adult male, 572 mm TL, 71° 7.45′ S, 176° 23.743′ E, 12 Mar 2002, 1280–1300 m depth; NMNZ P.038602, 1 adult male, 572 mm TL, 72° 18.00′ S, 179° 16.500′ W, 25 Feb 2002, 832–1067 m depth; NMNZ P.038603, 1 adult female, 510 mm TL, 72° 18.00′ S, 179° 16.500′ W, 25 Feb 2002, 832–1067 m depth; NMNZ P.038617, 1 male, 494 mm TL, 1 adult female 584 mm TL, 71° 17.70′ S, 178° 23.700′ W, 06 Mar 2002, 991–1052 m depth; NMNZ P.038618, 2 adult females, 510 and 562 mm TL, 1 adult male, 544 mm TL, 72° 32.40′ S, 179° 20.100′ W, 23 Feb 2002, 831–912 m depth; NMNZ P.038626, 1 adult female, 557 mm TL, 71° 47.70′ S, 177° 25.800′ W, 26 Jan 2002, 757–784 m depth; NMNZ P.038649*, 1 adult female, 590 mm TL, 71° 24.60′ S, 177° 28.200′ W, 20 Jan 2002, 890–999 m depth; NMNZ P.038653, 1 adult female, 530 mm TL, 75° 47.10′ S, 169° 10.800′ W, 09 Feb 2002, 894–1117 m depth; NMNZ P.038657, 1 adult female, 585 mm TL, 71° 24.60′ S, 177° 28.200′ W, 20 Jan 2002, 890–999 m depth; NMNZ P.038781, 1 adult female, 577 mm TL, 71° 14.58′ S, 176° 28.608′ E, 03 Mar 2002, 1118–1295 m depth; NMNZ P.038818, 1 adult female, 592 mm TL, 71° 22.498′ S, 176° 47.9993′ E, 30 Jan 2003, 1385–1450 m depth; NMNZ P.038824, 1 adult male, 530 mm TL, 61° 15.00′ S, 55° 20.00′ W, 16 Mar 2003; NMNZ P.038831*, 1 adult female, 543 mm TL, 61° 15.00′ S, 55° 20.00′ W, 17 Mar 2003; NMNZ P.038834*, 1 adult male, 523 mm TL, 61° 15.00′ S, 55° 20.00′ W, 16 Mar 2003; NMNZ P.038835*, 1 adult female, 495 mm TL, 61° 15.00′ S, 55° 20.00′ W, 16 Mar 2003; NMNZ P.040066, 1 adult male, 593 mm TL, 71° 44.2550′ S,

Table 4 *Bathyraja arctowskii*, morphometrics of left scapulocoracoid based on dissected elements. Proportional values are expressed as percentages of the element's maximum length

	Adult female, ZMH 115243, 330 mm disc width		Adult male, ZMH 115243, 300 mm disc width	
	mm	% max. length	mm	% max. length
Maximum length	40.9	100.0	34.7	100.0
Maximum height	25.3	61.9	27.0	77.8
Height at rear corner	21.6	52.8	22.5	64.8
Pre-mesocondyle-length	10.5	25.6	13.2	38.0
Post-mesocondyle-length	29.4	71.9	22.5	64.8
Anterior dorsal fenestra height	4.2	10.2	4.7	13.5
Anterior dorsal fenestra length	4.5	11.0	4.0	11.5
Anterior ventral fenestra height	5.9	14.3	4.8	13.8
Anterior ventral fenestra length	4.6	11.3	3.5	10.1
Height ant. dorsal + ant. bridge + ant. ventral fenestra combined	11.0	26.8	10.1	29.1
Height largest postdorsal fenestra	5.6 (1st)	13.6	5.7 (1st)	15.2
Length largest postdorsal fenestra	7.8 (1st)	19.1	5.8 (1st)	16.7
Height 2nd largest postdorsal fenestra	2.1	5.1	6.2	17.9
Length 2nd largest postdorsal fenestra	2.4	14.4	5.0	14.4
Height smallest postdorsal fenestra	1.0	2.5	–	–
Length smallest postdorsal fenestra	0.9	2.2	–	–
Height largest postventral fenestra	3.4 (1st)	8.3	3.0	8.6
Length largest postventral fenestra	6.3 (1st)	15.3	2.9	8.4
Height smallest postventral fenestra	1.3	3.2	1.0	2.9
Length smallest postventral fenestra	1.9	4.5	1.0	2.9
Total number postdorsal fenestrae	5–6		2	
Total number postventral fenestrae	4		5	

171° 39.7650′ E, 05 Feb 2004, 400–415 m depth; NMNZ P.040340, 1 adult female, 533 mm TL, 1 adult male, 565 mm TL, 71° 42.3450′ S, 172° 1.9000′ E, 05 Feb 2004, 621–636 m depth; NMNZ P.040570, 1 female, 462 mm TL, 72° 45.67′ S, 174° 21.900′ E, 15 Jan 2004, 398–420 m depth; NMNZ P.040900, 1 adult female, 555 mm TL, 71° 30.50′ S, 178° 0.60′ W, 19 Feb 2004, 1048 m depth; NMNZ P.041370, 1 adult female, 525 mm TL, 73° 12.20′ S, 177° 24.602′ W, 28 Dec 2004, 705–789 m depth; NMNZ P.041374, 1 adult female, 540 mm TL, 72° 8.60′ S, 178° 19.800′ W, 12 Jan 2005, 789–900 m depth; NMNZ P.041380, 1 female and 1 male specimen, one has 550 mm TL, 75° 15.00′ S, 174° 7.200′ W, 07 Jan 2005, 1206–1270 m depth; NMNZ P.041381, 2 adult males, 545 and 550 mm TL, 72° 15.20′ S, 178° 55.200′ W, 19 Jan 2005, 781–832 m depth; NMNZ P.041382, 1 adult female, 575 mm TL, 72° 14.20′ S, 178° 43.000′ W, 12 Jan 2005, 774–842 m depth; NMNZ P.041383, 2 adult females, 515 and 560 mm TL, 75° 24.30′ S, 172° 29.550′ W, 09 Jan 2005, 1156–1224 m depth; NMNZ P.041384, 1 female, 440 mm TL, 75° 11.40′ S, 175° 3.150′ W, 31 Jan 2005, 1091–1166 m depth; NMNZ P.041385, 1 adult male, 565 mm TL, 72° 15.20′ S, 179° 7.802′ W, 19 Jan 2005, 831–996 m depth; NMNZ P.041392, 1 adult male, 530 mm TL, 75° 33′ S, 170° 1.80′ W, 04 Feb 2005, 985–1065 m depth; NMNZ P.041394, 1 adult male, 490 mm TL, 75° 10′ S, 175° 6.00′ W, 07 Feb 2005, 1013–1242 m depth; NMNZ P.041395, 1 juvenile specimen, 225 mm TL, 75° 33.40′ S, 170° 4.600′ W, 05 Feb 2005, 965–1072 m depth; NMNZ P.041418, 1 adult male, 580 mm TL, 75° 0.00′ S, 174° 0.00′ W, 07 Feb 2005, 984 m depth; NMNZ P.041445, 1 adult female, 555 mm TL, 66° 29.80′ S, 78° 19.200′ E, 09 Mar 2005, 790–972 m depth; NMNZ P.042224, 1 adult male, 565 mm TL, 72° 0.30′ S, 178° 24.900′ W, 11 Jan 2006, 867–954 m depth; NMNZ P.042225, 1 adult male, 600 mm TL, 71° 34.80′ S, 178° 26.10′ W, 11 Jan 2006, 869–1001 m depth; NMNZ P.042226, 1 specimen, 540 mm TL, 72° 2.70′ S, 178° 46.500′ W, 12 Jan 2006, 1041–1160 m depth; NMNZ P.042244, 1 female, 470 mm TL, 71° 21.90′ S, 116° 32.100′ W, 07 Feb 2006; NMNZ P.042721, 1 adult male, 595 mm TL, 72° 3.15′ S, 174° 14.850′ E, 23 Jan 2007, 1189–1522 m depth;

Table 5 *Bathyraja arctowskii*, morphometrics of two egg capsules cataloged under ZMH 9014, all values given in millimeters

	empty egg capsule	egg capsule with embryo
ECTL_1, egg case total length incl. length of bent horns (along curve)[1]	141.5	146.4
ECTL_2, egg case total length incl. horizontal length of bent horns[2]	121.8	120.2
ECL, egg case length; measured longitudinally between the anterior and posterior apron borders[3]	77.6	76.1
AAL, anterior apron length[4]	5.1	5.1
PAL, posterior apron length[4]	12.6	12.9
ABW, anterior border width; distance between the bases of the anterior horns[3]	20.1	20.0
PBW, posterior border width; distance between the bases of the posterior horns[3]	21.0	21.1
MAW, maximum case width; transverse width of the case in its lateral plane at its widest part of the case[3]	42.3	40.7
MIW, minimum case width; transverse width of the case in its lateral plane at its narrowest part of the case[3]	34.5	34.4
LKW, lateral keel width; distance from the capsule keel junction to the keel edge[3]	1.5	0.6
CBL, central body length (excl. aprons)[1]	61.5	58.4
CBW, central body width (excl. lateral keels)[1]	39.1	39.9
CH, Capsule height (maximum height)[5]	18.9	18.9
AHL_1, anterior horn length; distance from the horn base to the tips (along curve)[3]	34.0	39.0
PHL_1, posterior horn length; distance from the posterior horn base to the tips (along curve)[3]	46.0	49.0
AHL_2, anterior horn length; horizontal length between perpendicular lines[1]	24.9	25.0
PHL_2, posterior horn length; horizontal length between perpendicular lines[1]	37.5	34.5

[1] Newly introduced measurement, [2] measured after Treloar et al. (2006), [3] measured after Ebert and Davis (2007), [4] measured after Concha et al. (2009), [5] measured after Concha et al. (2012)

NMNZ P.043593, 1 specimen, 73° 15.3000′ S, 178° 44.2650′ E, 19 Feb 2008, 760–770 m depth; NMNZ P.043642, 1 immature male, 72° 19.1050′ S, 175° 29.5050′ E, 21 Feb 2008, 980 m depth; NMNZ P.046622, 1 juvenile female, 271 mm TL, 71° 4.450′ S, 179° 52.200′ E, 31 Dec 2009, 1179–1342 m depth; NMNZ P.046624, 1 juvenile specimen, 165 mm TL, 71° 1.900′ S, 179° 38.15′ E, 01 Jan 2010, 1066–1334 m depth; NMNZ P.051853, 1 adult specimen, 606 mm TL, 65° 15.12′ S, 175° 32.52′ W, 03 Jan 2011, 1652–1685 m depth; NMNZ P.051854, 1 adult specimen, 572 mm TL, 72° 7.58′ S, 176° 18.60′ W, 29 Dec 2010, 825–855 m depth; NMNZ P.051855, 1 adult specimen, 586 mm TL, 72° 7.58′ S, 176° 18.60′ W, 29 Dec 2010, 825–855 m depth.

Egg capsules ($n = 43$): Syntypes: IRSNB 25 [orig. 3005], 71° 19′ S, 87° 37′ W, 27–28 May 1898, 435 m depth; IRSNB 26 [orig. 3006], 70° 23′ S, 82° 47′ W, 7–8 Oct 1898, 400 m depth; IRSNB 27 [orig. 3007], 70° 15′ S, 84° 06′ W, 19–20 Dec 1898, 569 m depth; ZMH 9014, 1 empty egg capsule and 1 egg capsule with 1 near-term male embryo, 120 mm TL, 61° 13.9′ S, 56° 25.4′ W, 21.11.96, 403–415 m depth; ZMH 9015, 7 egg capsules with early embryos, 60° 57.6′ S, 55° 11.8′ W, 25.11.96, 326–380 m depth; ZMH 9016, 1 egg capsule with early embryo, 61° 00.6′ S, 55° 07′ W, 25.11.96, 145–156 m depth; ZMH 9017, 4 egg capsules with early embryos, 61° 43.3′ S, 59° 12.5′ W, 27.11.96, 573–590 m depth; ZMH 123265 (ex ISH 203-1987), 5 egg capsules, 61° 13.12′ S, 56° 06.42′ W, 16.12.87, 230–250 m depth; ZMH 123275 (ex ISH 199-1987), 1 egg capsule, 60° 52′ S, 55° 31.48′ W, 14.12.87, 264–267 m depth; ZMH 123276 (ex ISH 202-1987), 19 egg capsules, 61° 20.18′ S, 56° 08.24′ W, 16.12.87, 295–311 m depth; ZMH 123277 (ex ISH 204-1987), 1 egg capsule, 61° 09.18′ S, 56° 11.06′ W, 16.12.87, 387–426 m depth.

Diagnosis

Bathyraja arctowskii is a small (to 61 cm TL) species of the genus *Bathyraja* with the following set of characters: disc evenly inverse heart-shaped (disc margins distinctly undulated in adult males, not or slightly undulated in others), with broadly rounded outer corners and with body length to mid-cloaca shorter than or equal to tail length from mid-cloaca. Preorbital snout length 8.1–16.2% TL, depending on ontogenetic stage, and distance between first gill slits 14.2–15.9% TL. Orbits moderately large, horizontal diameter 1.3–1.8 times interorbital width. Upper side of disc and tail entirely rough prickly with dermal denticles, underside smooth. Except for alar thorns of mature males, no thorns on disc but only a median row of 19–30 small thorns along tail to first dorsal fin. The thorns become smaller and more widely spaced posteriorly in subadults and adults and are generally wider spaced in large juveniles to adults as compared with small juveniles. Bases of

Table 6 Tissue samples used for molecular analyses

Species	Identifier	TePapa catalog no.	Locality
Bathyraja arctowskii	GN 17896	P.038649/TS2	-71.41, 177.47
Bathyraja arctowskii	GN 17897	P.038831/TS3	-61.25, -55.33
Bathyraja arctowskii	GN 17898	P.038834/TS3	-61.25, -55.33
Bathyraja arctowskii	GN 17899	P.038835/TS3	-61.25, -55.33
Bathyraja cf. *eatonii*	GN 15726		-66.85, 64.93
Bathyraja cf. *eatonii*	GN 17861	P.038826/TS3	Off South Shetland Islands
Bathyraja cf. *eatonii*	GN 17862	P.038827/TS3	Off South Shetland Islands
Bathyraja cf. *eatonii*	GN 17864	P.038829/TS2	Off South Shetland Islands
Bathyraja cf. *eatonii*	GN 17855	P.038825/TS2	Off South Shetland Islands
Bathyraja cf. *eatonii*	GN 17856	P.040069/TS2	-71.50, 171.79
Bathyraja cf. *eatonii*	GN 17857	P.040095/TS2	-71.72, 171.8
Bathyraja cf. *eatonii*	GN 17859	P.040345/TS2	-72.03, 173.25
Bathyraja eatonii	GN 15722		-52.25, 76.68
Bathyraja eatonii	GN 15724		-52.25, 76.68
Bathyraja eatonii	GN 15727		-51.98, 77.43
Bathyraja irrasa	GN 15711		-51.95, 76.90
Bathyraja maccaini	GN 15715		-66.63, 72.90
Bathyraja maccaini	GN 15716		-66.63, 72.90
Bathyraja maccaini	GN 15717		-66.72, 73.00
Bathyraja maccaini	GN 15719		-66.63, 72.90
Bathyraja maccaini	GN 15720		-66.70, 61.42
Bathyraja maccaini	GN 17865	P.036191/TS2	-75.72, 168.80
Bathyraja maccaini	GN 17866	P.036196/TS2	-75.72, 168.80
Bathyraja maccaini	GN 17867	P.038832/TS3	-61.25, -55.33
Bathyraja maccaini	GN 17868	P.038833/TS2	-61.25, -55.33
Bathyraja maccaini	GN 17869	P.038836/TS3	-61.25, -55.33
Bathyraja maccaini	GN 17870	P.040064/TS2	-71.72, 171.80
Bathyraja maccaini	GN 17871	P.040065/TS2	-71.70, 172.09
Bathyraja maccaini	GN 17872	P.040335/TS2	-72.070, 172.92
Bathyraja maccaini	GN 17874	P.040897/TS3	-77.33, -160.42
Bathyraja maccaini	GN 17875	P.040898/TS4	-77.33, -160.42
Bathyraja meridionalis	GN 17876	P.042494/TS3	-53.23, -42.37
Bathyraja meridionalis	GN 17877	P.042495/TS3	-55.44, -36.26
Bathyraja meridionalis	GN 17880	P.042505/TS3	-55.16, -36.37
Bathyraja meridionalis	GN 17881	P.042507/TS3	-55.17, -36.37
Bathyraja murrayi	GN 15714		-52.55, 75.06
Bathyraja sp.	GN 17854	P.043485/TS2	-76.77, 167.83

low, more or less equal-sized dorsal fins confluent or with short interspace. Postdorsal tail section very short, 1.7–5.2% TL, with low epichordal caudal lobe which is confluent with second dorsal fin. Dorsal ground color plain dark to medium grayish-brown, often with mostly indistinct scattered pale and dusky spots on disc, posterior pelvic lobes and on sides of tail, occasionally with transverse white pseudoocellus stripe on inner posterior pectorals. Underside mostly plain white or pale, often with gray marked cloaca and gray spots on belly to gill region, occasionally gray spotted posterior pectoral margins, origin and sides of tail, or tail partly dark. Mouth cavity and underside of nasal curtain at least partly, usually completely pigmented medium to dark grayish from very small juvenile stages onwards. Opened clasper tip shows all components typical for *Bathyraja* species, of which most apparent a long and deep pseudosiphon (ps) along outer edge of

Table 7 Possible ontogenetic changes of *Bathyraja arctowskii* based on values for subadult plus adult specimens, juveniles, and a male embryo

Character	Subadults and adults (*n* = 4, 424–535 mm TL)	Juveniles (*n* = 6, 135–333 mm TL)	Male embryo (*n* = 1, 120 mm TL)
Snout angle	110–120°	125–133°	140°
Preorbital snout length	11.4–16.2% TL	9.6–11.6% TL	8.1% TL
Preorbital snout length/internarial width	3.7–5.3 times	2.5–3.6 times	2.2 times
Preoral snout length	11.1–15.2% TL	9.0–11.3% TL	8.8% TL
Prenasal snout length	9.1–12.9% TL	7.4–9.4% TL	7.4% TL
Orbit, horizontal diameter	4.1–4.8% TL	4.6–5.8% TL	5.4% TL
Eyeball, horizontal diameter	3.4–3.7% TL	3.9–4.6% TL	4.4% TL
Interspiracular width	7.0–7.9% TL	7.9–8.8% TL	8.7% TL
Tail height at pelvic tips	2.0–2.2% TL	2.3–3.0% TL	4.3% TL
Tail width/height at pelvic tips	1.5–1.8 times	1.1–1.5 times	1.1 times
Tail height at 1st dorsal-fin origin	0.7–0.9% TL	0.9–1.3% TL	1.3% TL
Tail width/height at 1st dorsal-fin origin	1.7–2.6 times	1.1–1.8 times	1.4 times
Lateral tail fold length	44.3–47.7% TL	35.0–47.6% TL	32.8% TL
Ventral head length	25.0–28.0% TL	21.5–25.9% TL	–
Dorsal head length	17.6–21.6% TL	16.8–18.7% TL	14.2% TL
Nasal curtain length	3.4–4.1% TL	2.8–3.4% TL	2.4% TL
Space between lobes of nasal curtain	4.0–5.3% TL	2.8–4.0% TL	3.3% TL
Snout tip to mid-cloaca	45.6–49.6% TL	41.9–45.6% TL	41.3% TL
Snout tip to 1st hemal spine	48.0–51.5% TL	43.8–48.2% TL	–
Mid-cloaca to 1st dorsal-fin origin	38.4–42.8% TL	44.1–46.4% TL	46.7% TL
Mid-cloaca to 2nd dorsal-fin origin	42.5–47.4% TL	48.2–50.4% TL	52.3% TL
Mid-cloaca to tail tip	49.4–52.7% TL	53.2–59.3% TL	60.2% TL
Mid-cloaca to tail tip/snout tip to mid-cloaca	1.0–1.2 times	1.2–1.4 times	1.5 times
Dorsal color pattern of light dots and streaks	Usually faded	Distinct to mostly faded in large juveniles	Distinct even in preserved condition

dorsal lobe, as well as a massive projection (pj) over entire length of the inner ventral lobe. Clasper terminal skeleton with distal processes of dorsal marginal cartilage (forming external pseudorhipidion) and ventral marginal cartilage (forming external projection), three dorsal terminal cartilages (with dt1 very large and encapsulating terminal skeleton), ventral terminal, and one accessory terminal cartilage. Sexual dimorphism apparent in scapulocoracoid, with post-mesocondyle length longer in females than in males.

Description The description refers to the primary adult male ZMH 120216 (ex ISH 489-1981). Values of 10 other primary specimens examined in detail are presented in parentheses, more complex differences between specimens are described separately. Where relevant, ratios are based on horizontal measurements unless otherwise stated. Detailed morphometric measurements and meristics are given in Table 1.

External morphology (Figs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, and 16). Disc evenly inverse heart-shaped, anterior margins undulated showing concavity at anterior sides of snout and at level of nape (disc margins not undulated in small juveniles and adult females, slightly undulated in large juveniles and subadults), outer corners of disc broadly rounded. Disc width 1.2 (1.2–1.4) times disc length, markedly wide. Axis of maximum disc width at 30.0% (24.2–31.9%) TL, or 54.1% (54.7–61.0%) of disc length, and distinctly posterior to shoulder girdle. Dorsal head length 19.9% (14.2–21.6%) TL. Snout tip somewhat pronounced, narrowly rounded; snout moderately elongated and pointed at 110° angle (112–120° in subadults and adult female, 125–133° in juveniles, 140° in male embryo), with preorbital length 13.6% (11.4–16.2% in subadults and adult female, 9.6–11.6% in juveniles, 8.1% in male embryo) TL and 3.8 (3.7–5.3 in subadults and adult female, 2.5–3.6 in juveniles, 2.2 in male embryo) times the narrow interorbital width. Orbit horizontal

Fig. 1 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, in total dorsal view. Scale bar: 5 cm

diameter 1.3 (1.3–1.8) times interorbital width and 1.5 (1.5–2.0) times length of spiracle depression; interspiracular space wide, 2.2 (2.2–2.6) times interorbital space; about 10 pseudobranchial folds in each spiracle. Tail slender, gradually tapering towards tip; a low triangle in cross-section, width at level of pelvic tips 1.5 (1.6–1.8 in adult female and subadults, 1.1–1.5 in juveniles, 1.1 in male embryo) times height, width at first dorsal-fin origin 2.6 (2.5 in adult female, 1.7–2.2 in subadults, 1.1–1.8 in male embryo and juveniles) times height; tail length from mid-cloaca 1.0 (1.0–1.2 in adult female and subadults, 1.2–1.4 in juveniles, 1.5 in male embryo) times distance snout tip to mid-cloaca. Both dorsal fins parallelogram-shaped with broadly rounded upper margin and somewhat frayed tip widely overhanging base end; posterior margin strongly inclined forward and concave; both dorsal fins about as long as high (first dorsal-fin base length 1.0–2.8 times height and second dorsal fin base length 1.3–2.6 times height in other specimens), base of first dorsal fin 1.6 (0.6–1.2) times that of second dorsal fin. Bases of both dorsal fins confluent without interspace (confluent or with very small

Fig. 2 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, in total ventral view. Scale bar: 5 cm

Fig. 3 *Bathyraja arctowskii*, ZMH 123230, primary adult female, 535 mm TL, in total dorsal view. Scale bar: 5 cm

interspace). Postdorsal tail short, 65.2% (47.4–155.6%) of second dorsal-fin base length, with a low and indistinct epichordal caudal fold confluent with second dorsal fin, height of epichordal lobe ~14% (0–~30%) of second dorsal-fin height; hypochordal caudal fold absent. Lateral tail folds along full tail length (along full length also in adult female and subadults but along about posterior two thirds to almost full length in juveniles and male embryo).

Ventral head length 28.0% (25.0–27.9% in adult female and subadults, 21.5–25.9% in juveniles, not measurable in male embryo) TL. Preoral snout length 1.9 (1.5–2.3) times internarial width and 1.6 (1.2–2.4) times mouth width, the latter 27.4% (22.9–36.7%) of ventral head length and 115.5% (97.5–129.4%) of internarial space; ventral head length 4.2 (3.2–4.3) times internarial space; distance between 5th gill slits 63.0% (58.5–81.9%) of distance between 1st gill

Fig. 4 *Bathyraja arctowskii*, ZMH 123230, primary adult female, 535 mm TL, in total ventral view. Scale bar: 5 cm

Fig. 5 *Bathyraja arctowskii*, ZMH 9014, near-term male embryo, 120 mm TL, in total dorsal view. Scale bar: 2 cm

slits, the latter 2.2 (2.1–2.4) times internarial space. Anterior nasal flaps rather small and smooth-edged. Outer edges of nasal curtain smooth and not notched, apices rounded, their outer margin smooth; rear margin of curtain weakly fringed by broad and fleshy fringes; isthmus deeply arc-shaped. Jaws weakly angled, with 23 upper and 24 lower parallel tooth rows (22–29 upper and 21–29 lower tooth rows; arrangement similar in subadult male but teeth in quincunx pavement pattern in females, juvenile males and male embryo); individual teeth with pronounced, triangular cusp becoming smaller towards jaw angles (similar in subadult male but with rather low cusp in females, juvenile males and male embryo). Anterior and posterior pelvic-fin lobes separated by a deep notch, posterior lobe with angular outer margin and rounded tip 1.6 (1.1–1.5) times longer than solid anterior lobe tapering to a blunt tip. Fully developed claspers long and slender, with terminal region only somewhat widened; distal half of clasper stem plus terminal region exceeding tips of posterior pelvic lobes; clasper postcloaca length 50.6% of tail length from mid-cloaca.

Squamation (Figs. 1, 2, 3, 4, 5, 6, 12, 13, and 14). No thorns on upper disc except for very elongated field of alar thorns across outer pectoral corners and parallel to anterior half of posterior margins; alar thorns hook-like and of non-retractable, permanently erect type; alar thorns set in three to five longitudinal and ~20 transverse rows (Fig. 12). Tail with ~26 median thorns from between pelvic and pectoral insertions to somewhat anterior to first dorsal-fin base; thorns become smaller and more widely spaced posteriorly (Figs. 13 and 14). Other specimens with about 19 to 30 median tail thorns, which become smaller and more widely spaced posteriorly in subadults and adults and are generally wider-spaced in large juveniles to adults as compared with small juveniles. No interdorsal thorns (none also in other specimens except for one tiny thorn in smallest juvenile female).

Dorsal surface almost completely and densely set with fine dermal denticles, including the integument covering the eyeballs, as well as caudal and dorsal fins, but somewhat more loosely set on pectoral centers and axils; posterior pelvic-fin lobes smooth. The spinulation is similar in adult female and subadult male except for the presence of a few denticles on centers of posterior pelvic-fin lobes. The subadult female is almost completely covered with fine dermal denticles as well, but with largely smooth pectoral centers, as well as smooth integument covering the eyeballs and posterior pelvic-fin lobes. Dorsal surface of juveniles completely and densely covered with fine dermal denticles except for a more loose

Fig. 6 *Bathyraja arctowskii*, ZMH 9014, near-term male embryo, 120 mm TL, in total ventral view. Scale bar: 2 cm

Fig. 7 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, head in dorsal view. Scale bar: 5 cm

Fig. 9 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, close-up of orbital and spiracular region. Scale bar: 2 cm

coverage of rostral sides in two specimens. Ventral surface completely smooth in adult male and all other specimens.

Coloration: when fresh (Figs. 15 and 16): medium to dark brown dorsally, disc and pelvic fins with pattern of light dots and streaks (more pronounced in juveniles). Occasionally, dorsally lively ornamented specimens are found (Fig. 15). Underside of disc and tail whitish; pale dark spots may be present on tail and centrally on disc. Mouth cavity and underside of nasal curtain at least partly, usually completely pigmented medium to dark grayish.

Color in preservative (Figs. 1, 2, 3, 4, 5, 6): pattern of light dots and streaks faded, particularly in adult specimens, some of which appear plain medium to dark brown. Ventral coloration rather beige than whitish, with dark spots still visible. Dark pigmentation of mouth cavity and underside of nasal curtain still conspicuous.

Clasper external morphology (Fig. 17, based on one badly disintegrated male from ZMH 115243 [ex ISH 689-1978]). Clasper stem a solid rod of equal width, with the glans only little widening and short. The apparent component of the dorsal lobe is a deep and long pseudosiphon (ps) along the outer margin extending over three fourths of the glans length. A cleft (cf) is found in distal half of the glans between the axial cartilage ridge and the inner wall of dorsal lobe. A narrow cartilage rod is situated medially in proximal glans, the pseudorhipidion (pr), which covers proximally the axial cartilage (ax). The latter continues visible on deeper level as a ridge from underneath tip of pr to the extreme tip of the glans. Very prominent component on entire length of ventral lobe is the somewhat twisted and long projection (pj), a firm cartilage covered by integument and connected to outer ventral lobe margin with integument. A deep and wide sentina hollow (sn, indicated hatched) underneath the pj and the integument spanning to outer ventral lobe margin runs out with its proximal wall as a narrow integument ridge diagonally across the axial cartilage to the proximal end of the cleft. Within the sentina, externally not visible, is the ax-blade-like tip of the sentinel (st) found as a sharp cutting tip edge of the at1 cartilage.

Fig. 8 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, head in ventral view. Scale bar: 5 cm

Fig. 10 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, close-up of mouth-nasal region. Scale bar: 2 cm

Fig. 11 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, pelvic region with tail origin and pair of claspers in dorsal view. Scale bar: 5 cm

Both outer surfaces of the clasper, as well as inner surfaces of the open glans are smooth without a trace of dermal denticles.

Clasper skeleton (Fig. 18, based on one primary and one additional male, both badly disintegrated, from ZMH 115243). Figure 18a+b shows the distal part of the clasper stem in dorsal and ventral views, with the axial (ax), dorsal marginal (dm), and ventral marginal (vm) cartilages and cartilages of the glans. Prominent cartilage in dorsal view is the dorsal terminal 1 (dt1) encapsulating nearly the entire terminal surface dorsally, showing longitudinal ridges and grooves and curving onto the ventral side around the axial. Very distally appears a blunt, short tip of the dm-cartilage, as well as a narrow, elongated distal process, the dorsal terminal 3 (dt3). The thin tip of the ax-cartilage the same length as the former one but curving outward to connect with the tip of the slender dt3-process. Tip of the vm-process (= pj externally) solid and curving a little downwards.

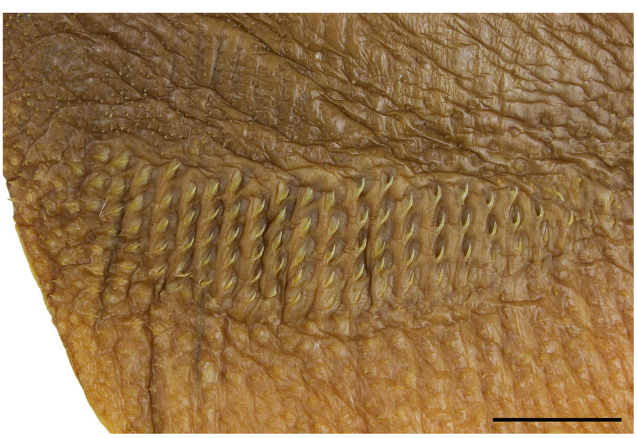

Fig. 12 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, left field of alar thorns. Scale bar: 2 cm

Ventral view of Fig. 18b shows the ventral part of the dt1 around the axial as well as the outer dorsal part of dt1 supporting the outer edge of external component pseudosiphon. The ventral terminal (vt) cartilage is an elongated drop-shaped plate, narrowing proximally, and positioned medially over the axial and ventral marginal (vm), but is not movable and does not appear as an external component in the glans. Prominent cartilage is the massive distal process of the vm = external component pj. The blunt distal end of the dm appears underneath the vm-process, as well as both slender distal tips of ax and dt3.

Figure 18c+d shows the terminal clasper skeleton in dorsal and ventral views, with dt1 and vt removed. The dorsal marginal cartilage (dm) occupies almost the entire dorsal surface, including the axial, from the stem to the distal tip and is difficult to interpret with its structures and distal tips. Tip of the vm-process sticking out at inner distal edge, and edge of the vm visible in proximal half. The ventral view (d) shows the vm-cartilage curving and widening distally, with its massive and long process (= external pj) inserting proximally underneath the outer edge of the vm, and the at1-cartilage inserting under inner distal edge. The slender, outward curving tip of the axial appears underneath the at1-level.

Figure 18e, with dt1 included, and f, without dt1, show the spread terminal skeleton. Most distally are visible the tips of the vm-process and the slender axial end connected to the slender dt3-process, also medially the dm-process (= external pr) and at outer left the tip of the at1-cartilage. Figure 18f shows the same arrangement of terminal cartilages without the capsule-shaped dt1 in the background.

Remark: this clasper skeleton is not yet fully calcified, or decalcified by preservation, partly still soft and flexible, but displays all external glans components and its skeleton cartilages. Exception is the slender distal outer edge process of the dm, which is connected with the extreme tip of the axial. A majority of *Bathyraja* species possesses in this position a dorsal terminal 2 (dt2) or dt3 cartilage, likewise connected with ax-tip. Such a separate dt3-cartilage is indicated in Fig. 18c along the outer dm-margin but may not yet be fully formed and calcified.

Therefore, the left clasper of another adult male (also from ZMH 115243), which was badly disintegrated as well but with claspers more hardened and more calcified skeleton, was dissected and skeletal elements were found identical with those of the male illustrated here. Contour of the questionable and better-calcified dt2 was more distinct and could be cut and lifted at the outer margin, and could thus be proven as a separate dt2 cartilage. However, the dt2 is plate-like and firmly attached with its entire lower surface to the dm surface. The dt2 has no joint connecting it with the dm and is static and not movable. Questionable remains, whether the long, thin and

Fig. 13 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, mid-section of tail in lateral view. Scale bar: 2 cm

hardly calcified distal extension of the dt2, connecting with a narrow tissue bridge to the distal end of the axial cartilage, is distal part of the dt2, or a separate dt3 cartilage. The delicate terminal cartilages of the very small, only 2 to 2.5 cm long glans do presently not allow a definitive decision on 2 or 3 dt-cartilages, but we tend here to 3 dt-cartilages. *Bathyraja* species with both, 2 and 3 dt-cartilages are known.

Cranium (Figs. 19 and 20). Table 2 provides cranial morphometrics taken from the four largest primary specimens at ZMH.

Although the crania did not depict very well on radiographs, as is typical for deep-water*Bathyraja* spp. due to their low calcification of cartilage, most cranial morphometrics could be measured with acceptable accuracy. The short anterior cranial fontanelle is broadly bullet- or spearhead-shaped; front part bluntly pointed, the fontanelle then gradually widens rearwards to widest part at about four fifths of fontanelle length but narrows again in posterior-most fifth of the fontanelle. The posterior cranial fontanelle is not or hardly visible on radiographs but appears to be an elongated, narrow triangle with tip pointing rearwards as vaguely visible in the radiograph of the cranium of the adult female (Fig. 20). As typical in *Bathyraja* crania, the rostrum narrows abruptly in front of the anterior fontanelle, and the uncalcified anterior two thirds of the very slender, undulated rostral cartilage are not depicted.

Ovoid nasal capsules large and strongly forwardly inclined at a 54–75° angle of their straight rear edges to longitudinal axis of cranium. Orbital region evenly deeply concave; otic region broadly bulky, with short occipital condyles and small jugal arches not or hardly exceeding the contour of the occiput rearward or laterally. Snout supported by forward extension of pectoral propterygia and radials extended to nearly snout tip and rostral node. Rostral shaft length 44.5–53.8% of cranium total and 80.9–116.5% of nasobasal length; maximum ethmoidal width 45.1–56.9% of cranium total length, 95.8–103.7% of nasobasal length, 2.9–3.4 times minimum dorsal interorbital width, and 1.7–1.9 times maximum width of otic region. Anterior fontanelle length 18.7–38.9% of rostral shaft and 10.1–17.9% of cranium total length, its length 0.9–1.8 times its maximum width, and its tip hardly extending into rostral shaft length.

Pelvic girdle (Figs. 21 and 22). Table 3 provides pelvic morphometrics taken from the four largest primary specimens at ZMH.

The maximum width of shoulder girdle, which shows a rather slender coracoid bar, and the maximum width of the pelvic girdle apparently show sexual dimorphism, with dimorphism of shoulder girdle maximum width evidenced by ratio shoulder girdle maximum width / dorsal interorbital width (4.0 and 4.5 times in males, 5.4 times in adolescent female) and dimorphism of pelvic girdle shown by ratio maximum width of shoulder girdle / maximum width of pelvic girdle (1.4 and 1.5 in males, 1.8 in adolescent female). However, this assumption is based on only three specimens and the differences might also be the result of intraspecific variation. The ratios could not be taken for the adult female due to the shoulder girdle being severely damaged.

Pelvic girdle with massive ischiopubic bar, anterior contour nearly straight in both sexes at all sizes, posterior contour slightly concave in females and juvenile males but deeply so in adult males; prepelvic processes moderately long, solid, conical, and straight to somewhat inclined inwards, their length 3.2–4.4 times median thickness of ischiopubic bar. Iliac processes massive and curving inwards, with broad, quadrangular tip. Each iliac region with two foramina.

Fig. 14 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, tail end with dorsal fins and low epichordal caudal lobe. Scale bar: 2 cm

Fig. 15 *Bathyraja arctowskii*, adult male from the Atlantic sector (not retained), in fresh condition. Photograph taken and kindly provided by K.-H. Kock

Scapulocoracoid (Fig. 23). Left side elements were dissected of an adult male (a) and adult female (b), both ZMH 115243. Morphometrics and meristics of both elements are given in Table 4.

Scapulocoracoids of many *Bathyraja* species show in general an elongated rectangular appearance in lateral view, with very asymmetrical anterior position of the mesocondyle. Unlike the rather constant and often species-specific scapulocoracoid features in many rajid and arhynchobatid genera, with a marked sexual dimorphism in a few genera (e.g., *Psammobatis*, see McEachran 1983, or *Neoraja*, see Stehmann et al. 2008), a very different situation is found in the genus *Bathyraja*. In this latter genus, the degree of intraspecific variation of scapulocoracoid features is so great, independent of eventual sexual dimorphism but probably due to ontogenetic influences, that the investigation of just a single scapulocoracoid is in no way representative or diagnostic for a *Bathyraja* species.

Fig. 16 *Bathyraja arctowskii*, MNHN 1987–0232, adult male, 591 mm TL, from the Indian Ocean sector, in fresh condition. Photograph taken and kindly provided by Guy Duhamel

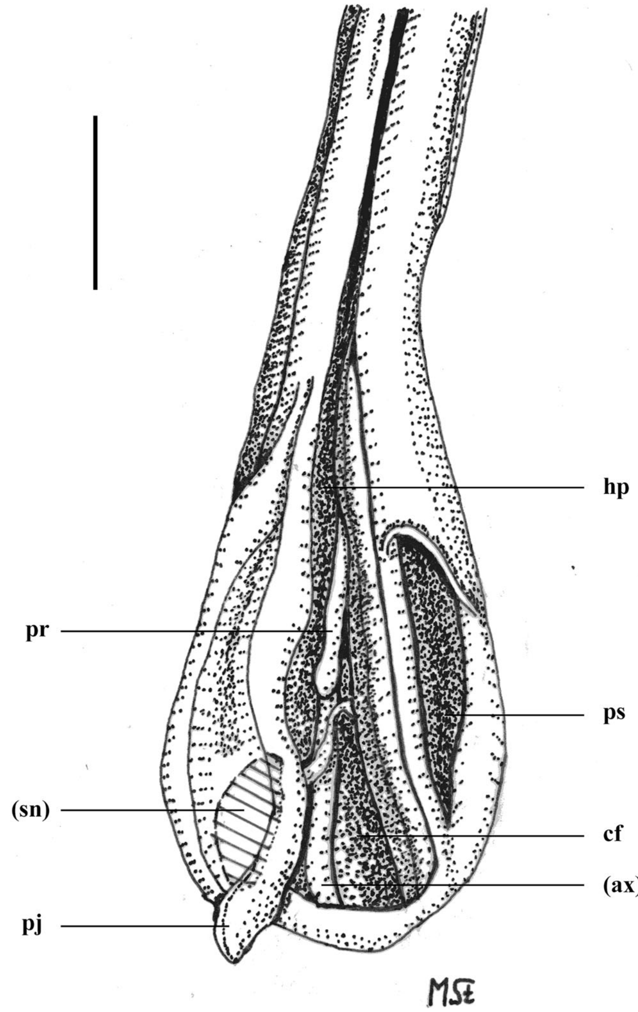

Fig. 17 *Bathyraja arctowskii*, ZMH 115243, left clasper glans opened. Scale bar: 1 cm

Figure 23 demonstrates for *B. arctowskii* both aspects, namely sexual dimorphism in overall shape, as well as distinct intraspecific natural variation in number, shape, and arrangement of postdorsal and postventral foramina. Elements of both sexes show a solid horizontal anterior bridge separating the anterior fenestra into a smaller anterior dorsal and an anterior ventral fenestra.

The adult male's element (Fig. 23a) shows a moderately short rectangular shape, with almost horizontal concave dorsal margin to the rounded rear corner, from which the nearly straight posterior margin slopes to the metacondyle. Two large postdorsal fenestrae are of similar size as the anterior dorsal

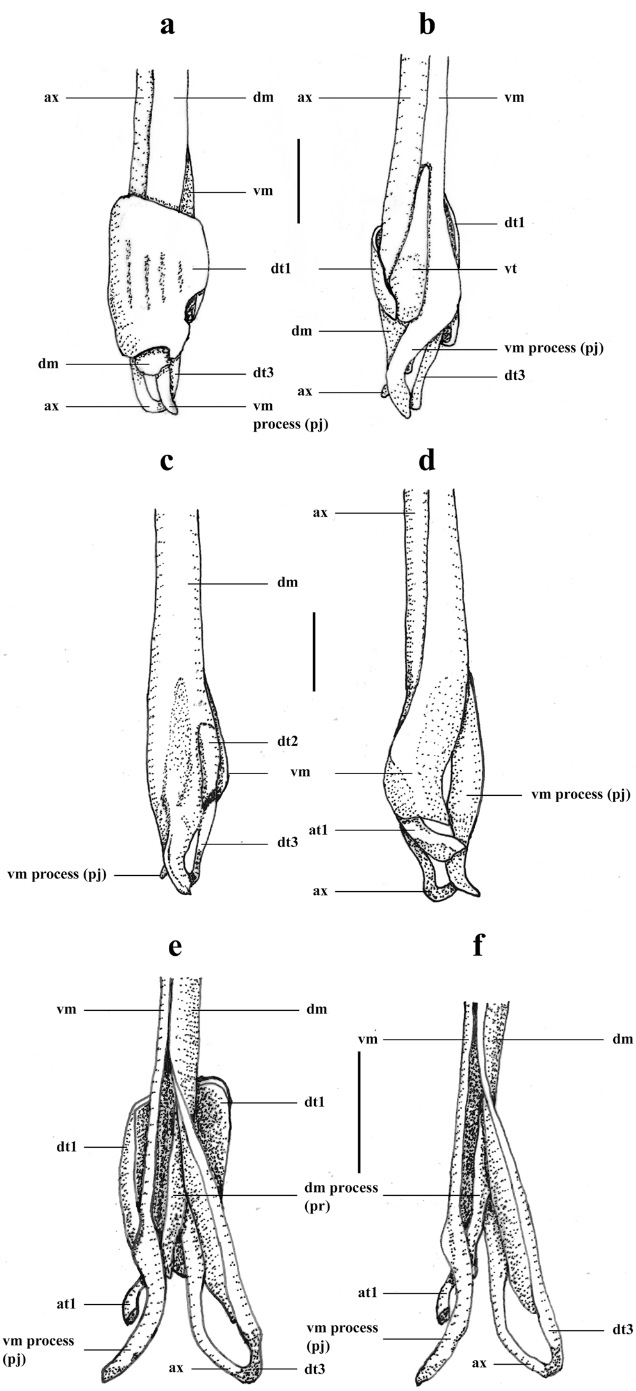

Fig. 18 *Bathyraja arctowskii*, ZMH 115243, dissected left clasper skeleton. **a**,**b** complete terminal skeleton in **a** dorsal and **b** ventral views; **c**,**d** terminal skeleton with dorsal terminal 1 and ventral terminal cartilages removed in **c** dorsal and **d** ventral views; **e**,**f** terminal skeleton in opened views with **e** and without **f** dorsal terminal 1 cartilage. Scale bars: 1 cm

fenestra. The anterior postdorsal fenestra is subcircular, longer, and higher than the adf, the posterior pdf is oblique narrowly oval, somewhat higher than the anterior pdf but only

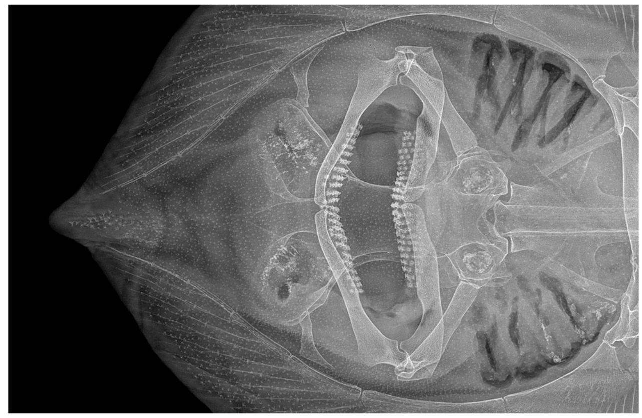

Fig. 19 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, radiograph of cranium and snout in dorsal view

half as wide as the latter. The five much smaller postventral foramina are a chain from about midlength of the mesocondyle to near the metacondyle; the second and last of these are larger than the remaining three small, rather pore-like postventral foramina.

In contrast is the adult female's element (Fig. 23b) of more elongated and distinctly rectangular shape, with an almost horizontal dorsal margin to a sharply marked rear corner, and the posterior margin is deeply concave and steeply sloping to the metacondyle. Much in contrast to the male's element are the five postdorsal foramina, in that the anterior one is a horizontally elongated fenestra being much longer than each of the anterior dorsal and ventral fenestrae. However, a stump at its lower edge indicates a former ligament bridge separating vertically this fenestra into two smaller ones. Level with its upper edge is a chain of three pore-like foramina, and below these a somewhat larger diagonally oval foramen. The large first postventral fenestra is of similar size as the anterior ventral fenestra, whereas the following three are

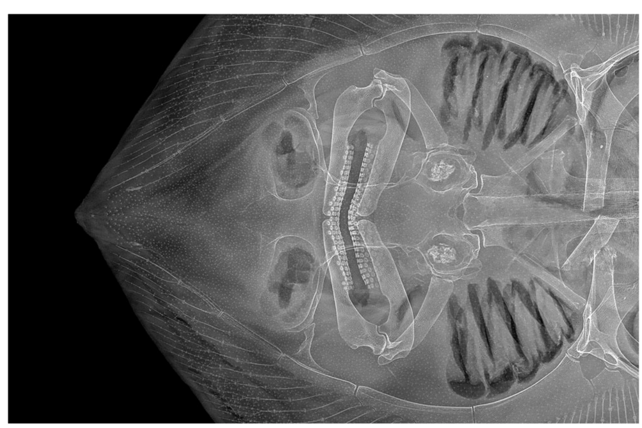

Fig. 20 *Bathyraja arctowskii*, ZMH 123230, primary adult female, 535 mm TL, radiograph of cranium and snout in dorsal view

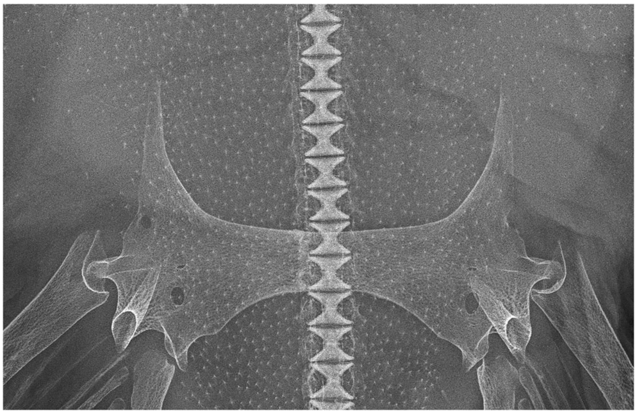

Fig. 21 *Bathyraja arctowskii*, ZMH 120216, primary adult male, 533 mm TL, radiograph of pelvic girdle in dorsal view

much smaller and a chain along the ridge between meso- and metacondyle.

Pre-mesocondyle length in the male 38.0% of maximum length and 58.7% of the post-mesocondyle length; in the female 25.6% and 35.7% respectively. Maximum length 1.3 times maximum height at scapular process in the male, 1.6 times in the female's element. Height at rear corner is 83.3% of the maximum height in the male, 85.3% in the female. The combined height of both anterior fenestrae is 37.4% of the maximum height at scapular process and 28.8% of the element's maximum length in the male, 43.3% and 26.8% in the female, respectively.

Skeletal meristics (from radiographs of all primary specimens except for male embryo; Table 1). Trunk vertebrae (Vtr): 30–37; predorsal tail vertebrae (Vprd): 66–80; terminal tail vertebrae (Vterm, approximately): 23–40; total vertebrae (Vtotal, approximately): 120–151; pectoral radials, left: 70–89, right: 70–90; pelvic radials, left: 4 + 16–5 + 20, right: 4 + 17–5 + 19.

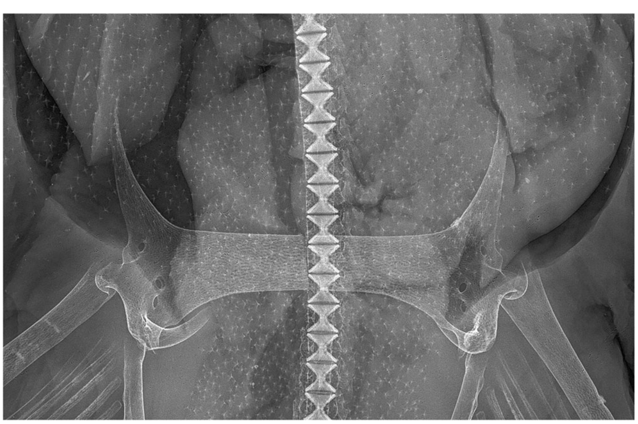

Fig. 22 *Bathyraja arctowskii*, ZMH 123230, primary adult female, 535 mm TL, radiograph of pelvic girdle in dorsal view. The cut pelvic girdle was assembled digitally

Egg capsule (Figs. 24, 25 and 26, based on two egg capsules cataloged under ZMH 9014 and one of the syntypes cataloged under IRSNB 25 [orig. 3005]). Table 5 provides morphometrics of the two egg capsules at ZMH.

Both surfaces of blackish-brown egg capsule smooth, with coverage of long, fine anchoring fibers. Extension of aprons two thirds onto horns. Upper side of egg capsule strongly convex, lower side moderately convex. Cross-section (anterior and posterior horns) depressed.

Size: *Bathyraja arctowskii* is one of the smallest species of the genus, reaching 61 cm TL. The largest recorded adult females are in the Atlantic a 608 mm TL specimen from off Elephant Island (ZMH 123243), in the Pacific a 610 mm TL specimen from the Ross Sea (NMNZ P.037551), and in the Indian Ocean a 555 mm TL specimen from Prydz Bay (NMNZ P.041445). The largest recorded adult males are in the Atlantic a 586 mm TL specimen from off King George Island (ZMH 123089), in the Pacific a 600 mm TL specimen from the Ross Sea (NMNZ P.042225), and in the Indian Ocean a 591 mm TL specimen from Prydz Bay (MNHN 1987-0232). The largest examined juvenile male has 384 mm TL, examined subadult males range from 361 to 450 mm TL, examined late subadult males range from 461 to 495 mm TL. The smallest examined adult male (NMNZ P.041394) has 490 mm TL. The size at hatching is about 12–13 cm TL based on primary male embryo ZMH 9014 and the smallest juvenile female examined in detail (ZMH 121822).

Molecular analyses: The tissue samples used for the molecular analyses are listed in Table 6. The maximum likelihood analysis of the aligned NADH2 sequence data confirm that *Bathyraja arctowskii* is a monophyletic lineage that is distinct from all other *Bathyraja* species from the region (Fig. 27). Phylogenetic inference based on the aligned NADH2 data set suggests that *B. arctowskii* is most closely related to a lineage of *Bathyraja* from the region that most closely resembles *B. eatonii* (identified as *B.* cf. *eatonii* in Fig. 27). The true *Bathyraja eatonii* appears more closely related to *B. irrasa*. *B. murrayi* and *B. meridionalis* (see Fig. 27). However, it is important that not too much be made of the phylogenetic placements presented herein as the inference is based on a single mitochondrial gene (see Naylor et al. 2012). More reliable phylogenetic inferences would require an assessment based on a large suite of mitochondrial and nuclear genes. The "take home message" from the mitochondrial data presented is that *B. arctowskii*, while being morphologically distinct, also appears to be molecularly distinct—at least, at the locus we have examined.

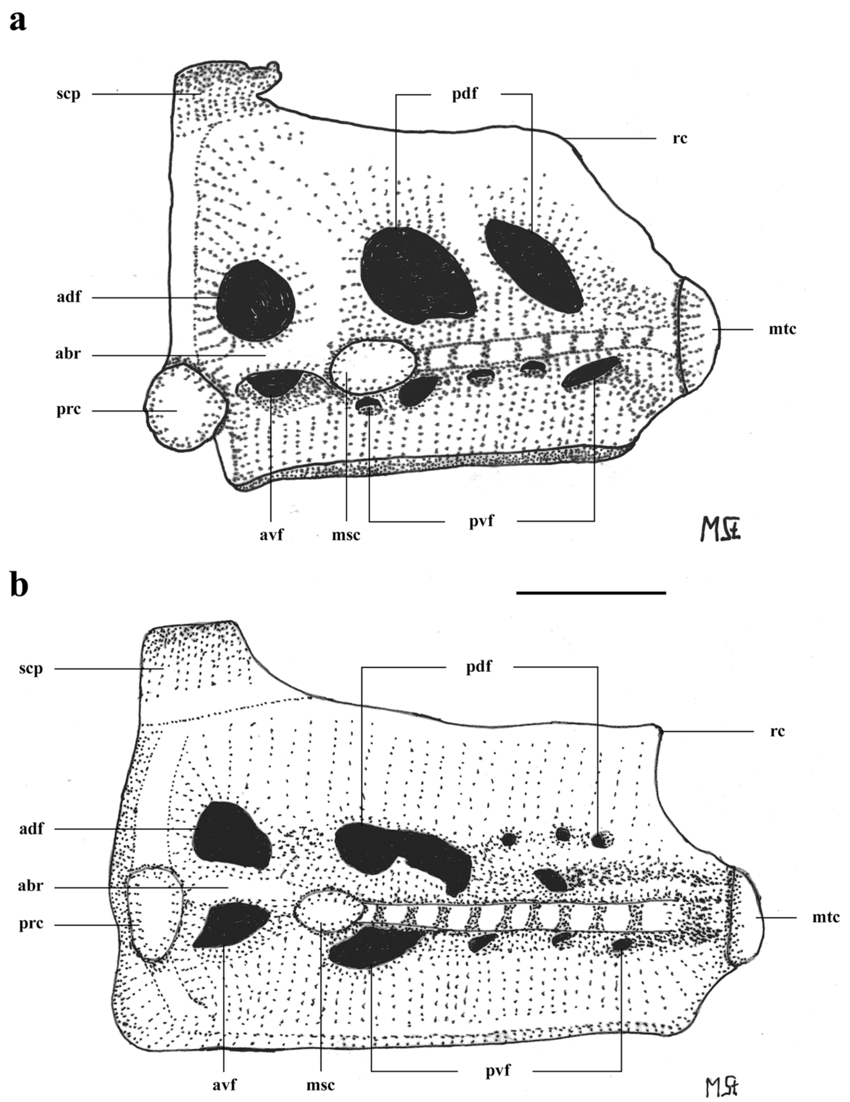

Fig. 23 *Bathyraja arctowskii*, ZMH 115243, dissected scapulocoracoids of **a** adult male and **b** adult female. Scale bar: 1 cm

Fig. 24 *Bathyraja arctowskii*, ZMH 9014, two egg capsules. **a**,**b** egg capsule with near-term embryo removed in **a** dorsal and **b** ventral views; **c**,**d** empty egg capsule in **c** dorsal and **d** ventral views. Scale bar: 2 cm

Fig. 25 *Bathyraja arctowskii*, one of three empty syntype egg capsules, IRSNB 25, in dorsal view (anterior to the right). Photograph kindly provided by Olivier Pauwels, © IRSNB

Distribution: *Bathyraja arctowskii* appears to be a wide-ranging, circumantarctic species with its center of distribution in the Atlantic sector of the Southern Ocean (Fig. 28). It is known from off the South Shetland, Brabant, and Biscoe Islands to the South-East Weddell Sea, from the Ross Sea in the Pacific sector, and two specimens (MNHN 1987-0232 and NMNZ P.041445) from Prydz Bay in the Indian Ocean sector of the Southern Ocean. The known depth distribution is 0–1685 m but the species is mainly found between 126 and 810 m depth based on ZMH material (excluding one lot of six specimens, ZMH 120223, from 0 to 140 m depth). Records deeper than 810 m are based solely on specimens from the NMNZ collection, indicating that the species possibly occurs in greater depths in the Pacific sector, albeit this may only be the result of differing fishery efforts in the respective depths. Most of the specimens caught deeper than 810 m were adults but adult specimens were also recorded from shallower depths elsewhere and juveniles in turn were also recorded deeper than 810 m and even below 1000 m.

Fig. 26 *Bathyraja arctowskii*, one of three empty syntype egg capsules, IRSNB 25, in ventral view (anterior to the right). Photograph kindly provided by Olivier Pauwels, © IRSNB

Remarks: The adult male generally corresponds well to the females, juvenile and subadult males, as well as the male embryo. The observed sexual dimorphism is typical for skates: adult male with anterior disc margins more undulated, alar thorns present, teeth with longer cusps and arranged in parallel rows (vs. quincunx pavement pattern), and pelvic girdle narrower with deeply (vs. slightly) concave posterior contour of ischiopubic bar.

Possible ontogenetic changes between the subadults plus adults ($n = 4$, 424–535 mm TL), juveniles ($n = 6$, 135–333 mm TL), and the male embryo ($n = 1$, 120 mm TL) are listed in Table 7. In addition, the median tail thorns become smaller and more widely spaced posteriorly in subadults and adults and are generally wider-spaced in large juveniles to adults as compared with small juveniles. Furthermore, the male embryo differs from all other specimens in a narrower disc (width 51.7% TL vs. 61.3–66.0% TL).

Discussion

As shown in the "Introduction" section, *Raja arctowskii* represents a unique case in skate taxonomy as it was named based only on three empty egg capsules. Therefore, it has remained impossible to assign any specimens to this species, and the species has remained a *nomen nudum* for a long time. The availability of a gravid female with egg capsules finally enabled to resolve this issue. Since this female was not found for the present study, other evidence was needed and found in the egg capsule with a male near-term embryo. The egg capsule unambiguously belongs to the same species as the empty syntype capsules and agrees well with all other examined capsules. The embryo itself corresponds well to all other examined specimens, juveniles and adults, thus evidencing their identity. The availability of adult male specimens further allowed for the generic assignment of the species to *Bathyraja*, in which it is one of the smallest species.

Compared with its congeners in the Southern Ocean, *Bathyraja arctowskii* is one of two smallest species reaching only 61 cm TL and maturing at around 36–50 cm TL. It can further be distinguished from its congeners by the—at least partial—dark pigmentation of the mouth cavity and underside of nasal curtain, which are light-colored in other species.

The only species in the region with similar maximum and egg capsule sizes, *B. murrayi* (Günther, 1880), reaches a slightly larger maximum size, i.e., 70 cm TL (Duhamel et al. 2005) and shows a white mouth cavity. *Bathyraja arctowskii* further differs from *B. murrayi* in the absence of thorns on the dorsal disc (Stehmann and Bürkel 1990): *B. murrayi* has a pair of distinct pre- and postorbital thorns, two or three on midline of nape, one or two on each shoulder, and usually one on mid-shoulder (vs. no thorns on dorsal disc); smaller additional

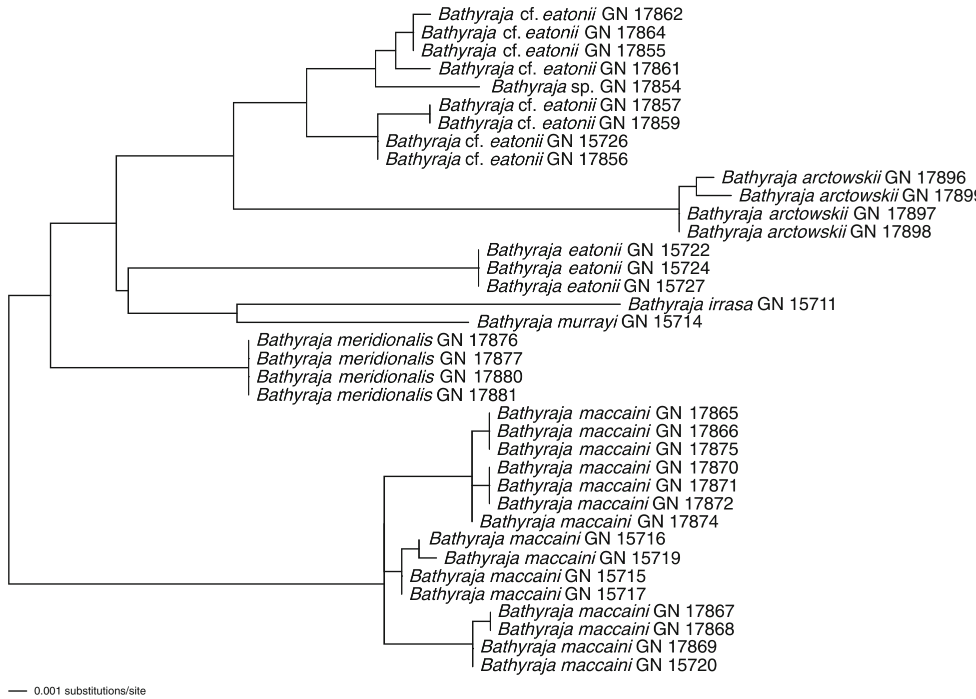

Fig. 27 Inferred phylogenetic relationships among taxa resulting from a Maximum Likelihood analysis of aligned NADH2 sequence data using the General Time Reversible model, modified to accommodate among site rate variation (ASRV) and a proportion of invariant sites (I) estimated from the data. The figure clearly shows *Bathyraja arctowskii* to represent a distinct lineage

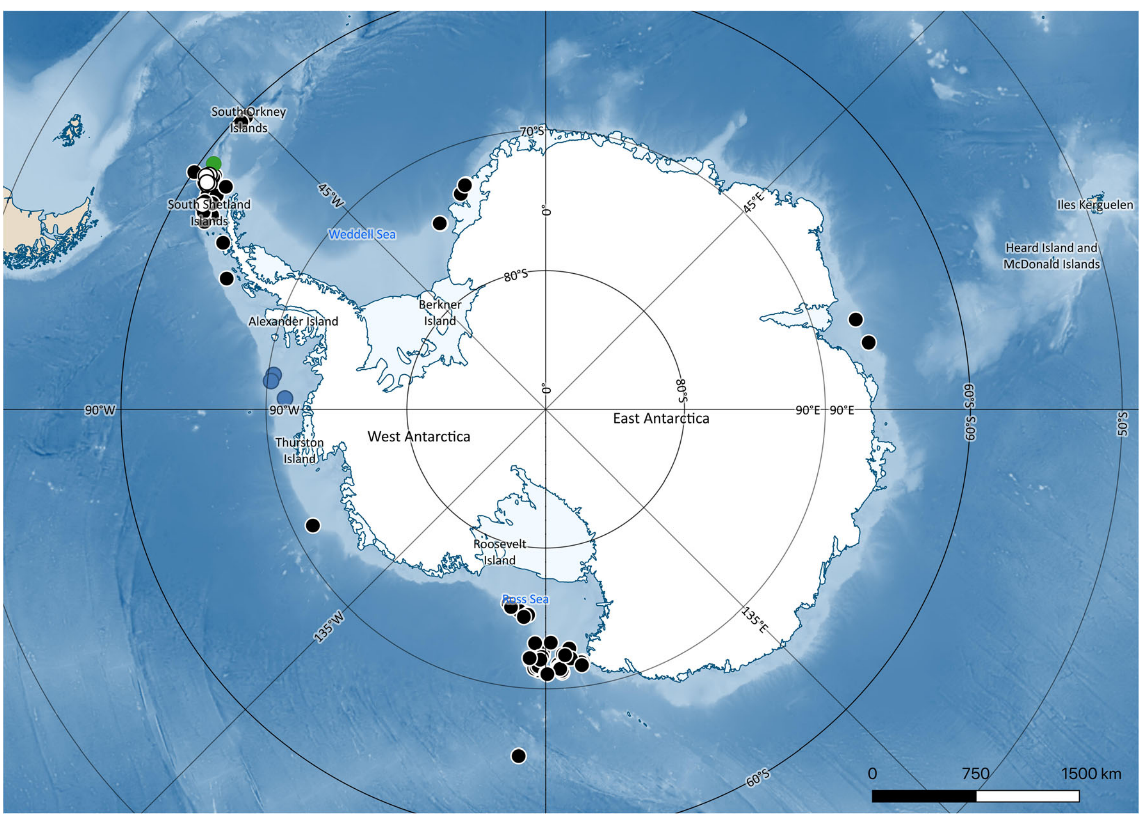

Fig. 28 Map of the Southern Ocean, showing catch locations of *Bathyraja arctowskii*: specimens listed under material examined (121 stations, 339 specimens; black spots, multiply overlapping), specimens from Bigelow & Schroeder (1965: two stations, two specimens; green spots), egg capsules from ZMH collection listed under material examined (eight stations, 40 egg capsules; white spots, overlapping), syntype egg capsules from IRSNB collection (three stations, three egg capsules; blue spots). Cartographic base from Matsuoka et al. (2018)

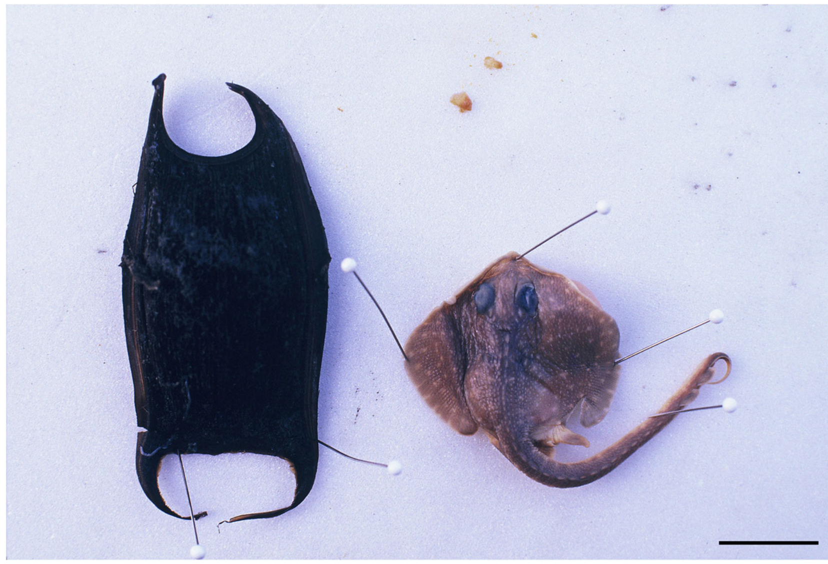

Fig. 29 *Bathyraja murrayi*, MTUF 26165, Kerguelen Islands, 14 Jan 1985, egg capsule (egg case length 59.8 mm, maximum case width 43.6 mm) with near-term embryo. Note thorns on trunk pronounced already in embryonic specimens. Photograph taken and kindly provided by Hajime Ishihara. Estimated scale bar: 2 cm

thorns may be present in supraorbital, supra- and interspiracular positions (vs. absent). Furthermore, *B. murrayi* has a very rough dorsal disc with additional coarse spinules and thornlets, particularly in large specimens, which are absent in *B. arctowskii*. Additionally, *B. murrayi* is only known from off the Kerguelen and Heard Islands, where *B. arctowskii* apparently does not occur, and large specimens tend to show a pair of (rarely more) light, dark-edged large pseudo-ocellar blotches on inner pectorals and individuals with solid or blotched broad dark ventral disc margins are common. Also, the egg capsule is shorter but broader than that of *B. arctowskii* (compare Figs. 24, 25 and 26 with Fig. 29). Measurements of nine egg capsules of *B. murrayi* in the MNHN collection, kindly provided by Guy Duhamel, Zouhaira Gabsi, and Jonathan Pfliger, indicate egg case lengths (ECL) of 57.0–67.2 mm and maximum case widths (MAW) of 40.6–48.6 mm. In *B. arctowskii*, ECL is 76.1–77.55 mm and MAW 40.72–42.33 mm. The presence of interspecific differences in the morphology of skate egg capsules has also been shown in previous studies (e.g., Ishiyama 1958b; Treloar et al. 2006; Ebert and Davis 2007; Ishihara et al. 2012; Porcu et al. 2017). Accordingly, egg capsule morphology can be very useful for distinguishing between different skate species, allows conclusions to be drawn on the habitat, and the capsule size also enables rough estimations of the size of adult animals.

Bathyraja irrasa Hureau & Ozouf-Costaz, 1980 also appears to be an allopatric species, only known from off the Kerguelen and Heard Islands. It is a much larger species, reaching ~120 cm TL (Weigmann 2016; Last et al. 2016b) to 140 cm TL (Duhamel et al. 2005), maturing size 86.5–121 cm TL and size at hatching 17.8–21.4 cm TL, and egg case 113.8 mm (excl. horns) long and 73.6 mm wide following Ishihara et al. (2012) or 9–10 cm long according to Duhamel et al. (2005). Like *B. arctowskii*, *B. irrasa* has a very rough dorsal disc but with disc margins and pelvic fins narrowly smooth (vs. prickly). Furthermore, *B. irrasa* has a pair of distinct preorbital thorns always present (vs. absent), additional smaller supra-and/or postorbital thorns may occur (vs. absent), and the number of median tail thorns is tendentially lower (9–23 vs. 19–30). Additionally, the ventral disc and pelvic fins are predominantly dark brown with an irregular-shaped broad whitish band from about mouth rearwards along two thirds of midbody (vs. predominantly whitish).

Bathyraja maccaini Springer, 1971 is also a much larger species, attaining ~120 cm TL, males maturing at ~94 cm TL following Last et al. (2016b), and with egg case 156.6 mm long and 80.0 mm wide (Ishihara et al. 2012). In contrast to *B. arctowskii*, *B. maccaini* has a dorsal disc largely smooth centrally in large specimens, with broad bands of spinules around outer disc margins, along midbody and on tail, and pectoral centers only loosely prickly even at small size. A pair of large thorns is always present pre- and postorbitally and on the shoulders (vs. absent) and the number of median tail thorns is lower (9–15 vs. 19–30).

Bathyraja meridionalis Stehmann, 1987 is the largest species in the region, reaching ~150 cm TL, males maturing at 132–142 cm TL, females at ~140 cm TL according to Last et al. (2016b) or attaining 158 cm TL, males maturing at 115–130 cm TL, females at 113–125 cm TL following Ebert (2016). In contrast to *B. arctowskii*, *B. meridionalis* has a dorsal disc covered with scattered, coarse, sharp prickles, more densely set only at anterior disc margins, in a broad band along midbody, and along sides of the tail. Pelvic fins largely smooth above (vs. spinules present at the rear margin of posterior pelvic-fin lobes) but ventrally a row of spinules scattered along

Table 8 Valid species of *Bathyraja* and *Rhinoraja*

Scientific name	Species authorship
Bathyraja abyssicola	(Gilbert, 1896)
Bathyraja aguja	(Kendall & Radcliffe, 1912)
Bathyraja albomaculata	(Norman, 1937)
Bathyraja aleutica	(Gilbert, 1896)
Bathyraja andriashevi	Dolganov, 1983
Bathyraja arctowskii	(Dollo, 1904)
Bathyraja bergi	Dolganov, 1983
Bathyraja brachyurops	(Fowler, 1910)
Bathyraja cousseauae	Díaz de Astarloa & Mabragaña, 2004
Bathyraja diplotaenia	(Ishiyama, 1952)
Bathyraja eatonii	(Günther, 1876)
Bathyraja fedorovi	Dolganov, 1983
Bathyraja griseocauda	(Norman, 1937)
Bathyraja hesperafricana	Stehmann, 1995
Bathyraja interrupta	(Gill & Townsend, 1897)
Bathyraja irrasa	Hureau and Ozouf-Costaz, 1980
Bathyraja ishiharai	Stehmann, 2005a
Bathyraja isotrachys	(Günther, 1877)
Bathyraja leucomelanos	Iglésias & Lévy-Hartmann, 2012
Bathyraja lindbergi	Ishiyama & Ishihara, 1977
Bathyraja longicauda	(de Buen, 1959)
Bathyraja maccaini	Springer, 1971
Bathyraja macloviana	(Norman, 1937)
Bathyraja maculata	Ishiyama & Ishihara, 1977
Bathyraja magellanica	(Philippi, 1902)
Bathyraja mariposa	Stevenson et al. 2004
Bathyraja matsubarai	(Ishiyama, 1952)
Bathyraja meridionalis	Stehmann, 1987
Bathyraja microtrachys	(Osburn & Nichols, 1916)
Bathyraja minispinosa	Ishiyama & Ishihara, 1977
Bathyraja multispinis	(Norman, 1937)
Bathyraja murrayi	(Günther, 1880)
Bathyraja pacifica	Last et al. 2016c
Bathyraja pallida	(Forster, 1967)
Bathyraja panthera	Orr, Stevenson, Hoff, Spies & McEachran, 2011
Bathyraja papilionifera	Stehmann, 1985
Bathyraja parmifera	(Bean, 1881)
Bathyraja peruana	McEachran & Miyake, 1984
Bathyraja richardsoni	(Garrick, 1961)
Bathyraja scaphiops	(Norman, 1937)
Bathyraja schroederi	(Krefft, 1968b)
Bathyraja shuntovi	Dolganov, 1985
Bathyraja simoterus	(Ishiyama, 1967)
Bathyraja smirnovi	(Soldatov & Pavlenko, 1915)
Bathyraja smithii	(Müller & Henle, 1838)
Bathyraja spinicauda	(Jensen, 1914)
Bathyraja spinosissima	(Beebe & Tee-Van, 1941)
Bathyraja trachouros	(Ishiyama, 1958a)
Bathyraja trachura	(Gilbert, 1892)
Bathyraja tunae	Stehmann, 2005b
Bathyraja tzinovskii	Dolganov, 1983
Bathyraja violacea	(Suvorov, 1935)
Rhinoraja kujiensis	(Tanaka, 1916)
Rhinoraja longicauda	Ishiyama, 1952
Rhinoraja odai	Ishiyama, 1958a
Rhinoraja taranetzi	Dolganov, 1983

edges of tail origin (vs. smooth). Median trunk and tail with a continuous row of 37–39 distinct thorns from nape to first dorsal fin and a smaller thorn interdorsally; median thorns on disc may be lost only in fully grown specimens (vs. no thorns on disc and usually no thorns interdorsally). Furthermore, the ventral surface, including pelvic fins and tail, is plain dark grayish-brown (vs. predominantly whitish).

Bathyraja eatonii (Günther, 1876) is the only congener of *B. arctowskii* in the Southern Ocean with no thorns on the dorsal disc or only 1 or 2 large median thorns on the nape/shoulder. *Bathyraja eatonii* is a much larger species, reaching ~126 cm TL, with size at hatching ~17.8 cm TL and egg cases 11–12 cm long (Duhamel et al. 2005; Last et al. 2016b). In contrast to *B. arctowskii*, large specimens of *B. eatonii* are mostly smooth on dorsal disc, with bands of fine and (with growth) coarser spinules along anterior margins, parallel to posterior margins and along midbody and tail; pectoral centers and pelvic fins usually smooth. Furthermore, *B. eatonii* has fewer median tail thorns (8–18 vs. 19–30).

Generic composition: *Bathyraja* currently contains 52 valid species. However, the four valid species presently assigned to *Rhinoraja* Ishiyama, 1952 likely belong to the same genus as the differentiation of both genera is questionable and solely relies on the presence or absence of a segmented rostral cartilage (Weigmann 2016). Unpublished mitochondrial molecular data collected by GJPN indicates that at least two of the four species of *Rhinoraja*, *R. longicauda* Ishiyama, 1952 and *R. taranetzi* Dolganov, 1983, are deeply nested within the genus *Bathyraja*, supporting Weigmann's (2016) hypothesis of congenerity. A list of the valid *Bathyraja* and *Rhinoraja* species, updated from Weigmann (2016, 2017) and considering Last et al. (2016a, b), can be found in Table 8.

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Key to the valid species of *Bathyraja* in the Southern Ocean:

1. Underside of disc largely or entirely dark, may become paler in large individuals 2
– Underside of disc white or largely so 3
2. Underside totally dark with small white marks only at nostrils, jaws, gills, tip of anterior pelvic lobe and tail origin; median row of about 40 thorns from nape to D1, but ~10 on disc often lost in adults; the largest species in the region, reaching ~150–158 cm TL and maturing at ~113–142 cm TL .... *B. meridionalis*
– Underside largely dark, paler in adults, but with an irregular white band from mouth along 2/3 of midbelly; preorbital thorns present, more at orbits may occur, but only 9–23 median thorns on tail; attains ~120–140 cm TL and matures at ~86.5–121 cm TL .... *B. irrasa*
3. Orbital and shoulder thorns always present 4
– No thorns on upper disc other than at most 1–2 on nape and mid-shoulder 5
4. Upper disc very rough with scattered coarse prickles and thornlets; thorns at orbits, on nape and shoulders. 21–26 distinct median thorns from nape to D1, reduced to 12–19 on tail in larger specimens; attains ~70 cm TL, egg cases ~6–7 cm long and 4–5 cm wide .... *B. murrayi*
– Upper disc partly prickly along margins, on midbody, and on tail; a massive thorn only in front of and behind each eye and on each shoulder; 8–15 median thorns only along tail; pectoral centers mostly smooth; reaches ~120 cm TL, egg cases ~16 cm long and 8 cm wide .... *B. maccaini*
5. At most 1–2 thorns on nape and mid-shoulder; band of densely set, fine prickles around disc and along midbody, with pectoral centers and rear margins smooth; 8–18 small median thorns along tail; mouth cavity white; attains ~126 cm TL, egg cases 11–12 cm long .... *B. eatonii*
– No thorns on upper disc, which is totally prickly; 19–3 small median thorns along tail; mouth cavity and underside of nasal curtain partly or totally pigmented dark; reaches ~61 cm TL, egg cases ~6–7 cm long .... *B. arctowskii*

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability All data generated or analyzed during this study are included in this published article.

Author contribution MFWS and SW conceived and designed research, conducted examinations, and wrote the first draft of the manuscript, GJPN conducted molecular analyses and contributed parts of the manuscript. All authors read and approved the final manuscript.

References

Bean TH (1881) Descriptions of new fishes from Alaska and Siberia. Proc U S Natl Mus 4(210):144–159

Beebe W, Tee-Van J (1941) Eastern Pacific expeditions of the New York Zoological Society. XXVIII. Fishes from the Tropical Eastern Pacific. [From Cedros Island, Lower California, South to the Galápagos Islands and Northern Peru.] Part 3. Rays, mantas and chimaeras. Zool Sci Contrib NY Zool Soc 26:245–280

Bigelow HB, Schroeder WC (1953) Fishes of the Western North Atlantic. Part two. Sawfishes, guitarfishes, skates and rays, Chimaeroids. Mem Sears Found Mar Res 1(2):1–588

Bigelow HB, Schroeder WC (1965) Notes on a small collection of rajids from the sub-Antarctic region. Limnol Oceanogr 10(Suppl):R38–R49

Clark RS (1926) Rays and skates, a revision of the European species. Fish Bd Scotland Sci Inv 1:1–66

Concha F, Hernández S, Oddone MC (2009) Egg capsules of the raspthorn sandskate, *Psammobatis scobina* (Philippi, 1857) (Rajiformes, Rajidae). Rev Biol Mar Oceanogr 44(1):253–256

Concha F, Oddone MC, Bustamante C, Morales N (2012) Egg capsules of the yellownose skate *Zearaja chilensis* (Guichenot 1848) and the roughskin skate *Dipturus trachyderma* (Krefft and Stehmann 1974) (Rajiformes: Rajidae) from the South-Eastern Pacific Ocean. Ichthyol Res 59:323–327

de Buen F (1959) Notas preliminares sobre la fauna marina preabismal de Chile, con descripción de una familia de rayas, dos géneros y siete especies nuevos. Bol Mus Nac Chile 27(3):171–201

Díaz de Astarloa JM, Mabragaña E (2004)*Bathyraja cousseauae* sp. n.: a new softnose skate from the southwestern Atlantic (Rajiformes, Rajidae). Copeia 2004(2):326–335

Dolganov VN (1983) Rukovodstvo po opredeleniyu khryashchevykh ryb dal'nevostochnykh morei SSSR i sopredel'nykh vod [Manual for identification of cartilaginous fishes of Far East seas of USSR and adjacent waters]. TINRO, Vladivostok

Dolganov VN (1985) A new species of skate from the southwestern Pacific Ocean. Biol Morya (Vladivostok) 1985(5):66–68

Dollo L (1904) Poissons. In: Expédition Antarctique Belge, Résultats du voyage du S.Y. Belgica en 1897-1898-1899, Zoologie. Imprimerie J.-E. Buschmann, Antwerpen, pp. 1–240

Duhamel G, Gasco N, Davaine P (2005) Poissons des îles Kerguelen et Crozet. Guide régional de l'océan Austral. Muséum national d'Histoire naturelle, Paris

Ebert DA (2016) Deep–sea cartilaginous fishes of the southeastern Pacific Ocean. FAO species catalogue for fishery purposes No. 10. FAO, Rome

Ebert DA, Davis CD (2007) Descriptions of skate egg cases (Chondrichthyes: Rajiformes: Rajoidei) from the eastern North Pacific. Zootaxa 1393:1–18

Forster GR (1967) A new deep-sea ray from the Bay of Biscay. J Mar Biol Assoc U K 47(2):281–286

Fowler HW (1910) Notes on batoid fishes. Proc Acad Nat Sci Phila 62: 468–475

Garrick JAF (1961) Studies on New Zealand Elasmobranchii. Part XIII. A new species of *Raja* from 1,300 Fathoms. Trans R Soc N Z 88(4):743–748

Gilbert CH (1892) Descriptions of thirty-four new species of fishes collected in 1888 and 1889, principally among the Santa Barbara Islands and in the Gulf of California. In: scientific results of explorations by the U. S Fish Commission steamer Albatross. Proc U S Natl Mus 14(880):539–566

Gilbert CH (1896) The ichthyological collections of the steamer Albatross during the years 1890 and 1891. Rep U S Fish Comm 19:393–476

Gill TN, Townsend CH (1897) Diagnoses of new species of fishes found in Bering Sea. Proc Biol Soc Wash 11:231–234

Günther A (1876) Remarks on fishes, with descriptions of new species in the British Museum, chiefly from southern seas. Ann Mag Nat Hist (Series 4) 17(101):389–402

Günther A (1877) Preliminary notes on new fishes collected in Japan during the expedition of H.M.S. 'Challenger'. Ann Mag Nat Hist (Series 4) 20(119):433–446

Günther A (1880) Report on the shore fishes procured during the voyage of H.M.S. Challenger in the years 1873–1876. In: Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. Zoology 1(part 6):1–82

Hanchet SM, Stewart AL, McMillan PJ, Clark MR, O'Driscoll RL, Stevenson ML (2013) Diversity, relative abundance, new locality records, and updated fish fauna of the Ross Sea region. Antarct Sci 25(5):619–636

Hubbs CL, Ishiyama R (1968) Methods for the taxonomic study and description of skates (Rajidae). Copeia 1968(3):483–491

Hulley PA (1970) An investigation of the Rajidae of the west and south coasts of southern Africa. Ann S Afr Mus 55(4):151–220

Hulley PA (1972) The origin, interrelationships and distribution of southern African Rajidae (Chondrichthyes, Batoidei). Ann S Afr Mus 60: 1–103

Hureau J-C, Ozouf-Costaz C (1980) Une nouvelle espèce de raie bathyale des îles Kerguelen *Bathyraja irrasa* n. sp. (Chondrichthyes, Rajidae). Cybium 4(9):19–29

Iglésias SP, Lévy-Hartmann L (2012)*Bathyraja leucomelanos*, a new species of softnose skate (Chondrichthyes: Arhynchobatidae) from New Caledonia. Ichthyol Res 59(1):38–48

Ishihara H, Treloar M, Bor PHF, Senou H, Jeong CH (2012) The comparative morphology of skate egg capsules (Chondrichthyes: Elasmobranchii: Rajiformes). Bull Kanagawa Prefect Mus (Nat Sci) 41:9–25

Ishiyama R (1952) Studies on the rays and skates belonging to the family Rajidae, found in Japan and adjacent regions. 4. A revision of three genera of Japanese rajids with descriptions of one new genus and four new species mostly occured in northern Japan. J Shimonoseki Coll Fish 2(2):1–34

Ishiyama R (1958a) Studies on the rajid fishes (Rajidae) found in the waters around Japan. J Shimonoseki Coll Fish 7(2/3):193–394

Ishiyama R (1958b) Observation of the egg-capsules of skates of the family Rajidae, found in Japan and adjacent waters. Bull Mus Comp Zool 118(1):1–24

Ishiyama R (1967) Fauna japonica. Rajidae (Pisces). Biogeographical Society of Japan, Tokyo

Ishiyama R, Ishihara H (1977) Five new species of skates in the genus *Bathyraja* from the western North Pacific, with reference to their interspecific relationships. Jpn J Ichthyol 24(2):71–90

Jensen AS (1914) The selachians of Greenland. Bianco Lunos Bogtrykkeri, København

Jones C, Damerau M, Deitrich K, Driscoll R, Kock KH, Kuhn K, Moore J, Morgan T, Near T, Pennington J, Schöling S (2009) Chapter 9. Demersal finfish survey of the South Orkney Islands. In: Van Cise AM (ed) AMLR 2008/2009 field season report – objectives, accomplishments and tentative conclusions, NOAA-TM-NMFS-SWFSC-445. U.S. Department of Commerce, National Oceanic & Atmospheric Administration, La Jolla, pp 49–66

Kalisz H (2013) The comparison of two undescribed species of skates, *Bathyraja* sp. 2 and *Bathyraja* sp. (c.f. *eatonii*) from the Antarctic waters of the South Orkney Islands. BSc thesis, Wilkes Honors College of Florida Atlantic University

Kendall WC, Radcliffe L (1912) The shore fishes. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz by the U.S. fish commission steamer 'Albatross' from October, 1904 to March, 1905, Lieut. Commander L.M. Garrett, U.S.N. commanding. Mem Mus Comp Zool 35(3):75–171

Krefft G (1968a) Knorpelfische (Chondrichthyes) aus dem tropischen Ostatlantik. Atlantide Rep 10:33–76

Krefft G (1968b) Neue und erstmalig nachgewiesene Knorpelfische aus dem Archibenthal des Südwestatlantiks, einschließlich einer Diskussion einiger *Etmopterus*-Arten südlicher Meere. Arch Fischereiwiss 19(1):1–42

Last PR, Séret B (2008) Three new legskates of the genus *Sinobatis* (Rajoidei: Anacanthobatidae) from the Indo-West Pacific. Zootaxa 1671:33–58

Last PR, Weigmann S, Yang L (2016a) Changes to the nomenclature of the skates (Chondrichthyes: Rajiformes). In: Last PR, Yearsley GK (eds) Rays of the world: supplementary information. CSIRO Special Publication. CSIRO Publishing, Melbourne, pp. 11–34

Last PR, Stehmann MFW, Séret B, Weigmann S (2016b) Softnose skates, family Arhynchobatidae. In: Last PR, White WT, de Carvalho MR, Séret B, Stehmann MFW, Naylor GJP (eds) Rays of the world. CSIRO Publishing, Melbourne, pp 364–472

Last PR, Stewart AL, Séret B (2016c) A new temperate deepwater skate of the genus *Bathyraja* (Rajoidei: Arhynchobatidae) from the South-West Pacific. Zootaxa 4132(1):107–117

Matsuoka K, Skoglund A, Roth G (2018) Quantarctica [Dataset]. Nor Polar Inst. https://doi.org/10.21334/npolar.2018.8516e961

McEachran JD (1983) Results of the research cruises of FRV "Walther Herwig" to South America. LXI. Revision of the South American skate genus *Psammobatis* Günther, 1870 (Elasmobranchii: Rajiformes, Rajidae). Arch Fischereiwiss 34(1):23–80

McEachran JD, Compagno LJV (1979) A further description of *Gurgesiella furvescens* with comments on the interrelationships of Gurgesiellidae and Pseudorajidae (Pisces, Rajoidei). Bull Mar Sci 29(4):530–553

McEachran JD, Miyake T (1984) Comments on the skates of the tropical eastern Pacific: one new species and three new records (Elasmobranchii: Rajiformes). Proc Biol Soc Wash 97(4):773–787

Müller J, Henle FGJ (1838–41) Systematische Beschreibung der Plagiostomen. Veit und Comp., Berlin

Naylor GJP, Ryburn JA, Fedrigo O, Lopez A (2005) Phylogenetic relationships among the major lineages of modern elasmobranchs. In: Hamlett WC (ed) Reproductive biology and phylogeny of chondrichthyes: sharks, rays and chimaeras, vol 3. Science Publishers, Endfield, pp 1–25

Naylor GJP, Caira JN, Jensen K, Rosana KAM, White WT, Last PR (2012) A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. Bull Am Mus Nat Hist 367:1–263

Norman JR (1937) Coast fishes. Part II. The Patagonian region. In: Discovery reports Vol. 16. University Press, Cambridge, pp. 1–150

Orr JW, Stevenson DE, Hoff GR, Spies IB, McEachran JD (2011) *Bathyraja panthera*, a new species of skate (Rajidae: Arhynchobatinae) from the western Aleutian Islands, and resurrection of the subgenus *Arctoraja* Ishiyama. NOAA Prof Pap NMFS 11:1–50

Osburn RC, Nichols JT (1916) Shore fishes collected by the "Albatross" expedition in Lower California, with descriptions of new species. Bull Am Mus Nat Hist 35:139–181

Philippi RA (1902) Descripcion de cinco nuevas especies chilenas: del órden de los plagióstomos. Anal Univ Chile 109:303–315

Porcu C, Marongiu MF, Bellodi A, Cannas R, Cau A, Melis R, Mulas A, Soldovilla G, Vacca L, Follesa MC (2017) Morphological descriptions of the eggcases of skates (Rajidae) from the central-western Mediterranean, with notes on their distribution. Helgol Mar Res 71(10):1–14

Sabaj MH (2019) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference, Version 7.1 (21 March 2019). Available from http://www.asih.org/ (accessed 11 Mar 2020)

Smith PJ, Steinke D, Mcveagh SM, Stewart AL, Struthers CD, Roberts CD (2008) Molecular analysis of Southern Ocean skates (*Bathyraja*) reveals a new species of Antarctic skate. J Fish Biol 73(5):1170–1182

Soldatov VK, Pavlenko MN (1915) Description of a new species of family Rajidae from Peter the Great Bay and from Okhotsk Sea. Annuaire Mus Zool Acad Imp Sci St Petersb 20:162–163

Springer S (1971) Three species of skates (Rajidae) from the continental waters of Antarctica. In: Llano GA, Wallen IE (eds) Biology of the Antarctic seas IV, vol 17. American Geophysical Union, Washington D.C., pp 1–10

Springer VG, Garrick JAF (1964) A survey of vertebral numbers in sharks. Proc U S Nat Mus 116(3496):73–96

Stehmann M (1970) Vergleichend morphologische und anatomische Untersuchungen zur Neuordnung der Systematik der nordostatlantischen Rajidae (Chondrichthyes, Batoidei). Arch Fischereiwiss 21(2):73–164

Stehmann M (1985) Ergebnisse der Forschungsreisen des FFS "Walther Herwig" nach Südamerika. LXIV. *Bathyraja papilionifera* sp. n. (Pisces, Batoidea, Rajidae), eine weitere neue Rochenart aus dem Südwestatlantik vom nordargentinischen Kontinentalabhang. Arch Fischereiwiss 36(1/2):195–211

Stehmann M (1987) *Bathyraja meridionalis* sp. n. (Pisces, Elasmobranchii, Rajidae), a new deep-water skate from the eastern slope of subantarctic South Georgia Island. Arch Fischereiwiss 38(1–2):35–56

Stehmann MFW (1995) First and new records of skates (Chondrichthyes, Rajiformes, Rajidae) from the West African continental slope (Morocco to South Africa), with descriptions of two new species. Arch Fish Mar Res 43(1):1–119

Stehmann MFW (2005a) *Bathyraja ishiharai* n. sp., a new deep-water skate from the eastern Indian Ocean on the Naturalist Plateau off southwestern Australia (Elasmobranchii, Rajiformes, Rajidae). J Ichthyol 45(suppl. 1):S39–S57

Stehmann MFW (2005b) *Bathyraja tunae* n. sp., a new deep-water skate from the western Indian Ocean (Chondrichthyes, Rajiformes, Rajidae). J Ichthyol 45(suppl. 1):S23–S38

Stehmann M, Bürkel DL (1990) Rajidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, pp 86–97

Stehmann MFW, Séret B, Costa EM, Baro J (2008) *Neoraja iberica* n. sp., a new species of pygmy skate (Elasmobranchii, Rajidae) from the southern upper slope of the Iberian Peninsula (Eastern North Atlantic). Cybium 32(1):51–71

Stevenson DE, Orr JW, Hoff GR, McEachran JD (2004)*Bathyraja mariposa*: a new species of skate (Rajidae: Arhynchobatinae) from the Aleutian Islands. Copeia 2004(2):305–314

Suvorov EK (1935)*Raja violacea*, a new species of ray from the Okhotsk Sea [in Russian with English summary]. Bull Acad Sci Math Nat 1935:431–433

Tanaka S (1916) Four new species of Japanese fishes [in Japanese]. Dobutsugaku Zasshi 28(331):173–174

Treloar MA, Laurenson LJB, Stevens JD (2006) Descriptions of rajid egg cases from southeastern Australian waters. Zootaxa 1231:53–68

Weigmann S (2016) Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. J Fish Biol 88(3):837–1037

Weigmann S (2017) Reply to Borsa (2017): comment on 'annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity by Weigmann (2016)'. J Fish Biol 90(4):1176–1181