NOAA Professional Paper NMFS 11

U.S. Department
of Commerce

March 2011

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NOAA Professional Papers NMFS

The NOAA Professional Paper NMFS (ISSN 1931-4590) series is published by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.
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Suggested reference

Orr, James W., Duane E. Stevenson, Gerald R. Hoff, Ingrid Spies, and John D. McEachran. 2011. *Bathyraja panthera*, a new species of skate (Rajidae: Arhynchobatinae) from the western Aleutian Islands, and resurrection of the subgenus Arctoraja Ishiyama. NOAA Professional Paper NMFS 11, 50 p.

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Bathyraja panthera, a new species of skate (Rajidae: Arhynchobatinae) from the western Aleutian Islands, and resurrection of the subgenus *Arctoraja* Ishiyama

James W. Orr (contact author)[1]
Duane E. Stevenson[1]
Gerald R. Hoff[1]
Ingrid Spies[1]
John D. McEachran[2]

[1] Resource Assessment and Conservation Engineering Division
Alaska Fisheries Science Center
National Marine Fisheries Service, National Oceanic and Atmospheric Administration
7600 Sand Point Way NE
Seattle, Washington 98115
Email address for contact author: James.Orr@noaa.gov

[2] Department of Wildlife and Fisheries Sciences
Texas A&M University
College Station, Texas 77843

Abstract—We provide morphological and molecular evidence to recognize a new species of skate from the North Pacific, *Bathyraja panthera*. We also resurrect the skate subgenus *Arctoraja* Ishiyama, confirming its monophyly and the validity of the subgenus. *Arctoraja* was previously recognized as a distinct subgenus of *Breviraja* and later synonymized with *Bathyraja* (family Rajidae). Although the nominal species of *Arctoraja* have all been considered synonyms of *Bathyraja parmifera* by various authors, on the basis of morphometric, meristic, chondrological, and molecular data we recognize four species, including the new species. Species of *Arctoraja* are distributed across the North Pacific Ocean and adjacent seas from southern Japan to British Columbia. *Bathyraja parmifera* is abundant in the eastern Bering Sea, Aleutian Islands, and northern Gulf of Alaska; *B. smirnovi* is a western Pacific species found in the Sea of Okhotsk and Sea of Japan; *B. simoterus* is restricted to waters around the northern and eastern coasts of Hokkaido, Japan; and the new species *B. panthera* is restricted to the western Aleutian Islands. *Bathyraja panthera* is diagnosed by its color pattern of light yellow blotches with black spotting on a greenish brown background, high thorn and vertebral counts, chondrological characters of the neurocranium and clasper, and a unique nucleotide sequence within the mitochondrial cytochrome oxidase gene. Furthermore, the species presently recognized as *Bathyraja parmifera* exhibits two haplotypes among specimens from Alaska, suggesting the possibility of a second, cryptic species.

Introduction

Recent bottom-trawl surveys conducted by the Alaska Fisheries Science Center (AFSC) of the National Marine Fisheries Service (NMFS) have resulted in the collection and subsequent discovery of several new species and records of fishes from the Aleutian Islands, including liparids (Orr and Busby, 2001, 2006; Orr, 2004; Orr and Maslenikov, 2007), zoarcids (Stevenson and Orr, 2006), and skates (Stevenson et al., 2004; Stevenson and Orr, 2005). Among those species that have been recognized as new but undescribed is a skate from the western Aleutian Islands previously identified as *Bathyraja parmifera* (Bean, 1881).

Skates of the family Rajidae, dominated by the genus *Bathyraja*, represent a substantial portion of the biomass of incidental species encountered by fisheries in the eastern Bering Sea (Spies et al., 2006; Stevenson et al., 2008). *Bathyraja* Ishiyama, 1958, comprising over 50 species (Stehmann, 2005; Ebert and Compagno, 2007), is the most diverse genus of the family, with its major center of abundance in the North Pacific where at least 25 species are distributed from Japan to California (Ishihara and Ishiyama, 1986; Ishihara, 1990; Stevenson et al., 2004; Ebert and Compagno, 2007). Twelve species are now considered valid in Alaskan waters (Stevenson et al., 2004; Stevenson and Orr, 2005; Stevenson et al., 2007) and further work is being conducted to clarify the status of suspected species complexes within the region. One of these complexes includes the most common species in Alaska, *Bathyraja parmifera*, the Alaska skate (Stevenson et al., 2008) of the subgenus *Arctoraja*.

Ishiyama (1958a) erected three subgenera, *Arctoraja*, *Bathyraja*, and *Notoraja,* for the Japanese skates of the widely distributed genus *Breviraja* Bigelow and Schroeder, 1948. The subgenus *Arctoraja* included two species of the North Pacific region, *B. parmifera* and *B. smirnovi* (Soldatov and Pavlenko, 1915), as well as Ishiyama's two new subspecies within *B. smirnovi*: *B. s. smirnovi* and *B. s. ankasube.* Later, Ishiyama (1967) described *Breviraja (Arctoraja) simoterus* based on specimens he had previously identified as *B. parmifera,* yet he did not list *B. parmifera* as a member of the subgenus. When Ishiyama and Hubbs (1968) elevated the subgenus *Bathyraja* to generic status, they considered *Arctoraja* and *Notoraja* to be synonyms of *Bathyraja*.

Although no comprehensive revision of the subgenus *Arctoraja* has been produced since Ishiyama's (1958a, 1967) seminal works, taxonomic reviews of North Pacific species of *Bathyraja* have come to contradictory conclusions on the status of *Bathyraja parmifera* and its close relatives. Ishihara and Ishiyama (1985, 1986) treated *B. parmifera*, *B. smirnovi*, and *B. simoterus* as distinct species, as do all recent Japanese authors (Nakaya, 1983, 1984; Nakaya and Shirai, 1992; Nakabo, 2000, 2002), distinguishing them within the context of dichotomous keys and checklists. In their phylogenetic analysis of the Rajidae, McEachran and Dunn (1998) listed all species in a generic classification of species, as did Stehmann (1986), McEachran and Miyake (1990), Compagno (1999), and Ebert and Compagno (2007) in their distributional analyses of species of the world. However, Dolganov (1983) referred *B. smirnovi* to *B. parmifera* and later examined the distribution of dorsal thorns and other morphological characters among "*B. parmifera*" of the North Pacific, conflating *B. smirnovi* and *B. simoterus* under *B. parmifera* (Dolganov, 2001; Dolganov and Korolev, 2006). Most Russian authors of checklists and ecological works (e.g., Dudnik and Dolganov, 1992; Fedorov, 2000; Sheiko and Fedorov, 2000; Fedorov et al., 2003; Orlov, 2003; Antonenko et al., 2007) have followed Dolganov's (1983, 2001) and Dolganov and Korolev's (2006) conclusions in print, and consequently their discussions of *B. parmifera* may refer to any of these closely related species. As other authors have suggested (Stehmann, 1986; Mecklenburg et al., 2002), we consider the nominal species *Raja obtusa*, described from the Bering Sea by Gill and Townsend (1897), to be a synonym of *B. parmifera*.

Herein we describe additional characters to support the resurrection of *Arctoraja* as a valid subgenus of *Bathyraja*. In our revision of *Arctoraja*, we use morphological and genetic data to describe a new species, *B. panthera*, and provide diagnoses, redescriptions, and distributions for all species.

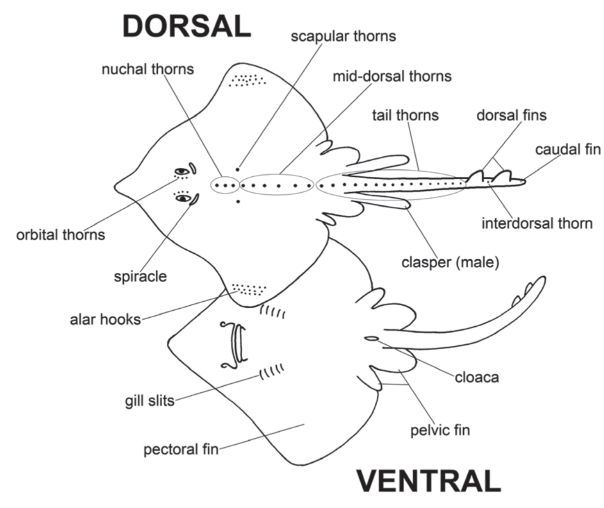

Figure 1

Selected terminology used to describe the external morphology of skates of the genus *Bathyraja*, subgenus *Arctoraja*.

Methods and materials

Most specimens of the new species were collected during the Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering (RACE) Division groundfish bottom trawl surveys or during other AFSC surveys conducted in the Aleutian Islands; archived material was also examined at other institutional collections. The word "tissue" associated with specimens in Material Examined indicates that tissue was also preserved in 95% ethanol for genetic analysis before the remainder of the specimen was fixed in 10% formalin.

Material listed under "Tissue with photo vouchers only" are tissues preserved in 95% ethanol taken from specimens that were photographed and then discarded at sea. Tissues from multiple specimens may be included under each catalog number; most of these individuals are separated by specimen numbers. Total lengths and sexes of specimens are provided when available.

Methods follow Stevenson et al. (2004) and Last et al. (2008). Body size is expressed as total length (TL), from tip of snout to tip of caudal fin. All measurements were made point to point, with either a steel ruler to the nearest millimeter or dial calipers to 0.1 mm. External measurements were made as described by Last et al. (2008), with the following exceptions: mouth width (two measurements: total width of the jaw cartilages and width of tooth bands); orbit length (longitudinal distance across orbit to cartilaginous rims); clasper length, from point of attachment with tail to distal tip of clasper; ventral head length (distance from tip of snout to anterior margin of coracoid bar along midline), and widths of first and fifth gill-slits.

We enumerate the following series of thorns on the dorsal midline (Fig. 1): nuchal thorns are those posterior to the head and extending from the anteriormost to the last thorn anterior to the scapular thorns; mid-dorsal thorns extend from the thorn after the last nuchal thorn to the last thorn immediately anterior to the pelvic horns; tail thorns extend from the first thorn posterior to the pelvic horns to the thorn immediately anterior to dorsal fin 1; and interdorsal thorns are those between the dorsal fins. Orbital thornlets are the series of small thorns on the medial rims of the orbits. Scapular thorns are paired thorns at the posterolateral margin of the scapulocoracoid.

For the new species, morphometric and meristic data are presented in the text as the measurement or count for the holotype followed by the range for other type material in parentheses. For *B. smirnovi*, for which only one paratype represents the known extant type material, data for the paratype are followed by the range for other material examined in parentheses. For other species, type material was not located or was disintegrated; therefore, the data are presented as the range for material examined. Morphometric and meristic data are summarized in Table 1.

Univariate analyses were conducted using SPSS for Windows (Release 11.5.1, SPSS Inc., Chicago, IL). To assess significant differences, arcsine-transformed morphometric ratios (with TL as denominator) and raw meristic characters were tested. Because of the low sample size for *B. simoterus*, the Games-Howell post hoc test for pair-wise comparisons, which accounts for unequal sample size and variances (Sahai and Ageel, 2000), was used to determine significant differences between species. Morphometric characters that met these assumptions (Table 1) were subjected to analysis of covariance (ANCOVA), using TL as covariate, and counts of meristic characters were subjected to analysis of variance (ANOVA).

To aid in discriminating the four species, a standard principal components analysis (PCA) was conducted on both morphometric and meristic characters. The analyses were conducted on the covariance matrix of log-transformed raw morphometric data and the correlation matrix of raw meristic data for those specimens for which all data were available, following Mayden and Kuhajda (1996). Differences between species were illustrated by plotting the individual scores from PC 2 versus PC 3 of the morphometric analysis, PC 1 versus PC 2 of the meristic analysis, and PC 2 of the morphometric analysis versus PC 1 of the meristic analysis. To analyze geographic variation within *B. parmifera*, data points were identified by reference to two zoogeographic regions: 1) the Aleutian Province, including the southern Bering Sea, Aleutian Islands, and Gulf of Alaska; and 2) a region comprising the combined Arctic and Kuril provinces, including the northern and western Bering Sea, eastern Kamchatka, and the Commander Islands (Logerwell et al., 2005). To analyze geographic variation within *B. smirnovi*, data points were also identified by reference to five regions: northern and southern Sea of Okhotsk, divided at 50°N; northern and southern Sea of Japan, divided at 40°N; and the Pacific Ocean side of Japan.

Skeletal measurements and illustrations for each species were taken from single dissected male specimens using the methods of Hubbs and Ishiyama (1968) and McEachran and Compagno (1979, 1982). Additional claspers of each species except *B. simoterus* were dissected, and two specimens of *B. parmifera* were prepared by boiling and dissection, to examine variation in clasper and other chondrological characters. Internal clasper components, as well as vertebrae and fin rays, of the holotype and allotype of *B. panthera* were verified by radiograph and computed axial tomographic (CAT) scans.

Egg capsule measurements follow Hubbs and Ishiyama (1968), with additions or modifications noted below, and are based on preserved capsules of *B. parmifera* and *B. panthera* collected from bottom trawls. Capsule length (CL) excludes horns, being the distance between the centers of the curved anterior and straight posterior capsule margins. Horn and capsule widths were measured with and without the lateral keel. Anterior horn width was measured at mid-horn length just posterior to the horn curl, irrespective of the respiratory fissure opening. Posterior horn width was measured at the base of the horn, level with the posterior capsule margin. The position of the byssal thread attachment point was measured from the anterior capsule margin to the center of the attachment of the byssal mass. Egg capsules of *B. parmifera* were verified by dissection from females; egg capsules of *B. panthera* were identified by geographic range, i.e., egg capsules of *Arctoraja* found only in the western Aleutian Islands. Egg capsules of *B. smirnovi* and *B. simoterus* were not available for examination, and data for these species were extracted from descriptions and illustrations in the published literature (Ishiyama, 1958b, 1967; Ishihara et al., 2005).

All illustrations were prepared by the second author from dissections executed by the third author. Institutional abbreviations are as listed at http://www.asih.org/codons.pdf or Leviton et al. (1985).

Samples for genetic analysis were processed following methods detailed by Spies et al. (2011). We sequenced the mitochondrial cytochrome oxidase subunit 1 (COI) gene from skeletal muscle tissue samples preserved in 95% ethanol taken from eight individuals of *B. panthera*, 33 *B. parmifera*, and six *B. smirnovi*, as well as from two formalin-fixed *B. simoterus*. Aligned consensus sequences were created using BioEdit 7.0.4.1 (Hall, 1999). Base positions were determined by alignment with the previously published sequences of Spies et al. (2006). After determining diagnostic sequence differences in the five haplotypes found among species of *Arctoraja*, we conducted a restriction fragment length polymorphism (RFLP) analysis on 179 additional samples of *B. panthera* and *B. parmifera* to quickly and inexpensively determine their haplotypes to examine geographic and depth distributions (Spies et al., 2011).

Table 1

Proportional morphometric (in percent total length) and meristic characters for species of the subgenus *Arctoraja* of *Bathyraja*. Range followed by mean ± standard deviation in parentheses. pan = *B. panthera*, par = *B. parmifera*, sm = *B. smirnovi*, si = *B. simoterus*. Species separated by < are significantly different. Species in parentheses and those separated by commas are not significantly different from one another. NS = non–significant. Missing values were not recorded.

	Bathyraja panthera			*Bathyraja parmifera*		*Bathyraja smirnovi*			*Bathyraja simoterus*		Significance	
	n	Holotype	Paratypes	*n*	Material examined	*n*	Paratype	Non–type material examined	*n*	Material examined		
Total length (mm)	39	980.0	197–1110	69	207–1150	71	525.0	237–1015	5	690.3–1006.2		
Disk width	31	69.4	64–74.3 (68.2 ± 2.6)	54	62.5–75 (70.7 ± 2.6)	71	68.3	65.9–82.2 (74.7 ± 3.1)	5	70.5–76.7 (74 ± 2.3)	<0.0001	pan<par<sm,si
Disk length	31	54.6	51.4–58.6 (55.3 ± 1.9)	54	53.8–60.7 (57.5 ± 1.6)	46	57.5	52.8–66 (58.9 ± 2.7)	5	56.6–58.1 (57.5 ± 0.6)		pan<par,si<sm,si
Snout to greatest disk width	30	30.1	23.9–37.3 (31.6 ± 3.2)	54	28.3–39 (34 ± 2.6)	44	38.1	29.9–41.9 (36.5 ± 3.2)	5	34.3–39.1 (36.3 ± 2.1)	<0.0001	pan<par,si<sm,si
Snout length	31	12.8	11.5–16 (13.6 ± 1.1)	54	12.9–17 (15 ± 1)	47	16.1	13.1–18.2 (15.6 ± 1.4)	5	13.2–15.8 (14.5 ± 1.1)		pan,si<par,si<sm,si
Head length	31	20.4	18.3–23.8 (20.8 ± 1.2)	54	19.6–24 (22.1 ± 1)	47	22.1	20.4–25.9 (23.2 ± 1.4)	5	21.4–24 (22.5 ± 1.1)		pan<par,si<sm,si
Orbit length	31	3.9	3–5.7 (4.3 ± 0.8)	54	2.6–4.8 (3.9 ± 0.5)	47	4.0	3.6–5.6 (4.5 ± 0.4)	5	4.3–5.3 (4.6 ± 0.4)		par<pan,sm,si
Orbit to spiracle length	31	5.0	4.7–6.8 (5.5 ± 0.5)	54	4.3–6.1 (5.2 ± 0.4)	47	5.3	4.4–6.4 (5.5 ± 0.4)	5	5.3–6.4 (5.8 ± 0.4)	<0.0001	par<pan,sm,si
Spiracle length	31	2.7	2.3–3.6 (2.9 ± 0.4)	54	2.1–3.5 (2.8 ± 0.3)	47	2.5	2.1–3.5 (2.9 ± 0.3)	5	2.7–3.3 (2.9 ± 0.2)		NS
Interorbital width	31	4.3	3.8–5 (4.3 ± 0.3)	54	3.9–5.7 (4.6 ± 0.4)	47	6.2	4.3–6.2 (5 ± 0.4)	5	4.6–5.1 (4.8 ± 0.2)	<0.0001	pan<par,si<sm,si
Interspiracular width	31	6.7	6.6–7.9 (7.2 ± 0.4)	54	6.3–7.8 (7.1 ± 0.4)	47	8.4	6.6–8.7 (7.6 ± 0.5)	5	7–7.6 (7.2 ± 0.2)		par,pan,si<sm
Outer spiracular width	21	11.8	11.5–13.2 (12.2 ± 0.6)	33	11–12.5 (11.8 ± 0.4)	33	12.8	10.9–13.9 (12.4 ± 0.7)	5	11.8–12.4 (12.2 ± 0.2)	<0.0001	par,si<pan,sm,si
Pretail length	31	49.5	44.2–57.1 (50 ± 3)	54	46.5–56.9 (52.6 ± 2.3)	48	52.4	47.8–58.4 (54.4 ± 2.4)	5	52.2–54.5 (53.3 ± 1.1)	<0.0001	pan<par,si<sm,si
Cloaca to 1st dorsal fin length	30	40.3	33.6–41.4 (38.4 ± 1.6)	54	31.9–41.7 (36.2 ± 2.1)	46	35.2	31–40.9 (35.1 ± 2.1)	5	34.3–39.6 (37 ± 1.9)	<0.0001	sm<si,par<pan,si
Cloaca to 2nd dorsal fin length	30	45.9	38.7–47.6 (44.1 ± 1.8)	54	37.1–47.8 (41.6 ± 2.1)	46	40.0	35.2–44.7 (39.4 ± 2.1)	5	38.4–44.2 (41.3 ± 2.1)	<0.0001	sm,si<par,si<pan
Interdorsal length	31	2.0	1.4–3.1 (2.1 ± 0.5)	54	1–3.9 (2.1 ± 0.6)	46	1.4	0.1–1.4 (0.7 ± 0.3)	5	0.5–1 (0.8 ± 0.2)	<0.0001	sm,si<par,pan
Tail length	30	52.6	44–54.1 (50.3 ± 2.3)	54	43.1–53.7 (47.7 ± 2.3)	48	46.7	41.6–50.4 (45.5 ± 2.1)	5	45.7–48.6 (47.1 ± 1)	<0.0001	sm,si<par,si<pan

continued

Table 1 (continued)

	Bathyraja panthera			*Bathyraja parmifera*		*Bathyraja smirnovi*			*Bathyraja simoterus*			
	n	Holotype	Paratypes	*n*	Material examined	*n*	Paratype	Non–type material examined	*n*	Material examined	Significance	
Caudal length	29	2.3	1.5–4.5 (2.4 ± 0.8)	54	0.8–3.5 (2.2 ± 0.5)	46	2.4	0.8–5.4 (2.5 ± 0.8)	5	2–3 (2.4 ± 0.4)		NS
Ventral snout length	31	11.2	9.6–15.1 (12.9 ± 1.3)	54	11.1–16.7 (14 ± 1.2)	46	15.2	10.8–18.2 (14.8 ± 1.6)	5	12.9–15.4 (14.1 ± 1.2)		pan,si<par,si<sm,si
Prenasal length	31	9.2	9.1–12.2 (10.7 ± 0.9)	54	10–14.9 (12 ± 1)	47	12.7	10.3–15.6 (13.1 ± 1.3)	5	10.8–13.6 (12 ± 1.2)	<0.0001	pan,si<par,si<sm
Head length at coracoid bar	31	28.1	25.2–30.3 (27.7 ± 1.4)	54	26.4–32.4 (29 ± 1.4)	46	30.1	25.6–33.1 (29.9 ± 1.9)	5	28–29 (28.6 ± 0.5)		pan,si<par,si<sm,si
Mouth width (cartilages)	31	10.8	8.1–12 (10 ± 1)	54	7.8–11.2 (9.8 ± 0.8)	46	10.3	8.3–11.6 (9.8 ± 0.6)	5	8.1–9.1 (8.8 ± 0.4)	0.0203	si<par,pan,sm
Mouth width (teeth)	22	8.0	7.1–8.8 (8.2 ± 0.4)	51	6.4–8.7 (7.5 ± 0.6)	43	5.8	5.8–9 (7.3 ± 0.8)	5	6.6–7.9 (7.1 ± 0.5)	<0.0001	par,sm,si<pan
Internarial width	31	6.6	5.8–7.6 (6.7 ± 0.4)	54	6.6–7.9 (7.2 ± 0.3)	46	7.3	6.7–8.3 (7.6 ± 0.4)	5	7–7.3 (7.1 ± 0.1)		pan<par,si<sm
Nasal curtain length	31	4.6	2.9–4.9 (4.2 ± 0.4)	54	2.6–5 (4 ± 0.5)	45	4.3	2.4–4.4 (3.4 ± 0.5)	5	2.6–4.2 (3.3 ± 0.7)	<0.0001	sm,si<par<pan
Nasal curtain width	31	9.7	7.9–10.2 (8.8 ± 0.6)	54	8.1–9.7 (8.8 ± 0.4)	44	9.2	8–10.6 (9.2 ± 0.6)	5	8.3–10 (9 ± 0.7)		NS
Gill slit 1 width	31	1.6	1–2 (1.5 ± 0.2)	54	1–2.1 (1.6 ± 0.2)	46	1.5	1.2–2.6 (1.7 ± 0.3)	5	1.6–2 (1.9 ± 0.2)	0.0015	pan<si<sm,par
Gill slit 5 width	31	1.4	0.6–1.5 (1 ± 0.3)	54	0.6–1.7 (1.1 ± 0.2)	46	1.3	0.8–1.9 (1.3 ± 0.2)	5	1.1–1.4 (1.3 ± 0.1)	<0.0001	pan<par<sm,si
Length between 1st gill slits	31	16.0	14.9–19.5 (16.8 ± 1.1)	54	15.7–18.9 (17.6 ± 0.8)	46	17.5	16.3–20.3 (18.1 ± 1.1)	5	17.8–18.2 (18 ± 0.2)		pan<par,sm<si
Length between 5th gill slits	31	11.5	9.8–14.5 (11.6 ± 1)	54	9.6–13.6 (12.1 ± 1)	46	12.8	10.3–15.4 (12.5 ± 1)	5	12–13.3 (12.6 ± 0.5)	0.0259	pan<par,si<sm,si
Anterior pelvic lobe length	31	12.2	8–14.5 (10.8 ± 1.9)	54	7.2–14.9 (10.8 ± 1.8)	46	9.6	9.4–16.5 (12.5 ± 1.8)	5	12.5–13.5 (12.9 ± 0.5)	<0.0001	par,pan<sm,si
Posterior pelvic lobe length	31	20.4	13.6–22.2 (17.3 ± 2.2)	54	14.1–22.7 (17.7 ± 1.9)	45	15.0	14.4–23 (17.2 ± 1.9)	5	15.8–19.9 (17.8 ± 1.5)		NS
Tail width at pelvic base	30	5.3	3.9–6 (5 ± 0.5)	54	3.7–6.2 (4.9 ± 0.6)	42	5.4	3.1–5.4 (4.5 ± 0.5)	5	3.9–5.7 (4.7 ± 0.7)	0.0050	sm,si<si,par,pan
Tail height at pelvic base	30	3.2	2.6–3.5 (3.1 ± 0.2)	54	2.4–3.5 (3 ± 0.3)	42	2.7	2.2–3.2 (2.8 ± 0.2)	5	2.7–4.2 (3.3 ± 0.6)		sm<si<par,pan

continued

Table 1 (continued)

	Bathyraja panthera			*Bathyraja parmifera*		*Bathyraja smirnovi*			*Bathyraja simoterus*		Significance	
	n	Holotype	Paratypes	*n*	Material examined	*n*	Paratype	Non–type material examined	*n*	Material examined		
Tail width at mid-length	30	3.2	2.4–3.7 (3.1 ± 0.3)	54	2.1–4.3 (3.1 ± 0.4)	42	3.0	1.8–3.6 (2.9 ± 0.4)	5	2–3.4 (2.8 ± 0.5)	0.0050	sm,si<(par,si),pan
Tail height at mid-length	30	2.1	1.4–2.3 (1.9 ± 0.2)	54	1.4–2.6 (1.9 ± 0.2)	42	1.5	1.4–2.1 (1.7 ± 0.2)	5	1.6–2.2 (1.8 ± 0.2)	<0.0001	sm<par,si,pan
Tail width at origin of dorsal fin 1	13	2.3	1.9–2.7 (2.2 ± 0.2)	18	1.5–2.7 (2.1 ± 0.3)	13		2–2.6 (2.3 ± 0.2)	2	1.9–2 (2 ± 0.1)		NS
Tail height at origin of dorsal fin 1	13	1.2	1.1–1.4 (1.2 ± 0.1)	18	1–1.6 (1.3 ± 0.1)	13		1–1.4 (1.2 ± 0.1)	2	1–1.2 (1.1 ± 0.1)		NS
Dorsal fin 1 length	31	3.8	2.8–4.5 (3.7 ± 0.4)	54	3–4.4 (3.6 ± 0.3)	47	3.3	2.8–4.5 (3.7 ± 0.4)	5	3.1–4 (3.6 ± 0.3)		NS
Dorsal fin 2 length	12	3.6	3–4.2 (3.5 ± 0.3)	9	2.5–3.8 (3.2 ± 0.4)	16		2.9–4.4 (3.8 ± 0.4)	5	2.3–3.8 (3.1 ± 0.6)	0.0059	si,par,pan<sm,pan
Dorsal fin 1 height	31	4.0	2.3–4.1 (3.2 ± 0.5)	54	1.8–4.3 (2.9 ± 0.6)	46	2.3	1.6–4.4 (2.8 ± 0.7)	5	2.2–3.1 (2.6 ± 0.5)		NS
Dorsal fin 1 origin to caudal-fin tip	31	11.9	9.2–14.7 (11.8 ± 1.3)	54	8.9–14.2 (11.5 ± 1.1)	47	11.6	8.4–13.4 (10.4 ± 1.1)	5	9.1–10.6 (9.8 ± 0.7)	0.0000	sm,si<par,pan
Dorsal fin 2 origin to caudal-fin tip	31	6.6	4.6–8.2 (6.2 ± 1)	54	4.3–7.8 (5.9 ± 0.7)	47	6.7	4.9–8.9 (6.2 ± 0.9)	5	5.3–5.9 (5.6 ± 0.3)		NS
Counts												
Teeth	37	27	24–31 (27.5 ± 1.8)	69	22–33 (27.3 ± 2.5)	45		18–29 (23.7 ± 2.8)	5	23–28 (26.2 ± 2)	<0.0001	sm<par,pan,si
Total vertebrae	12	127	118–129 (124.8 ± 3.2)	8	118–128 (120.8 ± 3.3)	8		118–127 (122 ± 3.7)	1	131	0.0002	par,sm<(pan,sm),si
Precaudal vertebrae	12	39	35–40 (37.8 ± 1.6)	8	32–40 (36.4 ± 2.5)	8		31–38 (34.3 ± 2.8)	1	41	0.0003	sm,(par,si)<pan, (par),si
Caudal vertebrae	13	88	81–94 (87.2 ± 3.3)	8	82–89 (84.4 ± 2.3)	8		83–96 (87.7 ± 4.5)	1	90	0.0003	par<pan, sm, si
Pectoral fin rays	13	86	82–90 (85.6 ± 2.1)	9	81–89 (84.2 ± 2.3)	8		82–92 (85.8 ± 3)	1	85		NS
Pelvic fin rays	21	23	22–27 (24.1 ± 1.6)	23	21–29 (25 ± 2.4)	8		21–26 (23.3 ± 2.1)	1	24		NS
Pseudobranchial folds	21	17	16–20 (17.7 ± 1.4)	67	14–19 (16.4 ± 1.4)	44		12–19 (15.6 ± 1.8)	4	12–19 (15.8 ± 3)	<0.0001	sm,si<par,si<pan

continued

Table 1 (continued)

	Bathyraja panthera			*Bathyraja parmifera*		*Bathyraja smirnovi*			*Bathyraja simoterus*		
	n	Holotype	Paratypes	*n*	Material examined	*n*	Paratype	Non-type material examined	*n*	Material examined	Significance
Counts (*continued*)											
Total dorsal thorns	39	34	31–42 (36.3 ± 2.4)	69	19–36 (29.7 ± 3.5)	45		20–35 (27.2 ± 3.6)	4	33–38 (36.5 ± 2.4)	<0.0001 sm<par<pan,si
Nuchal thorns	39	4	2–5 (3.5 ± 0.6)	69	1–4 (3 ± 0.7)	70	2	1–4 (2.7 ± 0.8)	5	3–4 (3.6 ± 0.5)	<0.0001 sm<par,si<pan,si
Scapular thorns	39	2	1–2 (1.4 ± 0.5)	69	1–3 (1.9 ± 0.4)	70	1	1–2 (1.1 ± 0.2)	5	1–3 (1.4 ± 0.9)	sm(si)<pan,si<par
Mid–dorsal thorns	39	7	6–10 (8 ± 1.1)	69	0–10 (6 ± 2.2)	70	0	0–4 (0.4 ± 0.8)	5	5–8 (6.4 ± 1.1)	<0.0001 sm<par,si<pan
Tail thorns	39	22	19–28 (23.1 ± 2)	69	15–23 (19.2 ± 1.8)	70	22	17–31 (24.3 ± 3.1)	5	22–28 (25.2 ± 2.6)	<0.0001 par<pan<sm,si
Interdorsal thorns	39	1	1–2 (1.7 ± 0.5)	69	1–3 (1.4 ± 0.5)	70	1	0–2 (0.5 ± 0.6)	5	1–1 (1 ± 0)	<0.0001 sm<par,si<pan

Results

Univariate statistical analysis

Among morphometric characters that met assumptions of normality, 16 characters were significantly different between at least one pair of species of *Arctoraja* (Table 1). The characters most useful to distinguish species include interdorsal length and disc width, which distinguish *B. panthera* and *B. parmifera* from *B. smirnovi* and *B. simoterus* (Fig. 2). With the exception of the orbits and spiracles, the anterior portion of the body of *B. panthera* is shorter and narrower than in *B. parmifera*, as demonstrated by significant differences in disc width, snout length, head length, prenasal length, widths of gill slits 1 and 5, and the lengths between gill slits 1 and 5. *Bathyraja panthera* also has a longer orbit and spiracle region (orbit to spiracle length) and is longer posteriorly, as we found significant differences between the tail measurements of cloaca to dorsal fin 1 length, cloaca to dorsal fin 2 length, and tail length. The anterior part of the disc of *B. panthera* is significantly shorter and wider than in both *B. smirnovi* and *B. simoterus*, while tail and interdorsal lengths are greater. The anterior disc of *B. parmifera* is shorter and narrower than *B. simoterus*, which has a greater disc width, distance from snout to greatest disc width, snout length, head length, orbit to spiracle length, gill slit 5 width, and a longer anterior pelvic lobe. *Bathyraja parmifera* has a longer interdorsal length and greater distance from the origin of dorsal fin 1 to the caudal tip. *Bathyraja parmifera* is shorter and wider in the anterior part of the body, including the orbital and spiracular region, and has a longer tail than *B. smirnovi*. The interdorsal length of *B. parmifera* is also longer. Except for slight but significant differences in disc length, interspiracular width, head length at fifth gill slit, mouth width (cartilages), internarial length, dorsal-fin 2 length, and length from dorsal-fin 2 origin to caudal tip, body shape was not significantly different between *B. smirnovi* and *B. simoterus*.

Among meristic characters (Tables 2 and 3), *Bathyraja panthera* has a higher number of thorns in all series, except scapular, and a higher number of total vertebrae than *B. parmifera*. Counts of mid-dorsal and interdorsal thorns are also higher in *B. panthera* than in *B. simoterus*. Counts of all thorns, except for tail thorns, are greater in *B. panthera* than in *B. smirnovi*. Higher counts of scapular thorns are found in *B. parmifera*, while *B. simoterus* has a greater total number of vertebrae, total thorns, and tail

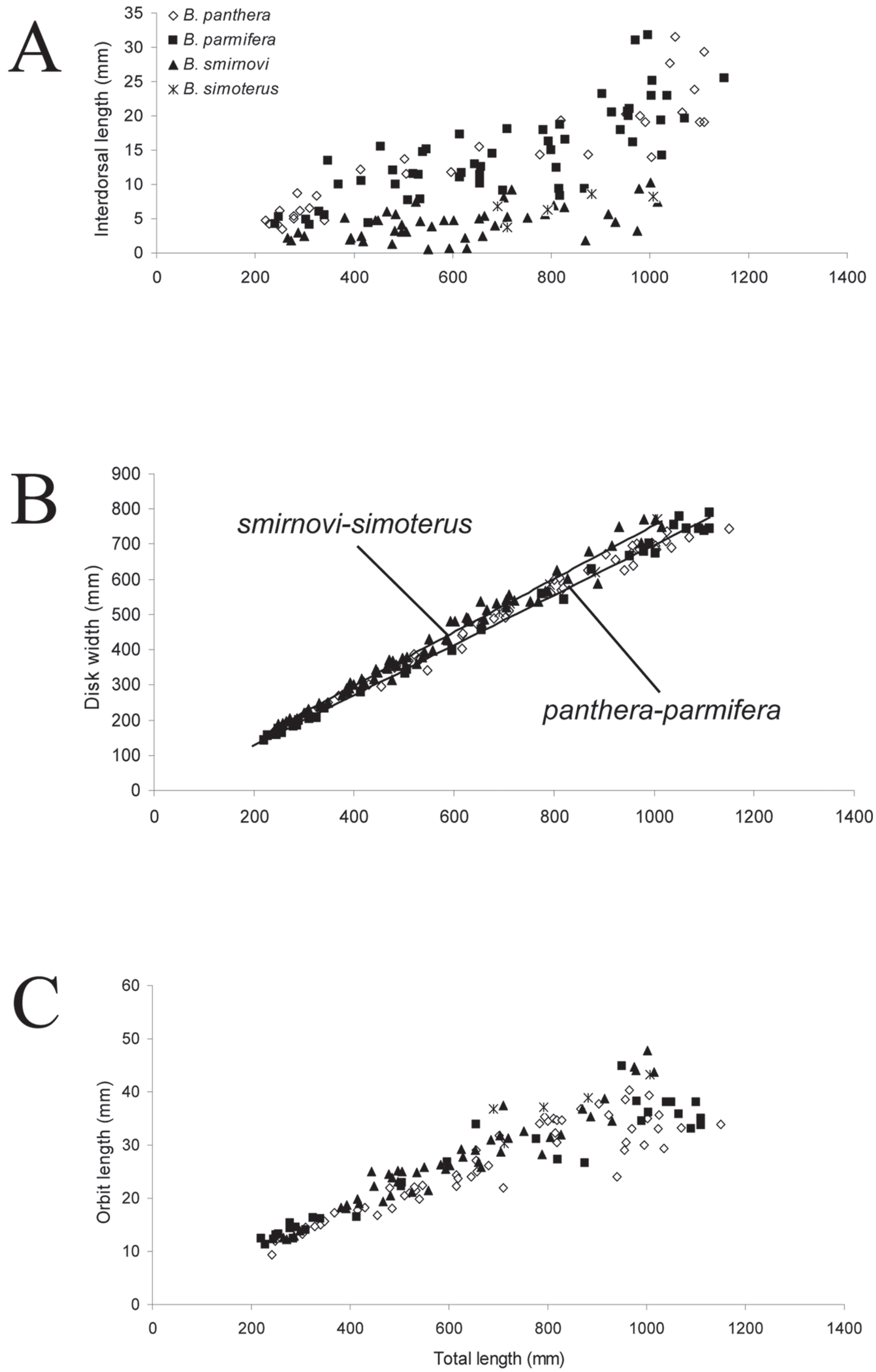

Figure 2

Plots of (A) interdorsal length, (B) disc width, and (C) orbit length versus total length of species of *Arctoraja*: *Bathyraja panthera* n. sp. (square), *B. parmifera* (diamond), *B. smirnovi* (triangle), and *B. simoterus* (star).

thorns. *Bathyraja parmifera* has a higher mean number of all dorsal thorns, except for those on the tail, than *B. smirnovi*. Counts of total and precaudal vertebrae and total dorsal, nuchal, middorsal, and interdorsal thorns are all significantly higher in *B. simoterus* than in *B. smirnovi*.

Table 2

Counts of total dorsal thorns, nuchal thorns, scapular thorns, mid-dorsal thorns, tail thorns, and interdorsal thorns of species of the subgenus *Arctoraja* of *Bathyraja*.

	Total dorsal thorns																								
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	*n*
B. parmifera	1		1	1	1	3	1	4	2	6	6	12	8	10	6	4	1	2							69
B. panthera													1		3	6	6	7	4	5	3	2	1	1	39
B. smirnovi		2	1	1	6	4	7	5	7	5	9	6	4	5	3	2	2	1							70
B. simoterus															1		1		1	2					5

	Nuchal thorns					
	1	2	3	4	5	*n*
B. parmifera	1	13	38	17		69
B. panthera		1	18	19	1	39
B. smirnovi	4	25	32	9		70
B. simoterus			2	3		5

	Scapular thorns			
	1	2	3	*n*
B. parmifera	10	57	2	69
B. panthera	22	17		39
B. smirnovi	66	4		70
B. simoterus	4		1	5

	Mid-dorsal thorns											
	0	1	2	3	4	5	6	7	8	9	10	*n*
B. parmifera	4	2	1	2	1	4	18	26	8	2	1	69
B. panthera							3	9	16	7	4	39
B. smirnovi	54	8	6	1	1							70
B. simoterus						1	2	1	1			5

	Tail thorns																	
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	*n*
B. parmifera	1	5	4	9	24	9	10	5	2									69
B. panthera					1	3	3	9	9	6	4		3	1				39
B. smirnovi			1	2	2	2	6	7	5	10	12	6	4	7	3	2	1	70
B. simoterus								1	1			1	1	1				5

	Interdorsal thorns				
	0	1	2	3	*n*
B. parmifera		40	28	1	69
B. panthera		13	26		39
B. smirnovi	40	28	2		70
B. simoterus		5			5

Table 3

Counts of total vertebrae, precaudal vertebrae, caudal vertebrae, pectoral-fin rays, and pelvic-fin rays of species of the subgenus *Arctoraja* of *Bathyraja*.

	Total vertebrae																	
	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	*n*
B. parmifera	1	1	1	2	4	1	5	3		3			1	1				23
B. panthera				1			1	3	4	2	3	1	3	2	2			22
B. smirnovi				2			1		1		1		1					6
B. simoterus																	1	1

	Precaudal vertebrae										
	31	32	33	35	36	37	38	39	40	41	*n*
B. parmifera		1		3	1	5	4	7	2		23
B. panthera				1	1	8	3	4	4	1	22
B. smirnovi	1	1	1	1		1	1				6
B. simoterus										1	1

	Caudal vertebrae																
	78	79	80	81	82	83	84	85	86	87	88	89	90	91	94	96	*n*
B. parmifera	1	2	1	1	4	1	6	3	2	1		1					23
B. panthera				1		1	1	4	4	5	4		1	1	1		23
B. smirnovi						1		1	1	1		1				1	6
B. simoterus													1				1

	Pectoral-fin rays												
	81	82	83	84	85	86	87	88	89	90	91	92	*n*
B. parmifera	1		5	4	3	3	4	1	2				23
B. panthera		1	1	2	2	6	5	2		2			21
B. smirnovi		1		1	4			1				1	8
B. simoterus					1								1

	Pelvic-fin rays										
	20	21	22	23	24	25	26	27	28	29	*n*
B. parmifera	1	1	3	3	2	5	3	2	1	3	24
B. panthera			1	10	5	1	2	3			22
B. smirnovi		1		1	2	3	1				8
B. simoterus						1					1

Multivariate statistical analysis

Plots of scores from a PCA of 30 specimens of *Arctoraja* with all meristic characters and the greatest number of morphometric characters available for those individuals revealed strong differences in meristic characters among all species, as well as morphometric characters useful for discrimination (Fig. 3). In the meristic PCA, PC1 explained 36.7% of total variation and was heavily loaded on thorn counts (middorsal, nuchal, interdorsal, and total thorns); PC2 explained 20.6%, being heavily loaded on caudal and total vertebrae, tail thorns, and scapular thorns (Table 4). Plotting scores of PC1 against PC2 separated all four species into distinct clusters (Fig. 3A). *Bathyraja panthera* was well separated from both *B. parmifera* and *B. smirnovi* along the PC1 axis, completely separated from *B. simoterus,* and nearly completely separated from *B. smirnovi* on the PC2 axis; *B. parmifera* was also well separated from *B. simoterus* on both the PC1 and PC2 axes and from *B. smirnovi* on the PC2 axis.

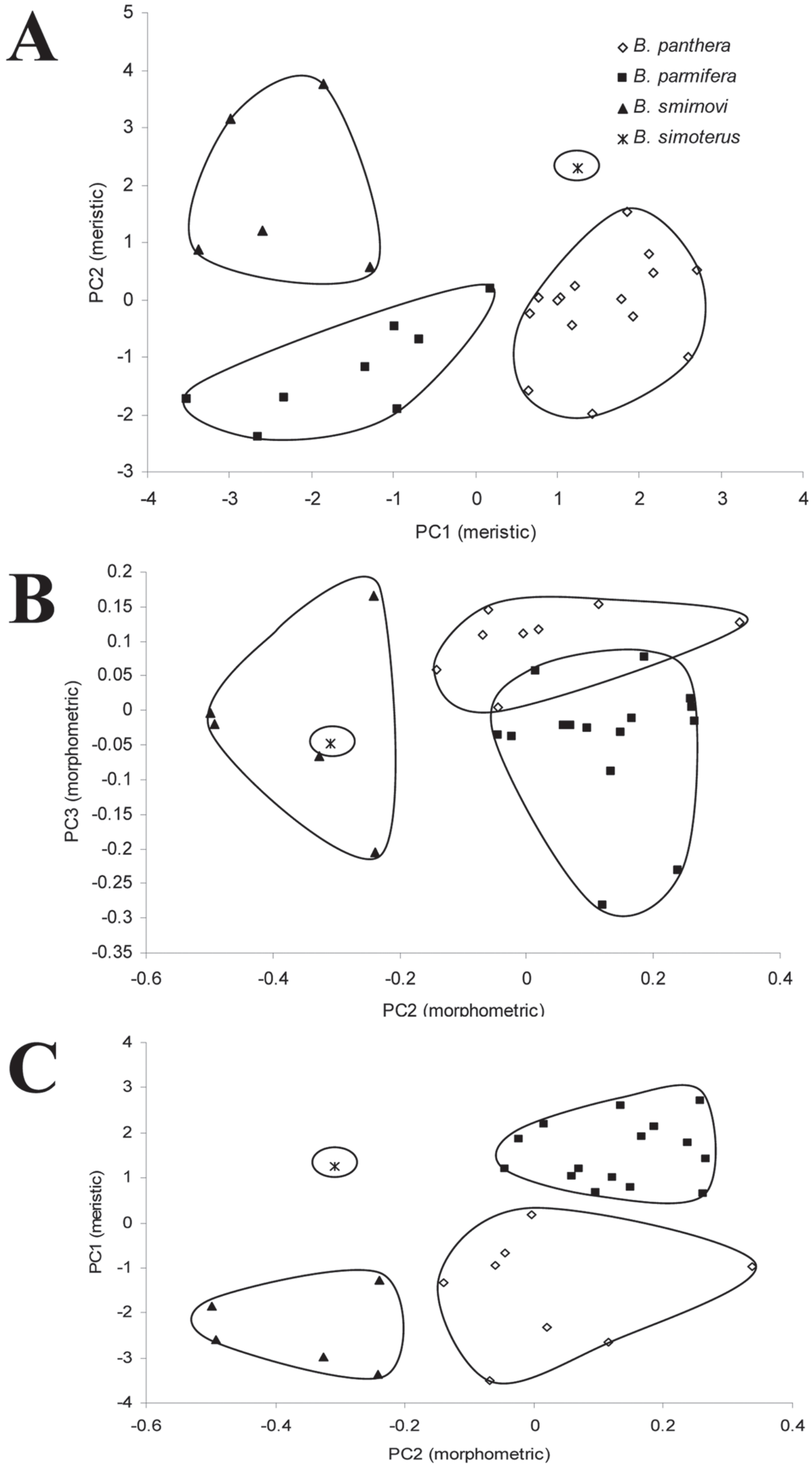

Figure 3

Plots of principal component (PC) scores for morphometric and meristic characters for individuals of species of *Arctoraja* for which all data were available: *Bathyraja panthera* n. sp. (square), *B. parmifera* (diamond), *B. smirnovi* (triangle), and *B. simoterus* (star). (A) Meristic characters only, (B) morphometric characters only, and (C) meristic (PC1) versus morphometric characters (PC2).

Table 4

Factor loadings for principal component (PC) analysis of meristic characters, including vertebrae, of species of *Arctoraja* from specimens examined having all characters used for multivariate analyses.

	PC1	PC2	PC3
Teeth	0.3255	0.0532	0.1799
Precaudal vertebrae	0.2773	–0.2158	–0.4934
Caudal vertebrae	0.1281	0.5841	–0.2703
Nuchal thorns	0.3348	–0.0055	0.3728
Scapular thorns	0.1145	–0.3815	–0.0424
Mid-dorsal thorns	0.4882	–0.1558	–0.0103
Tail thorns	–0.0324	0.5153	0.3772
Interdorsal thorns	0.3744	–0.1522	0.0697
Total dorsal thorns	0.4672	0.1306	0.2833
Total vertebrae	0.2787	0.3659	–0.5319

Bathyraja smirnovi and *B. simoterus* were separated on the PC1 axis.

In the morphometric PCA, all characters were positively loaded on PC1 (the size component; Table 5), which explained 93.0% of total variation. Among the shape components, PC2 explained 5.4%, being heavily loaded on interdorsal length, fifth gill slit width, and the length of the anterior pelvic-fin lobe; PC3 explained 2.3% and was heavily loaded on caudal-fin length and distances from dorsal-fin 2 and dorsal-fin 1 to caudal-fin tip (Table 5). In the plot of scores of morphometric PC2 vs. PC3 (Fig. 3B), two clusters separated primarily on the basis of interdorsal length were formed on the PC2 axis: one of *B. panthera* and *B. parmifera*, a second of *B. smirnovi* and *B. simoterus*. Plotting PC1 of the meristic PCA against PC2 of the morphometric PCA resulted in a complete separation of all species (Fig. 3C), as did the three-dimensional plot of scores of meristic PC1, meristic PC2, and morphometric PC2 (Fig. 4).

Although analyses of the few specimens with vertebral counts provided convincing evidence of species-level distinctions among the four species, we also analyzed a dataset of 122 specimens for which we had data for most morphometric and meristic characters. These analyses also revealed strong differences in meristic characters among all species and several morphometric characters useful for discrimination (Fig. 5). In the meristic PCA, PC1 explained 43.5% of total variation and was heavily loaded on middorsal and interdorsal thorns, teeth, and scapular thorns; PC2 explained 16.6%, being heavily loaded on tail, nuchal, and scapular thorns (Table 6). Plotting scores of PC1 against PC2 resulted in a nearly complete separation of *B. smirnovi* from the other three species on the PC1 axis; *B. panthera* and *B. parmifera* exhibited no separation on PC1

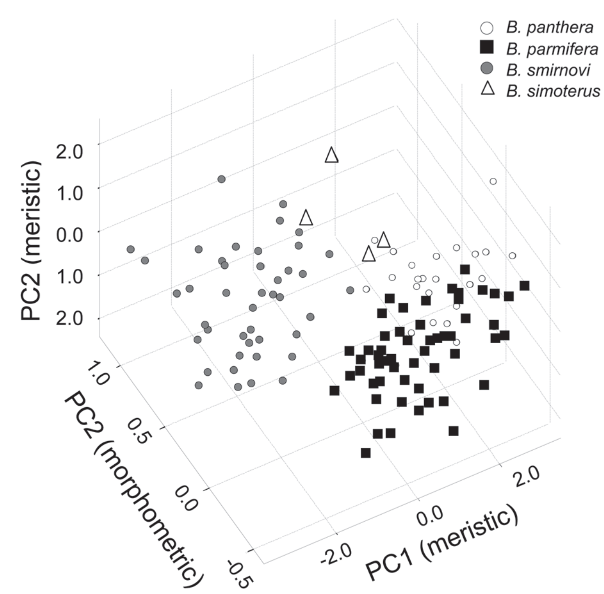

Figure 4

Three-dimensional plot of principal component (PC) scores for morphometric and meristic characters for individuals of species of *Arctoraja* for which all data were available: *Bathyraja panthera* n. sp. (open circle), *B. parmifera* (square), *B. smirnovi* (filled circle), and *B. simoterus* (triangle).

but only narrowly overlapped on the PC2 axis; and the cluster representing *B. simoterus* was widely separated from *B. parmifera* but nearly completely overlapped by the *B. panthera* cluster.

In the morphometric PCA, all characters were positively loaded on PC1, the size component, which explained 86.8% of total variation (Table 7). The first shape component, PC2, explained 9.0% of total variation, was negatively loaded on interdorsal width, and positively loaded on the width of gill slit 5, anterior pectoral lobe length, and prenasal length. The second shape component, PC3, explained an additional 1.4% of total variation. It was negatively loaded on dorsal-fin 1 height and anterior pectoral lobe length and positively loaded on prenasal length. Plotting scores of PC2 against PC3 produced a nearly complete separation between a cluster of the eastern North Pacific species (*B. parmifera* + *B. panthera*) and a cluster of the western North Pacific species (*B. smirnovi* + *B. simoterus*) on PC2. All species clusters nearly completely overlapped on the PC3 axis.

Plotting scores of meristic PC1 against morphometric PC2 (Fig. 5C) produced a cluster representing *B. smirnovi* completely separated from the cluster of *B. parmifera* + *B. panthera* together and narrowly overlapping with the cluster of *B. simoterus*. The cluster of *B.*

Table 5

Factor loadings for principal component (PC) analysis of morphometric characters of species of *Arctoraja* from specimens examined having all characters used for multivariate analyses, including vertebrae.

	PC1	PC2	PC3	PC4
Total length	0.1564	–0.0034	–0.0277	0.0202
Disk width	0.1666	–0.0642	0.0323	0.0185
Disk length	0.1665	–0.0352	0.0766	0.0111
Snout to greatest disk width	0.1659	–0.0845	0.0533	–0.0072
Snout length	0.1747	–0.0275	0.2526	0.0376
Head length	0.1692	–0.0537	0.1518	–0.0312
Orbit length	0.1292	–0.0240	–0.0471	–0.1766
Orbit to spiracle length	0.1451	–0.0070	–0.0735	–0.1732
Spiracle length	0.1760	–0.0125	0.0715	–0.0615
Interorbital width	0.1609	–0.0192	0.0205	0.1342
Interspiracular width	0.1471	0.0016	–0.0150	0.0609
Pretail length	0.1755	–0.0294	0.1126	–0.0103
Cloaca to 1st dorsal fin length	0.1481	–0.0039	–0.1302	–0.0193
Cloaca to 2nd dorsal fin length	0.1483	0.0346	–0.1189	–0.0224
Interdorsal length	0.1655	0.8711	0.1151	–0.0587
Tail length	0.1440	0.0346	–0.1428	0.0350
Ventral snout length	0.1625	–0.0431	0.3305	0.0241
Prenasal length	0.1638	–0.1003	0.2893	0.0971
Head length at coracoid bar	0.1738	–0.0160	0.1637	0.0283
Mouth width (cartilages)	0.1727	0.0576	0.1033	0.0761
Internarial width	0.1623	–0.0548	0.0753	–0.0122
Nasal curtain length	0.1488	0.1084	0.0220	0.1061
Nasal curtain width	0.1679	–0.0028	0.0293	0.0352
Gill slit 1 width	0.2015	–0.1042	0.1601	–0.2748
Gill slit 5 width	0.2254	–0.2921	0.0228	0.2618
Length between 1st gill slits	0.1663	–0.0079	0.0530	0.0449
Length between 5th gill slits	0.1753	–0.0309	0.0834	0.0080
Anterior pelvic lobe length	0.1640	–0.1824	–0.2449	–0.2604
Posterior pelvic lobe length	0.1737	–0.0165	–0.0808	–0.0732
Tail width at pelvic base	0.1577	0.0798	–0.0431	0.1203
Tail height at pelvic base	0.1592	0.0239	–0.0944	0.0029
Tail width at mid-length	0.1613	0.0300	0.0079	–0.0107
Tail height at mid-length	0.1556	–0.0298	–0.3432	0.2585
Dorsal fin 1 length	0.1322	0.0188	–0.1195	–0.0371
Dorsal fin 1 height	0.1780	0.1106	–0.3247	–0.4433
Dorsal fin 1 origin to caudal-fin tip	0.1278	0.1412	–0.2038	0.2608
Dorsal fin 2 origin to caudal-fin tip	0.1150	0.0241	–0.3689	0.4598

simoterus was completely separated from the cluster of *B. parmifera* + *B. panthera*.

Genetic analysis

Within a 557 base-pair segment of COI (see Table 1 of Spies et al., 2011), the new species *B. panthera* possesses a unique COI haplotype differing in at least two base pairs from all other species and known haplotypes of *Arctoraja*, as well as all other species of Rajidae examined. *Bathyraja parmifera* exhibits two haplotypes, but only the most common is known to be represented in specimens examined morphologically. The two western Pacific species, *B. smirnovi* and *B. simoterus*, have identical COI sequences. Together the two are distinguished from both *B. panthera* and *B. parmifera* at no fewer than five nucleotide positions.

Systematics

Bathyraja subgenus *Arctoraja* (Ishiyama, 1958)

Breviraja subgenus *Arctoraja* Ishiyama, 1958a:337 (type species *Raja smirnovi* Soldatov and Pavlenko, 1915).

Constituent species. The following four species are assigned to *Bathyraja (Arctoraja):*

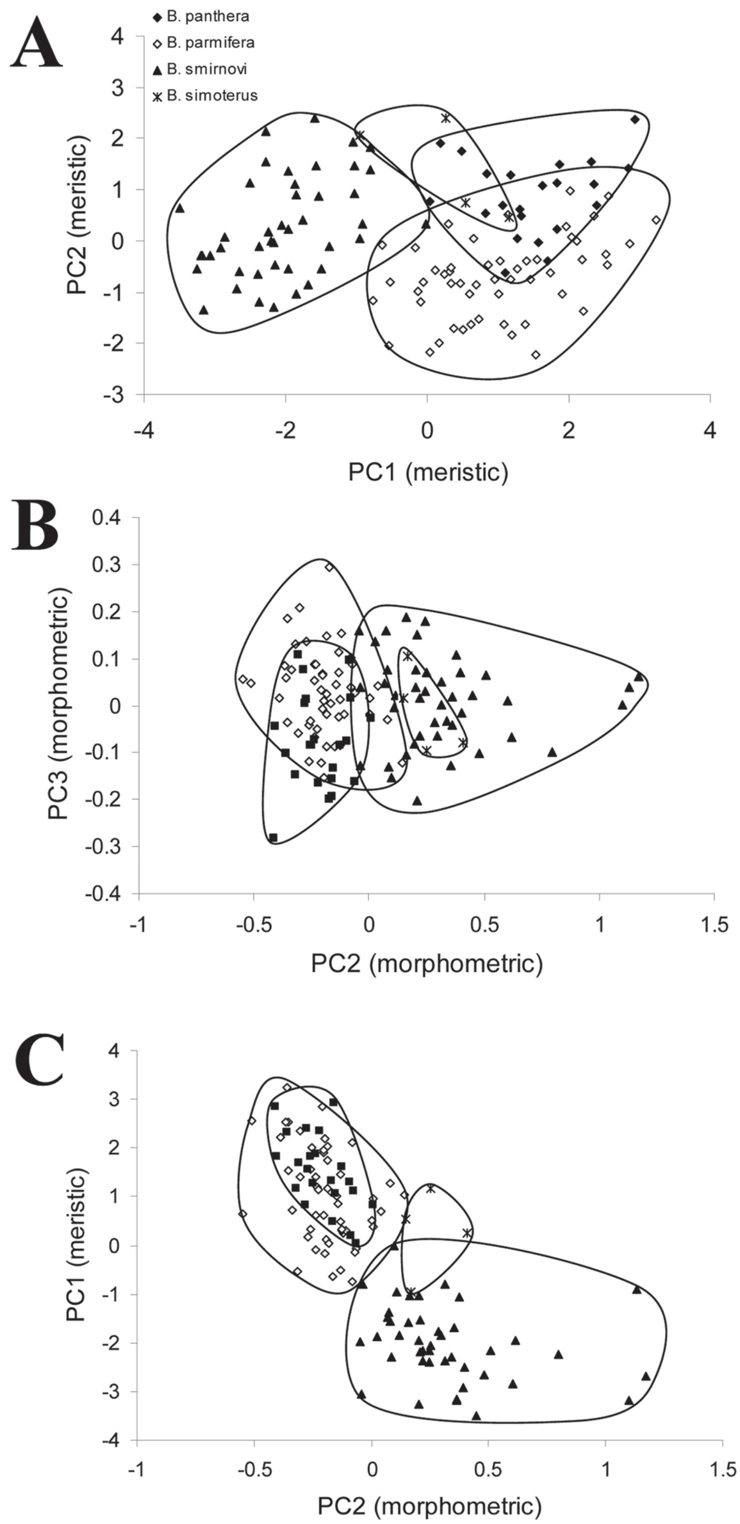

Figure 5

Plots of principal component (PC) scores for morphometric and meristic characters for maximum numbers of individuals examined of species of *Arctoraja* for which most data were available: *Bathyraja panthera* n. sp. (square), *B. parmifera* (diamond), *B. smirnovi* (triangle), and *B. simoterus* (star). (A) Meristic characters only, (B) morphometric characters only, and (C) meristic (PC1) versus morphometric characters (PC2).

Table 6

Factor loadings for principal component (PC) analysis of meristic characters of species of *Arctoraja* for specimens examined having all characters, except vertebrae, used for multivariate analyses.

	PC1	PC2	PC3
Teeth	0.4302	0.1293	–0.2358
Nuchal thorns	0.3086	0.5284	–0.1670
Scapular thorns	0.3720	–0.3618	–0.2057
Mid-dorsal thorns	0.4925	0.0141	–0.0498
Tail thorns	–0.2360	0.7339	–0.1409
Interdorsal thorns	0.4573	0.0805	–0.0646
Pseudobranchial folds	0.2719	0.1668	0.9207

Table 7

Factor loadings for principal component (PC) analysis of morphometric characters of species of *Arctoraja* for specimens examined having all characters, except vertebrae, used for multivariate analyses.

	PC1	PC2	PC3
Total length	0.1784	0.0161	–0.0504
Disk width	0.1778	0.0655	–0.0262
Disk length	0.1779	0.0439	–0.0523
Snout length	0.1694	0.0598	–0.1626
Head length	0.1710	0.0592	–0.0794
Orbit length	0.1386	0.0777	0.0297
Orbit to spiracle length	0.1634	0.0453	0.0226
Spiracle length	0.1931	0.0322	–0.0332
Interorbital width	0.1793	0.0685	–0.1416
Interspiracular width	0.1690	0.0564	–0.0582
Pretail length	0.1847	0.0506	–0.0802
Cloaca to 1st dorsal-fin length	0.1778	–0.0097	–0.0262
Cloaca to 2nd dorsal-fin length	0.1785	–0.0288	–0.0285
Interdorsal length	0.2204	–0.9451	–0.0786
Tail length	0.1751	–0.0266	–0.0299
Ventral snout length	0.1512	0.0562	–0.1711
Prenasal length	0.1574	0.0802	–0.1925
Head length at coracoid bar	0.1762	0.0472	–0.0760
Mouth width (cartilages)	0.1780	0.0067	–0.0589
Internarial width	0.1774	0.0687	–0.0830
Gill slit 1 width	0.2063	0.0570	–0.0355
Gill slit 5 width	0.2094	0.1650	–0.0682
Length between 1st gill slits	0.1798	0.0545	–0.0900
Length between 5th gill slits	0.1764	0.0580	–0.1495
Anterior pelvic lobe length	0.1588	0.1031	0.1509
Posterior pelvic lobe length	0.2020	0.0256	0.1037
Dorsal fin 1 length	0.1676	0.0277	0.0552
Dorsal fin 1 height	0.2102	–0.0028	0.6176
Dorsal fin 1 origin to caudal-fin tip	0.1670	–0.0807	–0.0420
Dorsal fin 2 origin to caudal-fin tip	0.1556	0.0063	–0.0176

Bathyraja panthera n. sp., *Bathyraja parmifera* (Bean, 1881), *B. smirnovi* (Soldatov and Pavlenko, 1915), and *B. simoterus* (Ishiyama, 1967).

Diagnosis. Species of *Bathyraja* with large maximum body size (>1000 mm TL), moderately long, blunt snouts (11–16% TL; 58–75% head length), and short tails that are much shorter than disc width (50–80% DW) (Figs. 6–9). Dorsal surface with coarse, broad-based, stellate denticles concentrated along anterior pectoral margins, anterior snout, along mid-disc, and in more or less regular rows along lateral margins of tail, with smaller denticles sparsely scattered over base of pectoral fin; midline of tail at base of thorns naked; interorbital area sparsely covered with coarse denticles. Ventrum naked, except for occasional small denticles on tip of snout. Orbital thornlets present along medial rim of orbits. Nuchal, scapular, and tail thorns large and strong; middorsal thorns absent or present, strong when present; thorns often strongly recurved at the tip. Claspers large with blunt tip; pseudosiphon 1 well developed, projection (= funnel of Ishiyama, 1958a; see Hulley, 1972) present, completely enclosed within glans; distal tip of axial flattened, dorsal terminal 1 well developed with medio-proximal shelf, dorsal terminal 2 forming strongly lobed ridge, bearing 4–5 hooked denticles (= "scales" of Ishiyama, 1958a) on dorsal surface. Vertebral counts high, total vertebrae 118–131 (precaudal vertebrae 31–41, caudal vertebrae 81–96). Ventrum pale, with few scattered gray blotches. Intestinal valves 11–13 (Ishiyama, 1967). Electric organ large, occupying distal half of tail (Ishiyama, 1967). Egg-capsule (Fig. 10) with wide keels, tapering horns, and a surface of smooth low ridges. The subgenus is united by at least five base positions in COI that differ from the 15 species of *Bathyraja* and one species of *Rhinoraja* from the North Pacific Ocean examined (Spies et al., 2011).

Description. Body moderately large (maximum length 139 cm TL; Stevenson et al., 2007). Disc 1.1–1.4 times as broad as long; maximum angle in front of spiracles about 130° in juveniles, about 120° in adults; snout tip usually strongly produced, anterior margin slightly convex to orbital region, straight to slightly concave to mid-nuchal region, concave to maximum disc width, lateral corners of disc abruptly rounded, posterior margin slightly convex. Mature males scalloped along anterior margin from level of orbits to nuchal region. Mature females more robust than mature males. Axis of greatest width 0.5–0.7 times distance from tip of snout to posterior tip of pectorals. Pelvic fins moderately incised; anterior lobe narrow to moderate and long, length 0.4–0.9 times posterior lobe. Tail short, length of tail from posterior margin of cloaca to tip 0.7–1.2 times distance from tip of snout to posterior margin

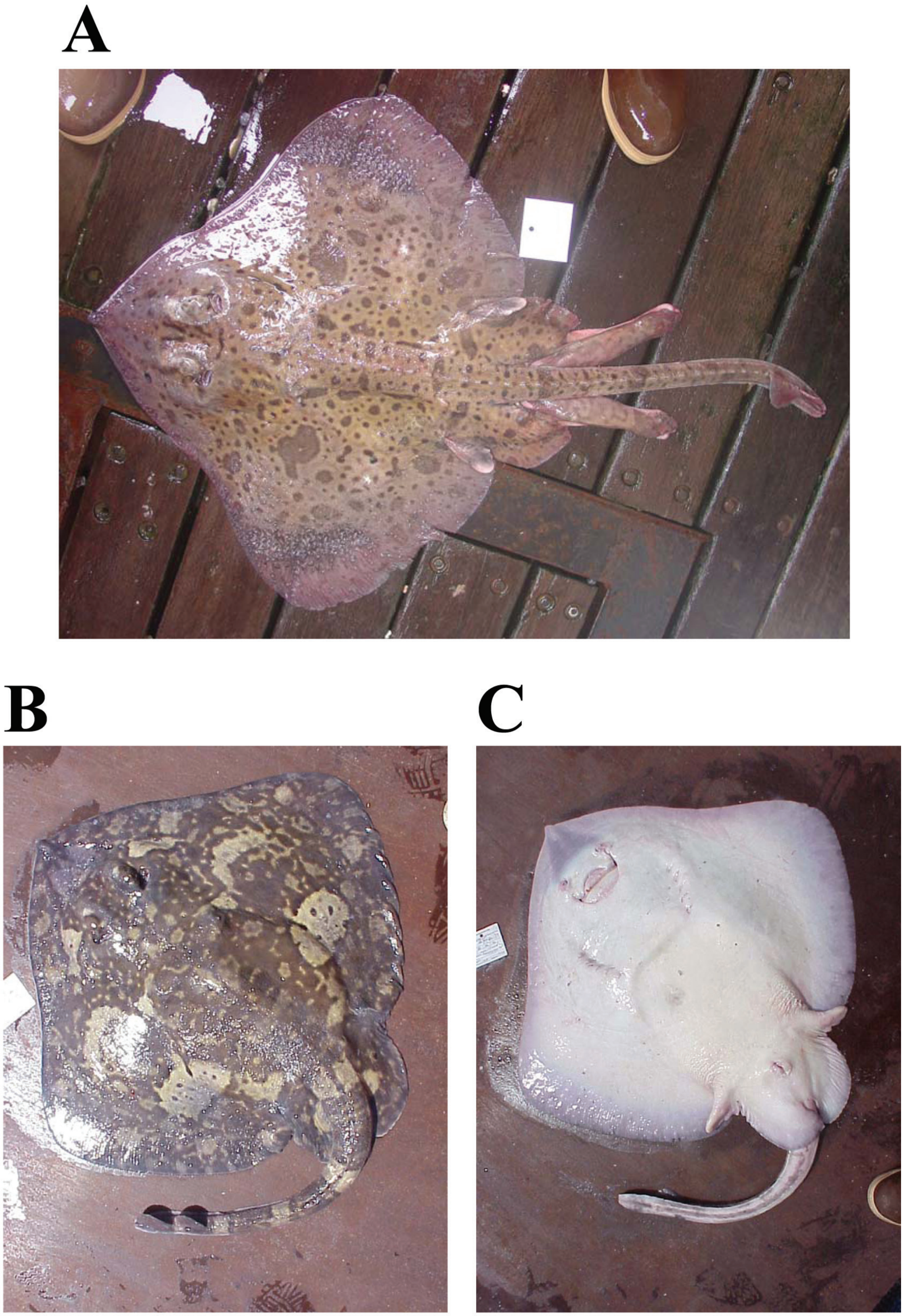

Figure 6

Bathyraja panthera n. sp.: (A) UW 116980, holotype, live male, 1003 mm TL; (B) UW 111889, paratype, live female, 1100 mm TL, dorsal view, and (C) ventral view.

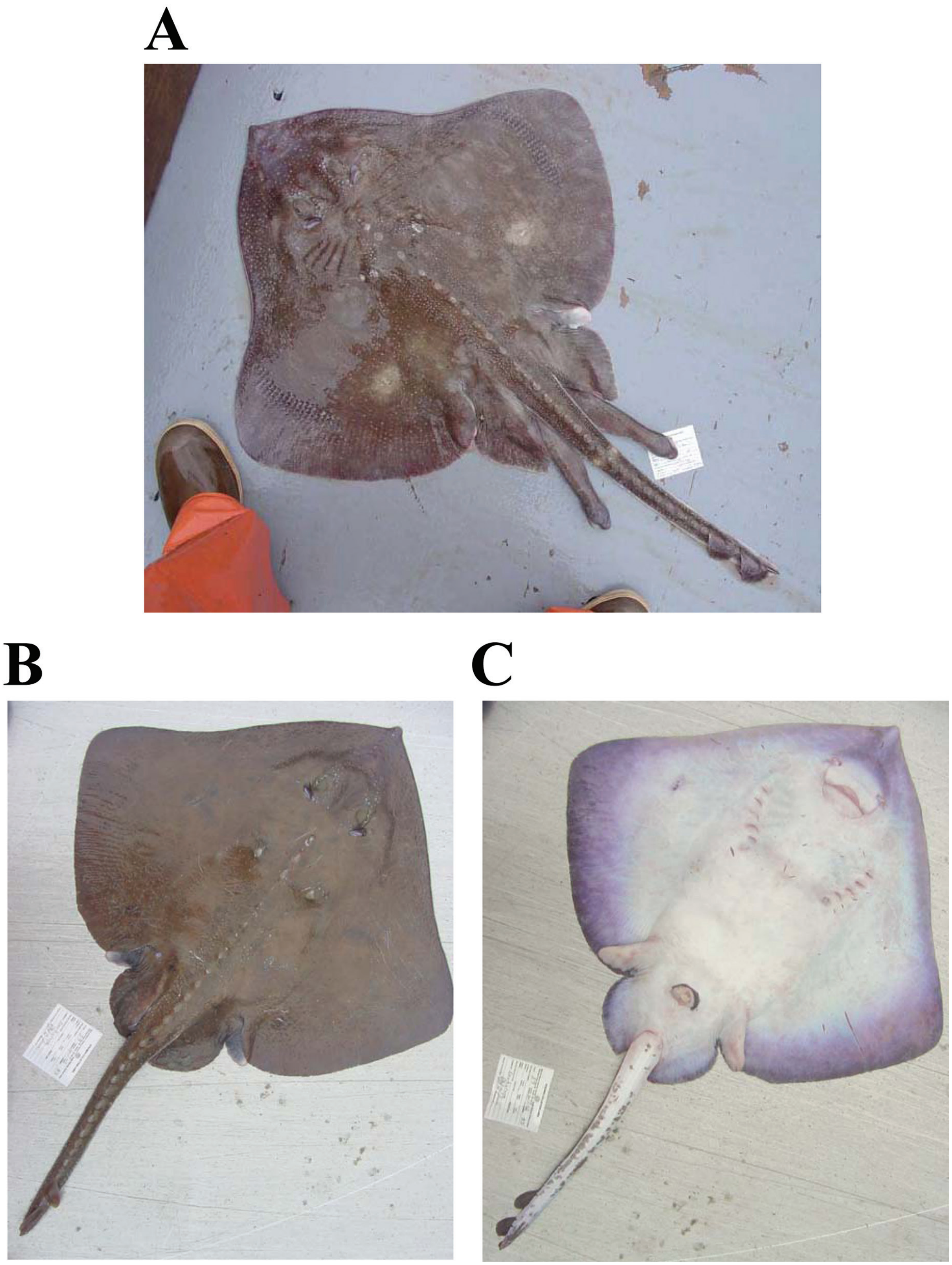

Figure 7

Bathyraja parmifera: (A) UW 113475, live male, 1023 mm TL; (B) live female, ca. 710 mm TL, dorsal view, and (C) ventral view. Female captured at 60.38°N, 178.65°W, 295 m depth, and released at sea.

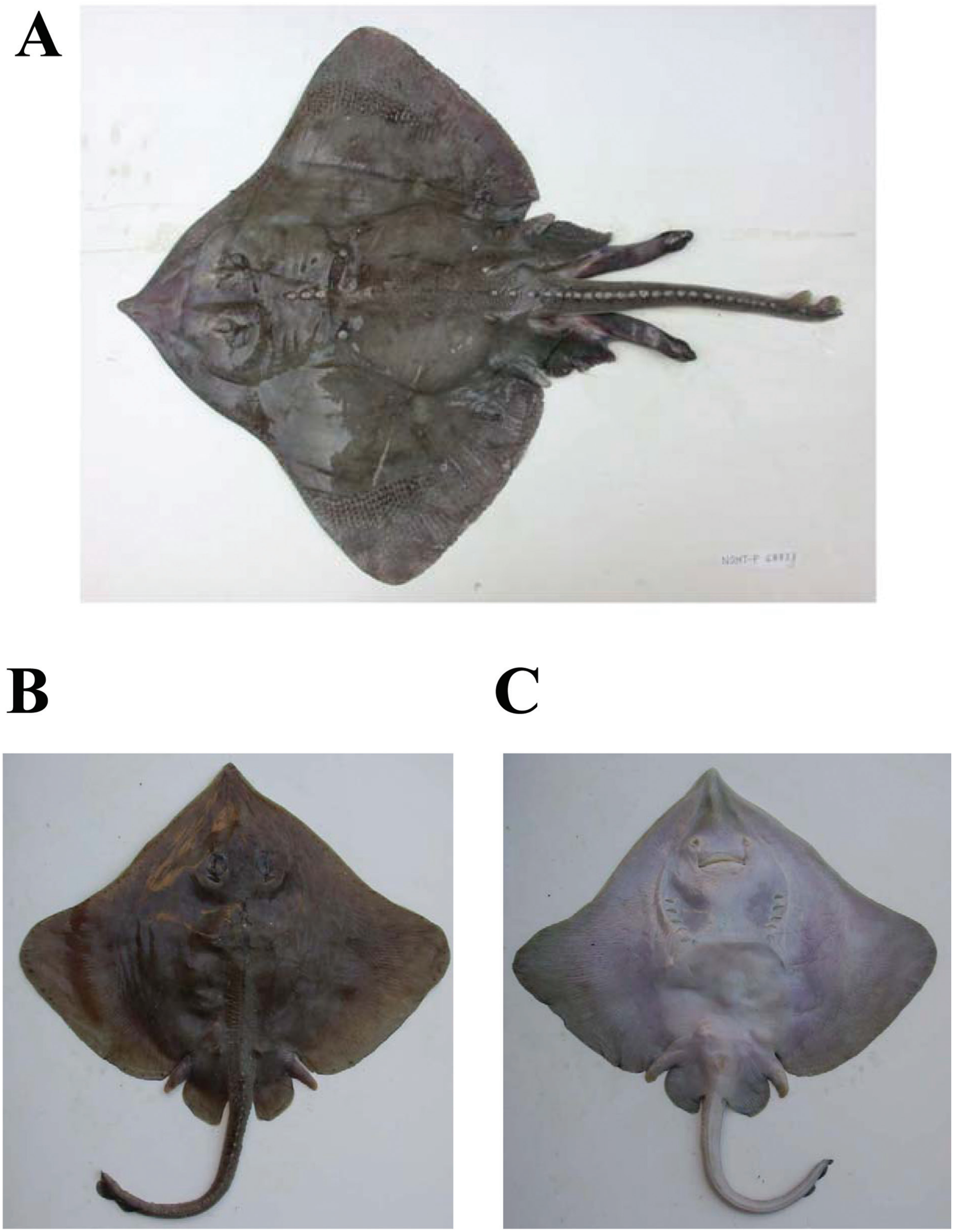

Figure 8

Bathyraja smirnovi: (A) NSMT-P 68833, live male, 979 mm TL; (B) NSMT-P 76122, live female, 478 mm TL, dorsal view, and (C) ventral view.

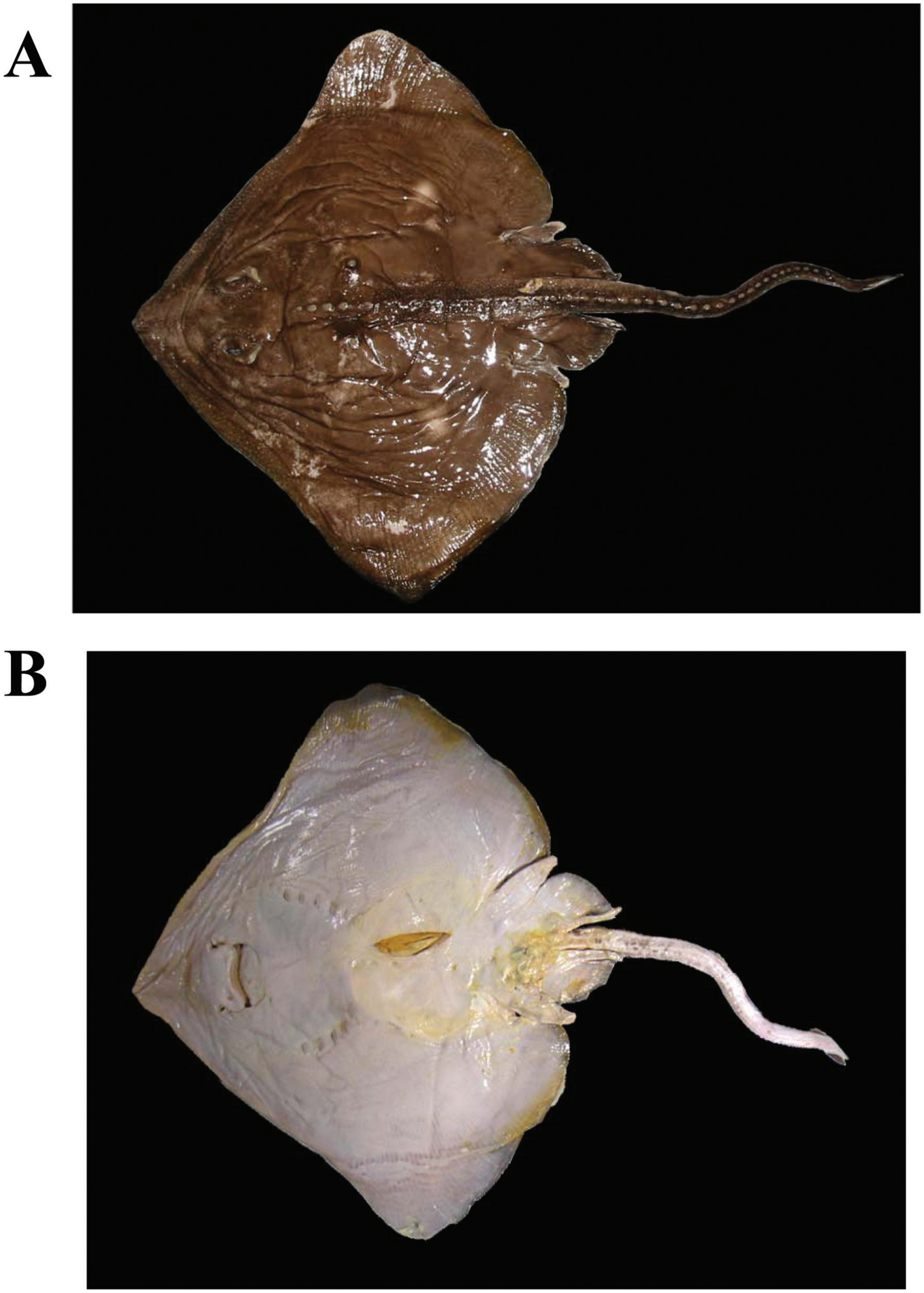

Figure 9
Bathyraja simoterus: (A) HUMZ 143347, preserved male, 711 mm TL, dorsal view, and (B) ventral view.

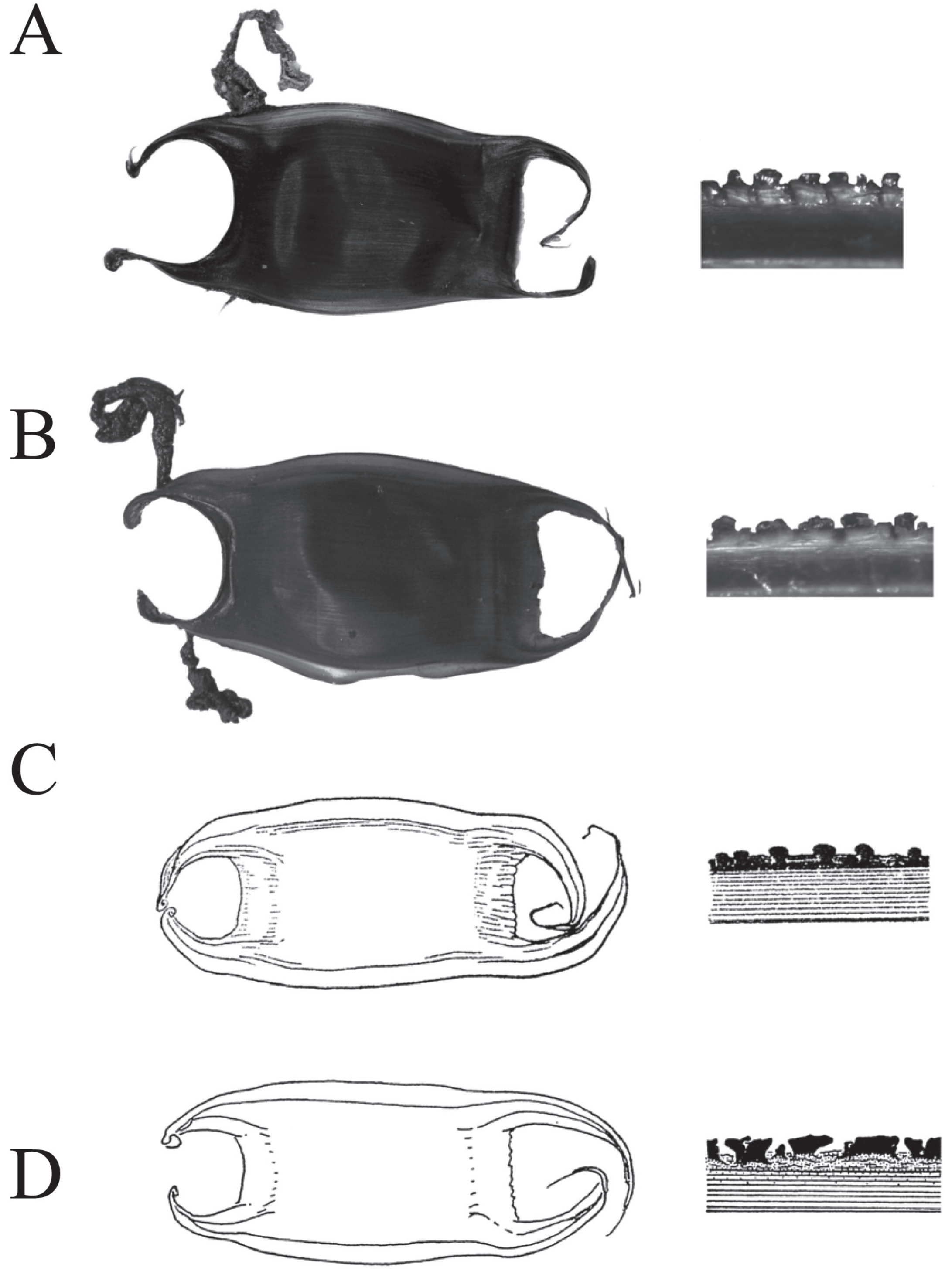

Figure 10

Whole egg capsules and cross sections of the dorsal longitudinal ridges of egg capsules of species of subgenus *Arctoraja*: (A) *Bathyraja panthera* n. sp., TCWC 12056.02, 130 mm CL; (B) *B. parmifera*, UW 119315, 130 mm CL; (C) *B. smirnovi*, ca. 125 mm CL (after Ishiyama, 1958b); (D) *B. simoterus*, ca. 125 mm CL (after Ishiyama, 1967).

of cloaca. Tail moderately depressed, with lateral fold along ventrolateral surface originating at base of tail to three-quarters length of tail and running to caudal tip. Caudal fin length greater than one-half base of second dorsal fin.

Preorbital snout length 2.2–5.9 times orbital length and 2.6–4.1 times interorbital width; preoral snout length 1.4–2.4 times internarial distance. Interorbital distance 0.7–1.7 times orbit length; orbit length 0.9–2.3 times spiracle length. Anterior nasal flap laterally expanded and moderately notched with moderate triangular process at posterior border of nostril; posterior nasal flap coarsely fringed and weakly developed. Mouth width 11.0–17.5% of disc width. Upper and lower jaws slightly arched. Teeth in 18–33 rows, with short pointed, recurved cusps extending from round base and in quincunx arrangement in both sexes, larger and more widely spaced in males. Pseudobranchial folds 12–20.

Distance between first gill slits 2.1–2.9 times internarial distance; length of first gill slits1.0–2.4 times length of fifth gill slits. First dorsal fin approximately equal in size and shape to second; interdorsal length narrow to wide, 2–110% of first dorsal-fin base; second dorsal fin separated from moderately well-developed epichordal lobe of caudal fin.

Dorsal surface with coarse, broad-based, stellate denticles concentrated along anterior pectoral margins, anterior snout, mid-disc, and lateral margins of the tail, with smaller denticles sparsely scattered over base of pectoral fin; midline of tail at base of thorns naked; denticles on sides of tail aligned in more or less defined rows; interorbital area sparsely covered with coarse denticles; denticles with stellate bases and posteriorly directed recurved spines. Ventrum naked, except for occasional small denticles on snout tip. Orbital thornlets lining anterior and posterior rims of orbits. Disc with strong thorns: nuchal thorns 1–5, scapular thorns 1–3, middorsal thorns absent or present, when present 1–10, tail thorns 15–31, interdorsal thorns present or absent, when present 1–3.

Neurocranium relatively short and broad, width about equal to nasobasal length, total cranial length about twice its width (Figs. 11–13, Table 8). Rostral cartilage with slender, flexible, unsegmented shaft, length about equal to nasobasal length; rostral appendices narrow, poorly calcified, separated from rostrum for about 30% appendix length, appendix length about 30% of rostrum length; rostral base somewhat broad, width about 30% of rostrum length. Dorsal fontanelles one or two. Interorbital width about 35% nasobasal length, least width of basal plate about 25% nasobasal width. Postorbital region of cranium moderately broad, width across otic capsules about 50% nasobasal length.

Scapulocoracoid an elongate rectangle in lateral view, height greatest anteriorly and decreasing slightly posteriorly, height about 75% length (Fig. 14, Table 8). Rear corner rounded or markedly produced. Mesocondyle situated anteriorly on lateral face, postmesocondyle distance about twice premesocondyle distance. Anterodorsal and anteroventral fenestrae subcircular, separated by a robust anterior bridge. Postdorsal foramina 3–5 and postventral foramina 5–7, varying in size. Pectoral radials 81–92.

Pelvic girdle somewhat broad, with straight or slightly arched puboischiadic bar (Fig. 15, Table 8). Lateral prepelvic processes well developed, slightly recurved, length 30–40% maximum width of pelvis in males. Iliac processes well developed, one to three obturator foramina on each side. Pelvic radials I, 21–29. Predorsal vertebral count 118–131: trunk vertebrae 32–41, predorsal caudal vertebrae 81–96.

Clasper (Figs. 16 and 17) moderately robust to robust, fleshy, with expanded glans, 50–75% tail length in mature males; pseudosiphon formed within inner dorsal lobe, ventral margin of pseudosiphon formed by lobed ridge, inner dorsal surface of lobe bearing 4–5 large, hooked denticles (= scales of Ishiyama, 1958a); pseudorhipidion formed by the dorsal marginal, a narrow ridge of soft tissue extending distally from pseudorhipidion; inner ventral lobe with bulbous projection extending to about the distal end of the lobed ridge, falling well short of distal margin of glans; spike small, rounded and buried in soft tissue. Small denticles present or absent externally on distal portion.

Axial cartilage compressed distally, bowed laterally, extending distally well beyond dorsal and ventral marginal cartilages, distal tip rounded or pointed in lateral profile; dorsal marginal cartilage more or less shorter than ventral marginal, extending distally to about half to the full length of dorsal terminal 2, tapering to a point distally, forming pseudorhipidion; ventral marginal cartilage laterally expanded at level of hypopyle, a distolateral sinusoidal or straight rod-like portion extending distally beyond dorsal marginal cartilage to about half the length or beyond the distal tip of dorsal terminal 2, tip bluntly pointed, forming projection, completely contained within glans. Dorsal terminal 1 large, ring like, proximal margin strongly concave with pronounced medio-proximal shelf for insertion of the dilatator muscle, articulating ventrally with the ventral terminal, dorsolateral margin forming dorsal half of pseudosiphon; dorsal terminal 2 bearing 4–5 large, hooked denticles on dorsal external surface, forming lobed dorsal ridge on distoventral half of pseudosiphon; dorsal terminal 3 subcylindrical, attached along medial margin of dorsal terminal 2, rounded or bluntly pointed distally, forming portion of dorsomedial surface of pseudosiphon; ventral terminal cartilage lanceolate or tear-drop shaped, with broad distal end, about twice the length of dorsal terminal 2; acces-

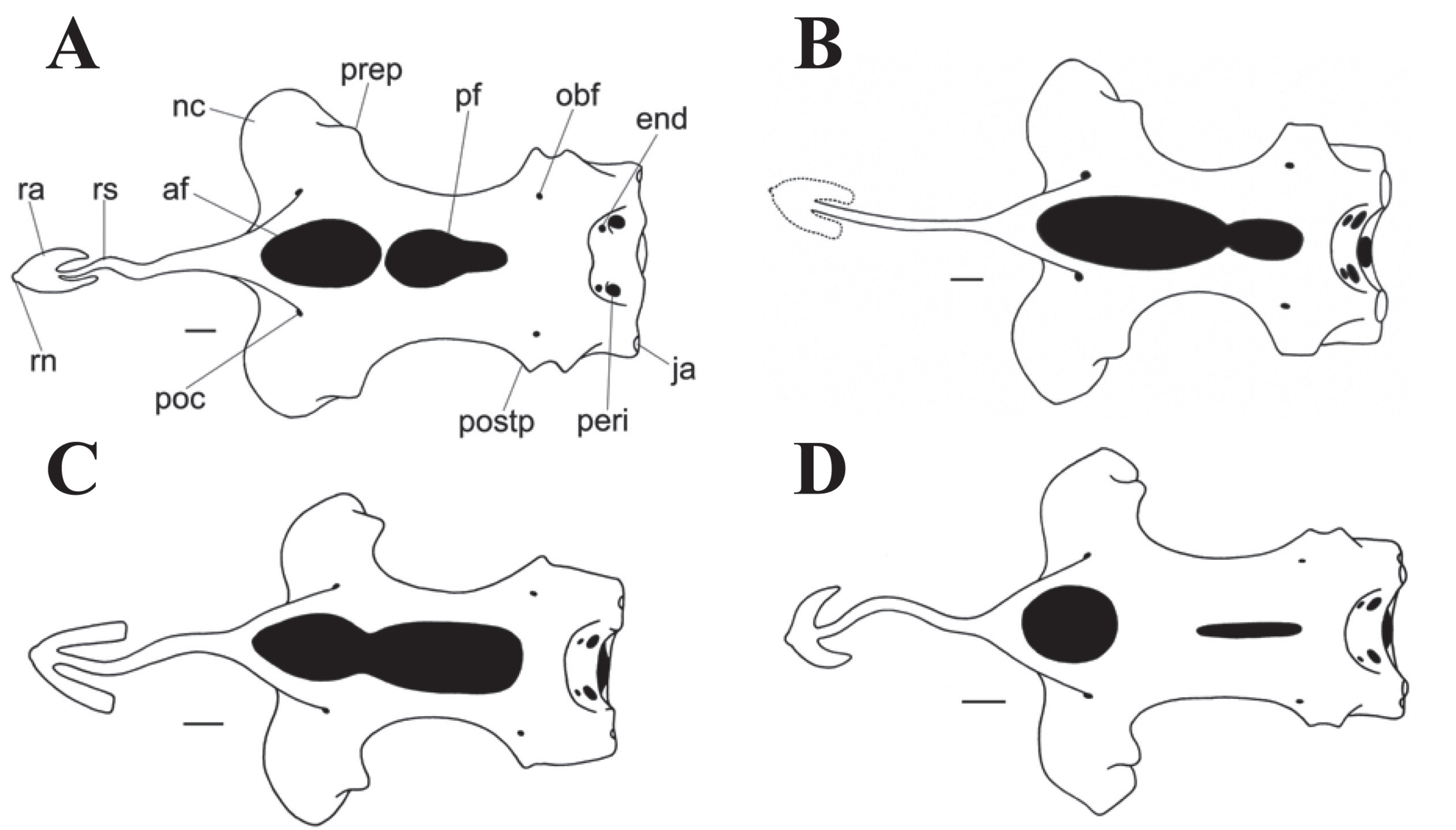

Figure 11

Dorsal view of neurocrania of males of species of the subgenus *Arctoraja:* (A) *Bathyraja panthera* n. sp., paratype, UW 111888, 1090 mm TL; (B) *B. parmifera,* UW 22336, 1002 mm TL; (C) *B. smirnovi,* HUMZ 152289, 704 mm TL; (D) *B. simoterus,* HUMZ 143369, 690 mm TL. af = anterior fontanelle, end = endolymphatic foramen, ja = jugal arch, nc = nasal capsule, obf = otic branch of facial nerve foramen, peri = perilymphatic foramen, pf = posterior fontanelle, poc = preorbital canal foramen, postp = postorbital process, prep = preorbital process, ra = rostral appendix, rn = rostral node, rs = rostral shaft. Scale bar = 10 mm.

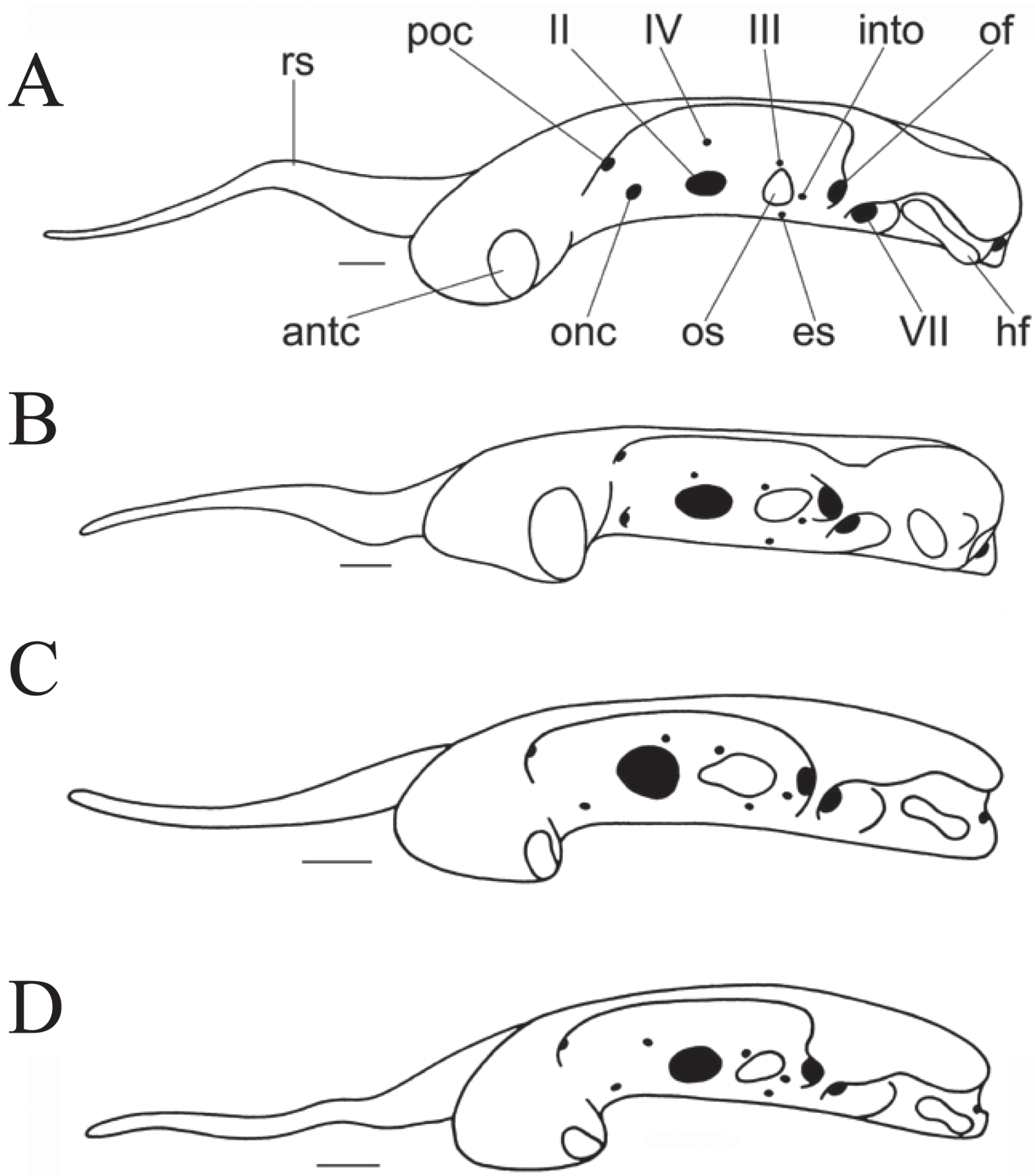

Figure 12

Lateral view of neurocrania of males of species of the subgenus *Arctoraja*: (A) *Bathyraja panthera* n. sp., paratype, UW 111888, 1090 mm TL; (B) *B. parmifera,* UW 22336, 1002 mm TL; (C) *B. smirnovi,* HUMZ 152289, 704 mm TL; (D) *B. simoterus,* HUMZ 143369, 690 mm TL. antc = antorbital condyle, es = efferent spiracular artery foramen, hf = hyomandibular facet, into = interorbital vein foramen, of = orbital fissure, onc = orbital nasal canal, os = optic stalk, rs = rostral shaft, II = optic nerve foramen, III = oculomotor nerve foramen, IV = trochlear nerve foramen, VII = hyomandibular branch of facial nerve foramen. Scale bar = 10 mm.

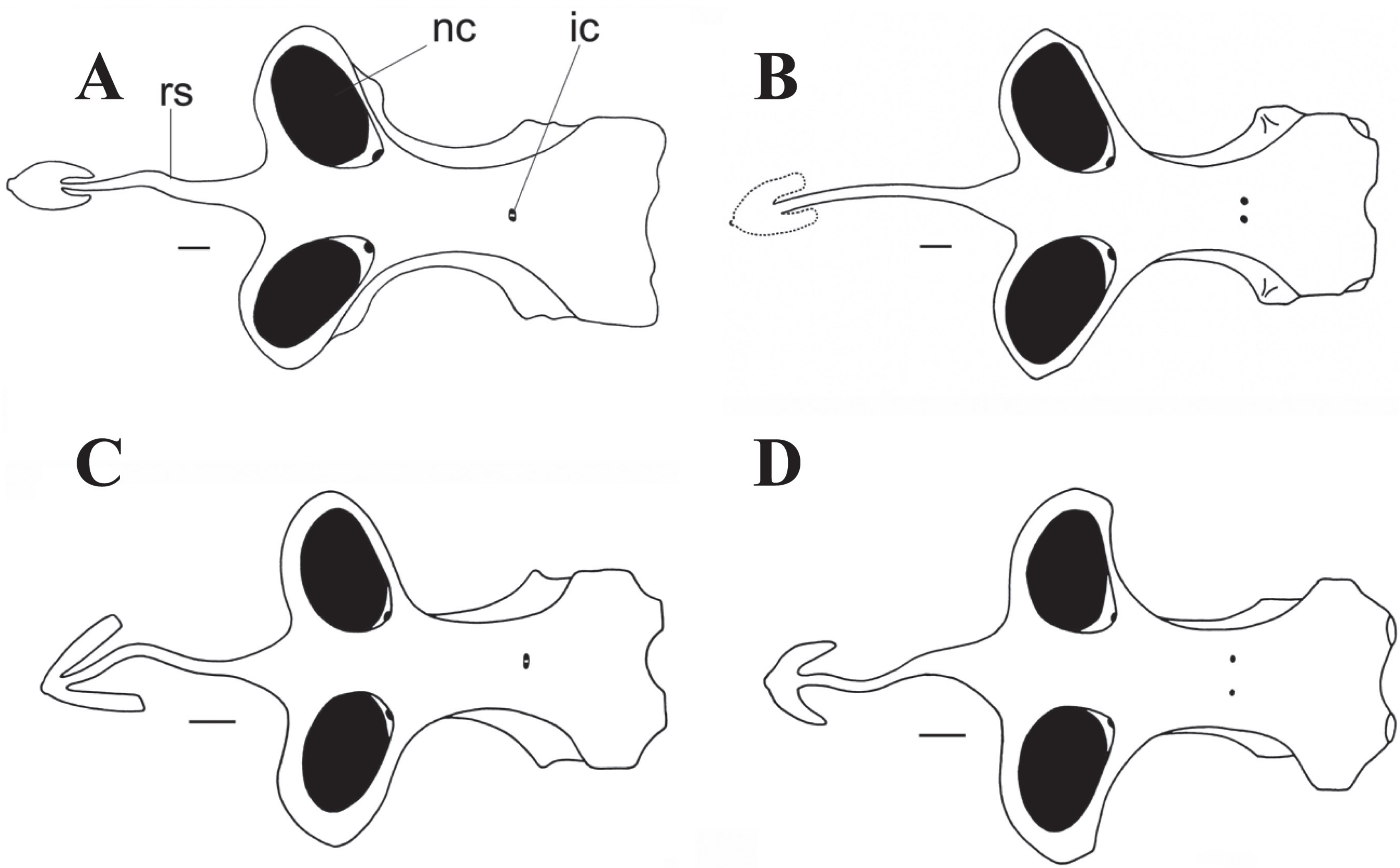

Figure 13

Ventral view of neurocrania of males of species of the subgenus *Arctoraja*: (A) *Bathyraja panthera* n. sp., paratype, UW 111888, 1090 mm TL; (B) *B. parmifera,* UW 22336, 1002 mm TL; (C) *B. smirnovi,* HUMZ 152289, 704 mm TL; (D) *B. simoterus,* HUMZ 143369, 690 mm TL. ic = internal carotid foramena, nc = nasal capsule, rs = rostral shaft. Scale bar = 10 mm.

Table 8

Cranial and scapulocoracoid proportions, expressed as percent of nasobasal length or scapulocoracoid length, respectively, of species of *Arctoraja*. Absent data were not available in prepared material.

	B. panthera	*B. parmifera*	*B. smirnovi*	*B. simoterus*
Cranium				
Nasobasal length (mm)	121.0	100.5	81.0	81.2
Cranial length	179.34	198.01	206.17	185.96
Cranial height	19.01	21.19	20.37	21.06
Rostral cartilage length	81.24	102.69	103.09	88.05
Prefontanelle length	80.58	99.90	97.53	77.59
Cranial width	90.50	104.18	94.69	103.69
Interorbital width	33.88	34.13	34.94	36.33
Rostral base	29.42	28.86	32.72	33.99
Anterior fontanelle length	27.27	24.58	75.93	30.42
Anterior fontanelle width	19.42	19.40	22.10	21.92
Posterior fontanelle length	28.51	47.76		23.40
Posterior fontanelle width	13.64	15.42	20.74	5.79
Rostral appendix length	21.49		35.80	27.96
Rostral appendix width	16.53		37.04	32.64
Rostral cleft length			20.99	10.47
Width across otic capsules	52.48	46.77	57.04	57.64
Least width of basal plate	23.97	26.67	26.30	28.08
Greatest width of nasal capsules	35.12	39.80	34.81	35.71
Internarial width	17.60	18.11	17.28	19.83
Scapulocoracoid				
Greatest length (mm)	88.5	75.5	58.8	55.7
Greatest height	66.10	74.83	61.56	67.32
Premesocondyle	31.98	36.56	36.56	36.80
Postmesocondyle	66.44	61.19	64.63	61.40
Postdorsal fenestra height	11.86	10.99	11.90	14.54
Postdorsal fenestra length	10.17	7.28	8.50	13.46
Anterior fenestra length	12.99	15.23	13.95	13.46
Anterior fenestra width	10.17	10.99	11.05	11.67
Height of rear corner	52.20	57.35	49.32	48.47

sory terminal 2 broadly triangular or subcylindrical, articulating proximally with ventral marginal cartilage, bluntly rounded distoventrally to form spike.

Egg capsule. Egg capsule large, maximum size 150 mm long by 90 mm wide (Ishiyama, 1967), approximately rectangular, widest near mid-length, with horn in each corner (Fig. 10); anterior margin rounded, posterior margin nearly straight, velum obsolete, lateral margins with pronounced keel. Anterior horns curled dorsally, shorter than posterior horns; posterior horns slightly curved ventrally. Byssal threads attached on or at the base of anterior horns. Exterior surface with smooth low longitudinal ridges, approximately 30–55 per centimeter, furnished with small tubercles, with domed or ridged apices; color light brownish green with lighter keels when freshly deposited, darkening to uniform black after extended exposure to seawater.

Etymology. The subgeneric name *Arctoraja* is derived from the Greek αρχτος, meaning "of the north," and the Latin *raja*, a "ray or skate."

Remarks. Ishiyama (1958a) united *B. parmifera* (which he later described as a new species, *B. simoterus*) and *B. smirnovi* in the subgenus *Arctoraja* on the basis of a nearly smooth dorsum, with scattered stellate denticles; smooth ventrum; moderately elongate and bluntly tipped flexible snout; short, depressed tail; reduced caudal fin; slender rostral cartilage; small rostral appendices; large anterior fontanelle; numerous (35–40 abdominal and 82–88 tail) vertebrae; numerous intestinal valves; a unique clasper, with pseudosiphon absent and specialized axial cartilage and dorsal terminal 1 cartilages; and unique egg capsule. Ishiyama (1967) later amended the diagnosis by deleting the absence of the pseudosiphon and the condition of dorsal terminal 1.

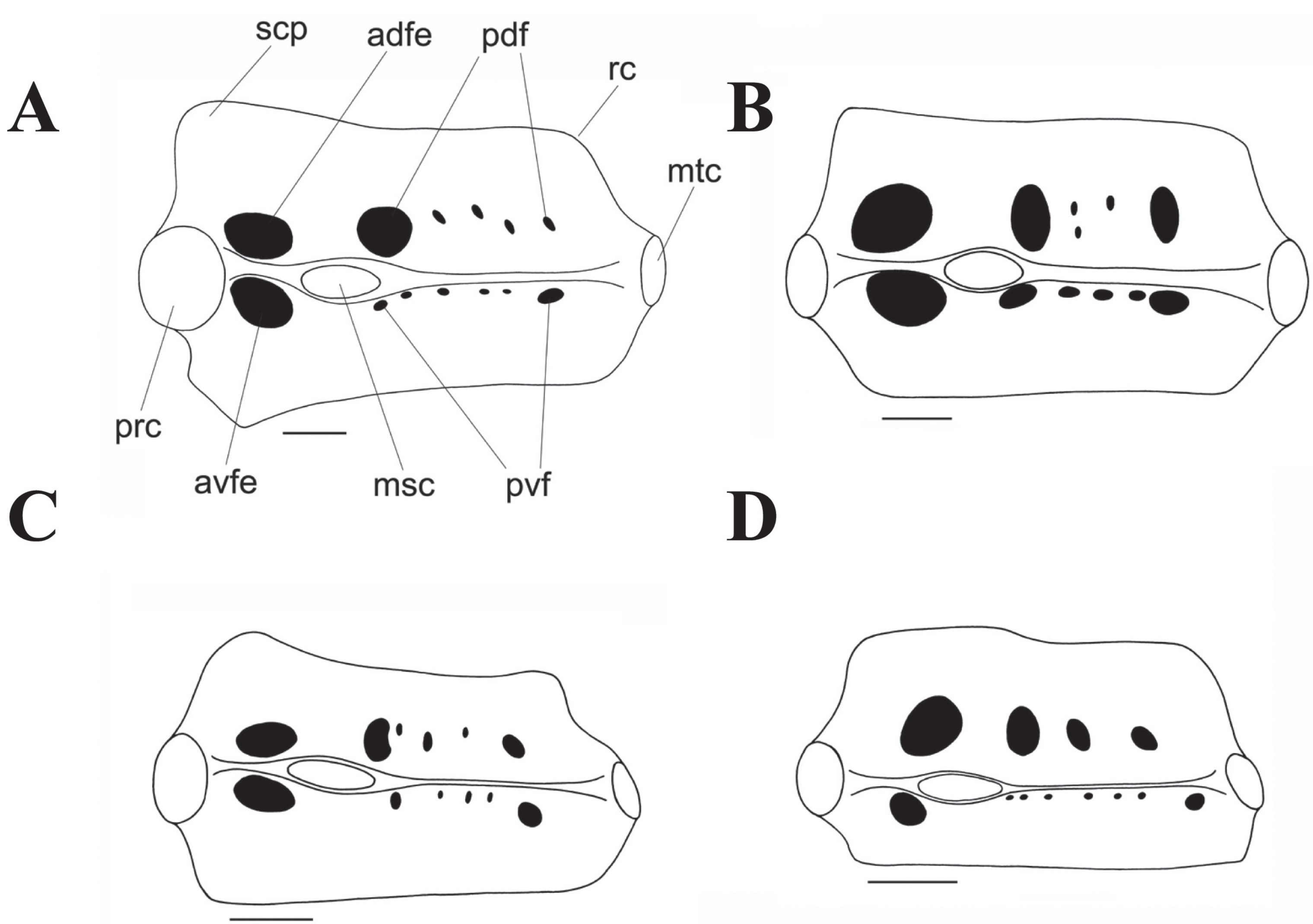

Figure 14

Lateral view of scapulocoracoids of males of species of the subgenus *Arctoraja*: (A) *Bathyraja panthera* n. sp., paratype, UW 111888, 1090 mm TL; (B) *B. parmifera*, UW 22336, 1002 mm TL; (C) *B. smirnovi*, HUMZ 152289, 704 mm TL; (D) *B. simoterus*, HUMZ 143369, 690 mm TL. adfe = anterodorsal fenestra, avfe = anteroventral fenestra, msc = mesocondyle, mtc = metacondyle, pdf = postdorsal foramina, prc = procondyle, pvf = postventral foramina, rc = rear corner, scp = scapular process. Scale bar = 10 mm.

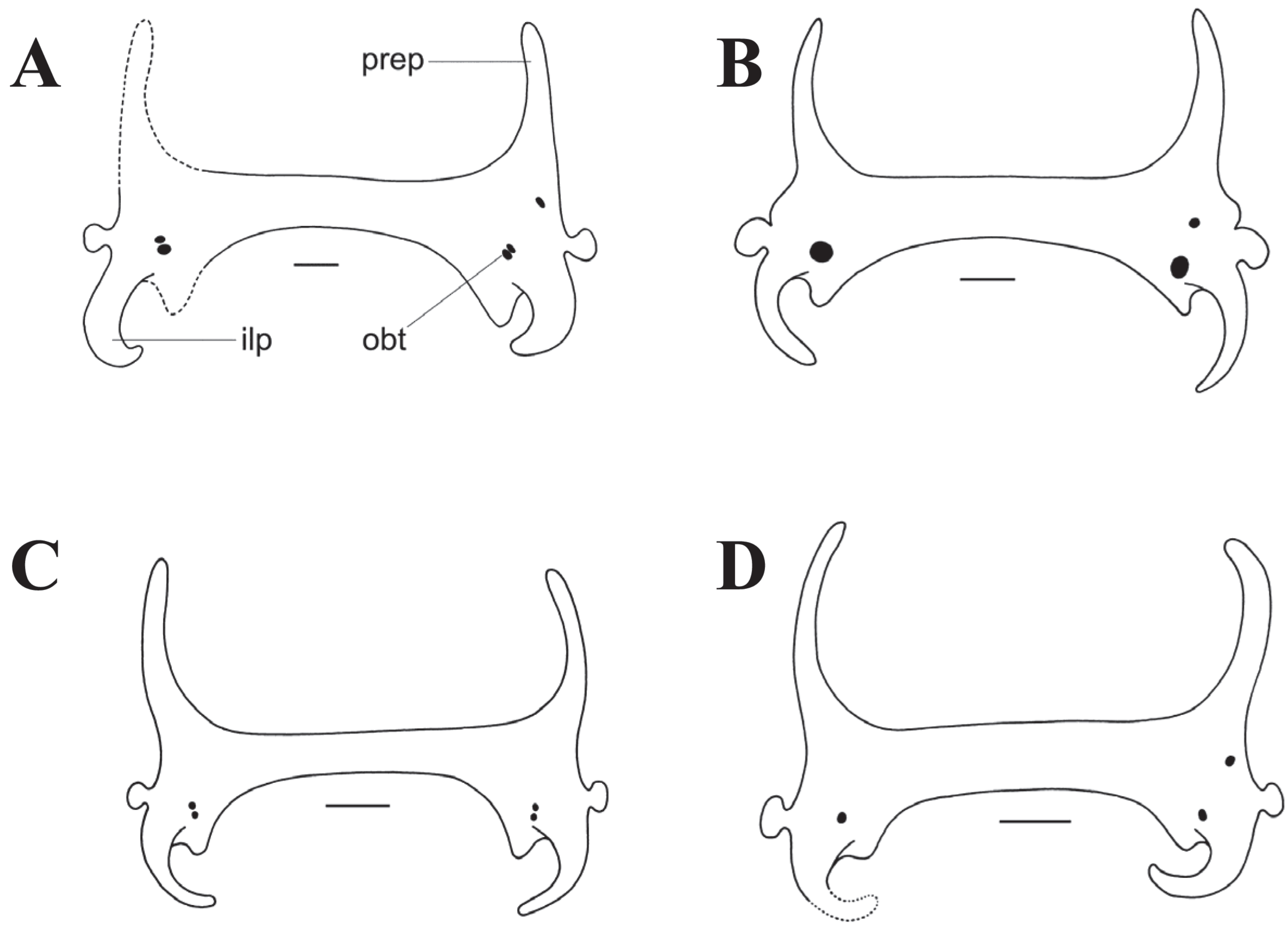

Figure 15

Dorsal view of pelvic girdles of males of species of the subgenus *Arctoraja*: (A) *Bathyraja panthera* n. sp., paratype, UW 111888, 1090 mm TL; (B) *B. parmifera,* UW 22336, 1002 mm TL; (C) *B. smirnovi,* HUMZ 152289, 704 mm TL; (D) *B. simoterus,* HUMZ 143369, 690 mm TL. ilp = iliac process, obt = obturator foramina, prep = prepelvic process. Scale bar = 10 mm.

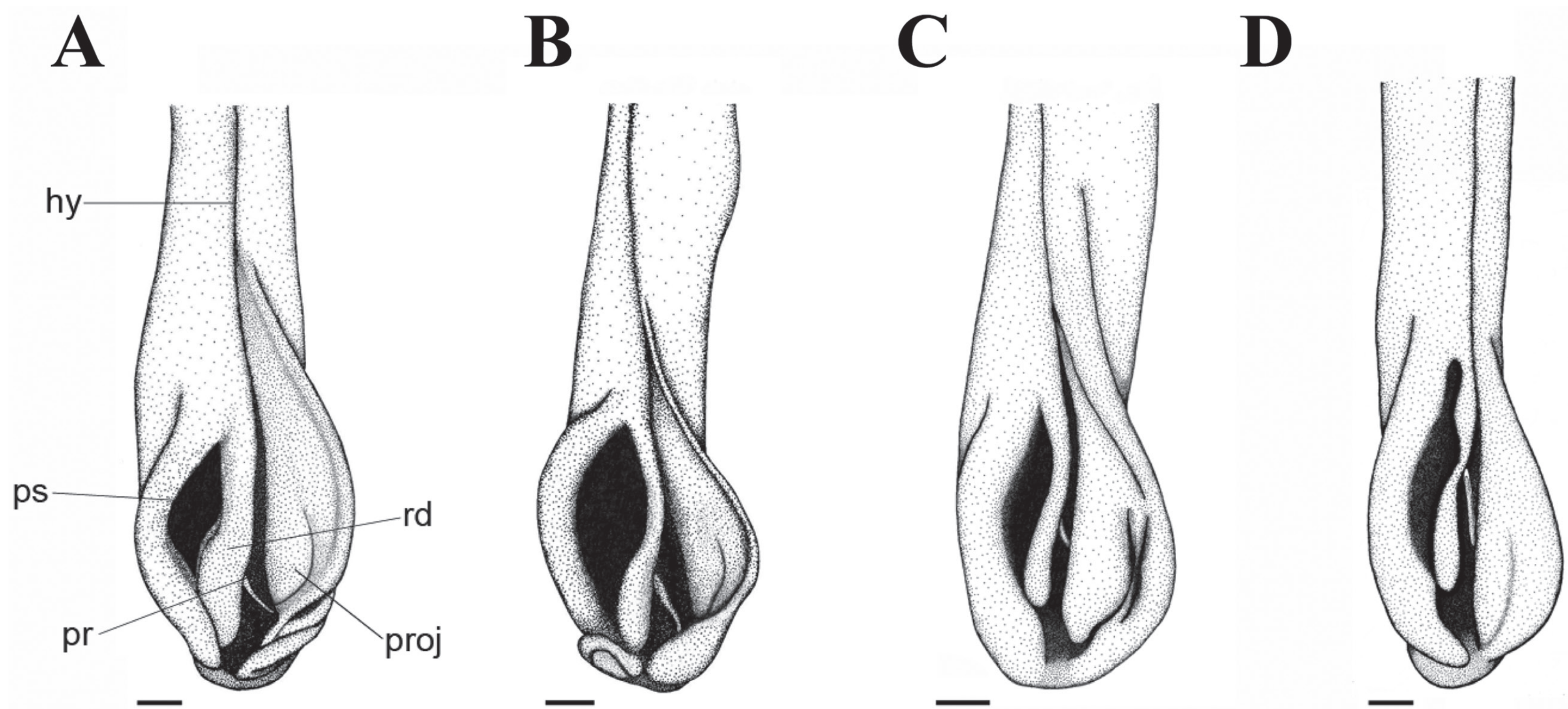

Figure 16

Lateral external view of right claspers of species of the subgenus *Arctoraja*: (A) *Bathyraja panthera* n. sp., paratype, UW 119267, 1080 mm TL; (B) *B. parmifera*, UW 150018, 1050 mm TL; (C) *B. smirnovi*, UW 114999, 1076 mm TL; (D) *B. simoterus*, HUMZ 143363, 1006 mm TL; splayed to show internal components. hy = hypopyle, pr = pseudorhipidion, proj = projection, ps = pseudosiphon, rd = lobed ridge. Scale bar = 5 mm (estimated for *B. simoterus*).

Monophyly of *Arctoraja* is also supported by changes in five bases in the COI gene (Spies et al., 2011). In all phylogenetic trees produced by analyses of our molecular data, a monophyletic *Arctoraja* was invariably present (Spies et al., 2011), one of the few groups supported unequivocally by these data.

Among North Pacific skates, only two species, *Bathyraja aleutica* and *B. interrupta*, bear superficial similarity to species of *Arctoraja*, but can be easily separated from them. Like members of *Arctoraja*, both species may have a full complement of relatively strong dorsal thorns. In *B. aleutica* these are complete, extending from the nuchal region to the wide interdorsal space. Denticles of *B. aleutica* are small and nearly uniformly cover the dorsum, unlike the denticles in adults of *Arctoraja* which are large and stellate, covering only the disc margin and midbelt. Denticles uniformly cover the tail in *B. aleutica*, but in *Arctoraja* they are absent from the base of the thorns and aligned in rows along the side of the tail. Neither species has orbital thornlets, although specimens of *B. interrupta* may have strong denticles along the orbital rims that contrast strongly with the often naked interorbital space. *Bathyraja interrupta* (perhaps representing a species complex; Stevenson et al., 2007) exhibits high variability and may either have reduced thorns in the middorsal series or completely lack them. When present, the thorns are never as strong as in species of *Arctoraja*. Denticles are also highly variable in *B. interrupta*, but unlike in species of *Arctoraja*, denticles are relatively small and are not aligned in rows on the tail. In addition, unlike the robust, bulbous claspers with a distinct pseudosiphon framed by the ridge in species of *Arctoraja*, claspers of *B. aleutica* are slender and have a narrow, slit-like pseudosiphon; claspers of *B. interrupta* are slender and entirely lack a pseudosiphon.

***Bathyraja (Arctoraja) panthera* n. sp.**
leopard skate
(Figures 2–6, 10–18; Tables 1–9)

Breviraja stellulata: Okada and Kobayashi, 1968:39–40, figs. 15a and 15b (non Jordan and Gilbert, 1880, new combination, misidentification, brief description, HUMZ 33542, 597 mm TL, female).

Holotype. UW 116980, 1 (1003 mm male), tissue, western Aleutian Islands, 53.1124°N, 170.9038°E, 99 m depth, 8 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 128.

Allotype. UW 113476, 1 (1050 mm female), tissue, western Aleutian Islands, 51.53°N, 178.56°E, 144 m depth, July 2003, E. A. Logerwell, FV *Pacific Explorer*, cruise 2003-01, haul 10, Genbank FJ869225.

Paratypes. A total of 43 specimens, 197–1110 mm TL. **Western Aleutian Islands:** UW 112328, 1 (1110 mm female), tissue, 52.9124°N, 170.815°E, 189 m depth, 30 July 2004, P. Von Szalay, FV *Sea Storm*, cruise 2004-01, haul 223, Genbank FJ869226; UW 47246, 1 (285 mm female), 52.2148°N, 179.9469°W, 96 m depth, 13 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 125; UW 47245, 1 (310 mm female), tissue, 51.9631°N, 178.1881°E, 258 m depth, 5 July 2002, J. W. Orr, FV *Vesteraalen*, cruise 2002-01, haul 149, Genbank DQ104921; UW 47248, 1 (220 mm female), 52.2227°N, 179.8239°W, 122 m depth, 13 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 126; UW 47251, 2 (225–228 mm females), 52.0244°N, 175.8883°E, 153 m depth, 7 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 104; UW 47252, 1 (245 mm female), 52.17452°N, 175.2372°E, 221 m depth, 8 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 107; UW 47244, 4 (255–290 mm males), 51.7163°N, 175.7853°E, 94 m depth, 7 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 100; UW 111889, 1 (1100 mm female), tissue, 51.8554°N, 178.2777°E, 92 m depth, 5 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 94, Genbank DQ104923; UW 119207, 2 (217–240 mm females), 51.8497°N, 177.4693°E, 107 m depth, 23 July 2006, P. Von Szalay, FV *Sea Storm*, cruise 2006-01, haul 184; UW 112324, 1 (1065 mm male), tissue, 52.5161°N, 174.4335°E, 188 m depth, 26 July 2004, P. Von Szalay, FV *Sea Storm*, cruise 2004-01, haul 201, Genbank FJ869221; UW 111478, 1 (197 mm male), 51.6921°N, 175.5521°E, 190 m depth, 1 August 1997, J. W. Orr, FV *Vesteraalen*, cruise 1997-01, haul 203; UW 46416, 1 (220 mm male), 53.1097°N, 170.9186°E, 102 m depth, 3 August 1997, J. W. Orr, FV *Vesteraalen*, cruise 1997-01, haul 216; UW 117313, 1 (900 mm male), tissue, 51.2587°N, 179.1183°E, 155 m depth, 17 July 2003, E. A. Logerwell, FV *Pacific Explorer*, cruise 2003-01, haul 18, Genbank FJ869223; UW 111888, 1 (1090 mm male), dissected, tissue, 51.7575°N, 175.6682°E, 90 m depth, 7 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 101; SIO 10-196 (ex UW 117501), 1 (1110 mm male), tissue, 51.7766°N, 175.9152°E, 86 m depth, 17 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 167; UW 116849, 3 (247–308 mm males), tissue, 52.2047°N, 179.9690°W, 93 m depth, 28 June 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 84; UW 116986, 1 (990 mm male), tissue, 51.7529°N, 175.6766°E, 91 m depth, 16 July 2006, FV *Sea Storm*, cruise 2006-01, haul 163; UW 119833, 4 (980 mm and *n* = 3, 99–112 mm, with tissue only; males), tissue, 53.1124°N, 170.9038°E, 99 m depth, 8 July 2006, B. Knoth and P. Munro, FV *Sea Storm*, cruise 2006-01, haul 128; UW 46451, 1 (245 mm male), 52.0320°N, 175.8788°E, 161 m depth, 1 August 1997, J. W. Orr, FV *Vesteraalen*, cruise 1997-01, haul 206; SIO 10-197 (ex UW 48590), 1 (325 mm female), 51.9965°N, 177.6465°E, 84 m depth, 27 June 2000, K. E. Pearson,

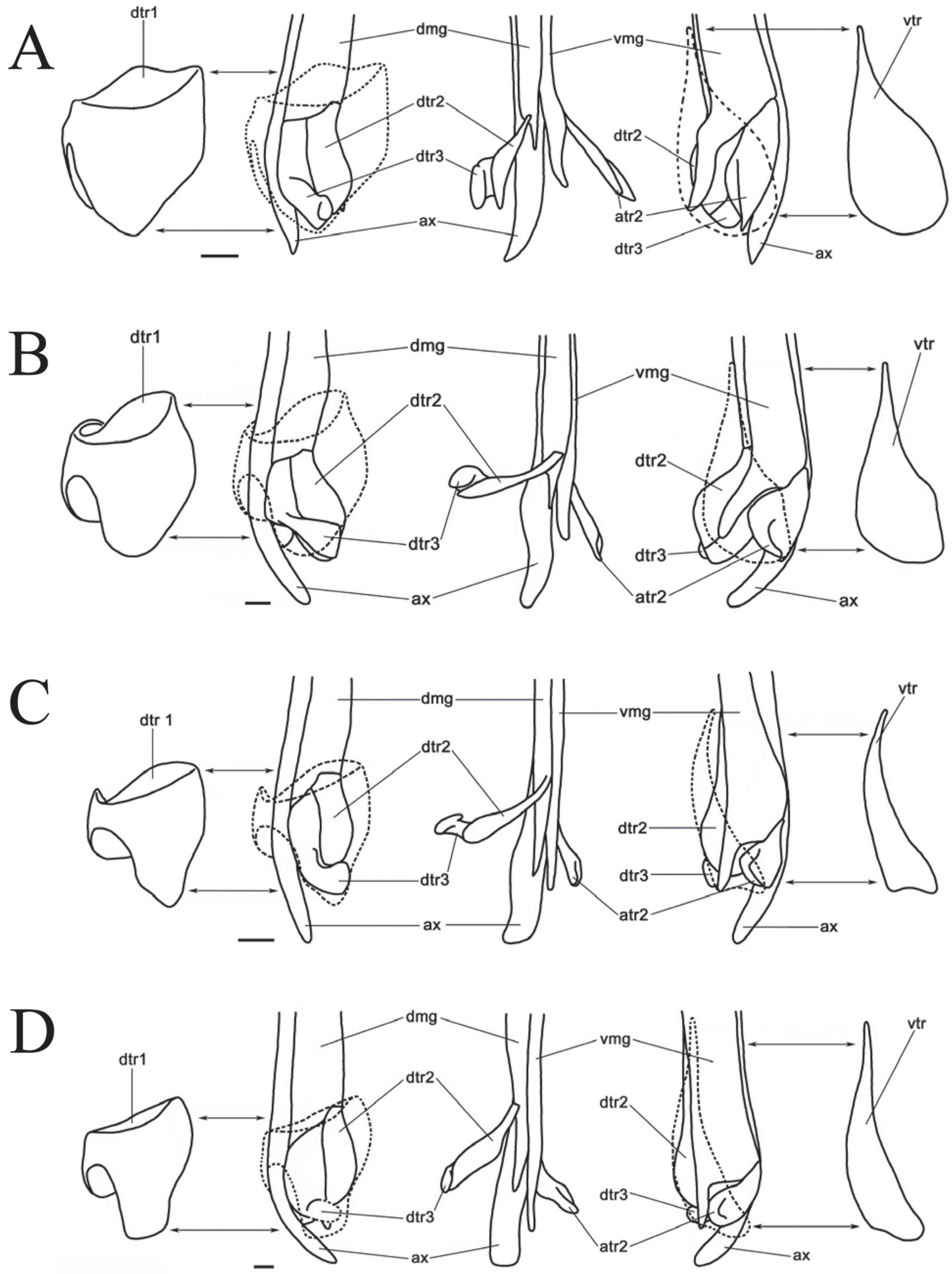

Figure 17

Dorsal (left), lateral (center), and ventral (right) views of clasper cartilages of species of the subgenus *Arctoraja*: (A) *Bathyraja panthera* n. sp., paratype, UW 119267, 1080 mm TL; (B) *B. parmifera,* UW 150018, 1050 mm TL; (C) *B. smirnovi,* UW 114999, 1076 mm TL; (D) *B. simoterus,* HUMZ 143363, 1006 mm TL. atr2 = accessory terminal cartilage 2, ax = axial cartilage, dmg = dorsal marginal cartilage, dtr1, dtr2, dtr3 = dorsal terminal cartilages 1, 2, and 3, vmg = ventral marginal cartilage, vtr = ventral terminal cartilage. Scale bar = 10 mm.

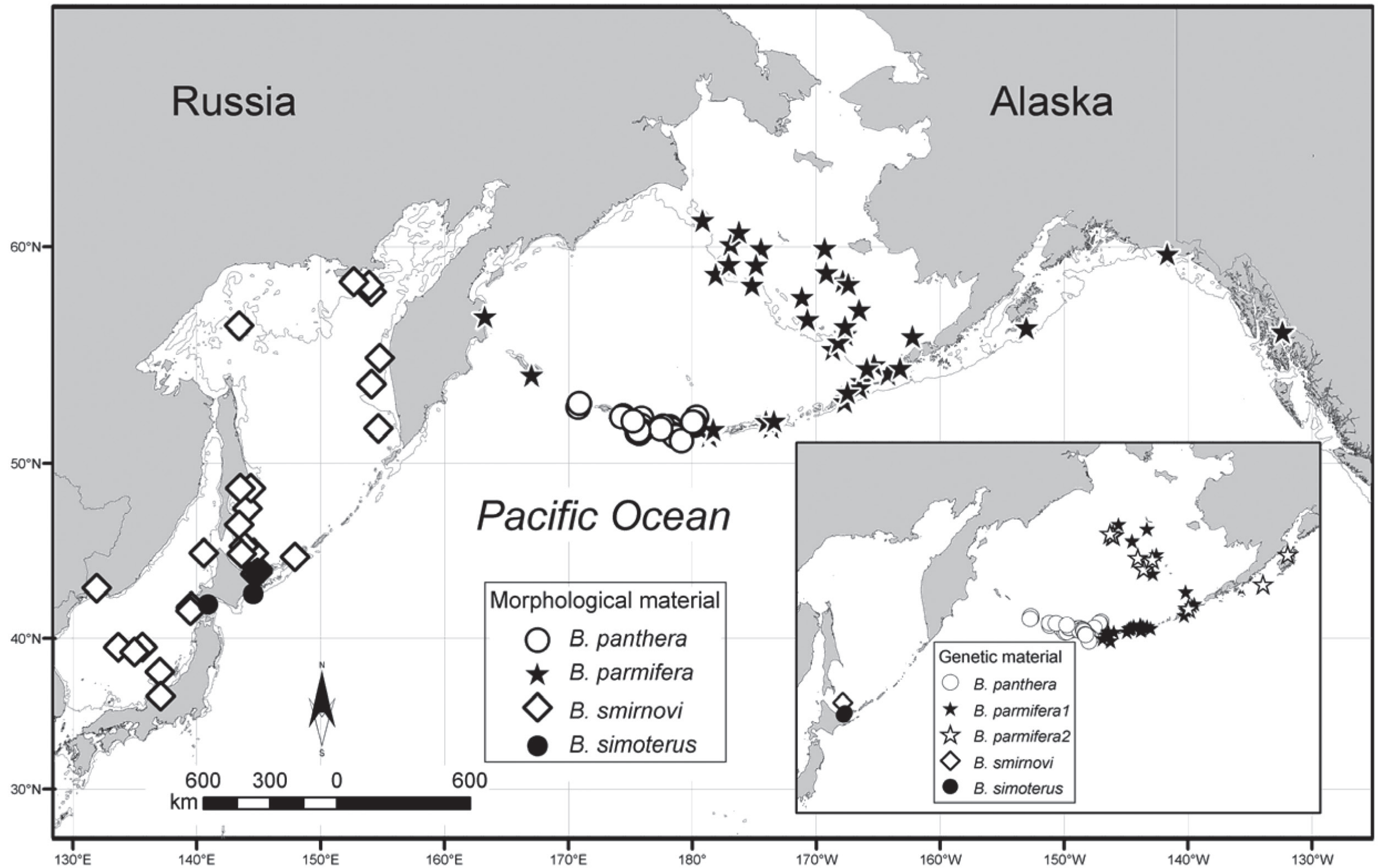

Figure 18

Distribution of species of the subgenus *Arctoraja* of *Bathyraja* based on material examined. Depth contour = 200 m.

FV *Dominator*, cruise 2000-01, haul 147; HUMZ 89385, 1 (951 mm male), Amchitka I., 51.482°N, 178.6242°E, 244 m depth, 9 August 1980; UW 116984, 1 (875 mm male), tissue, 52.2360°N, 175.2423°E, 150 m depth, 15 July 2006, FV *Sea Storm*, cruise 2006-01, haul 158, E. Jorgensen; UW 113471, 1 (820 mm female), tissue, 51.58°N, 178.45°E, 154 m depth, 15 July 2003, E. A. Logerwell, FV *Pacific Explorer*, cruise 2003-01, haul 8, Genbank FJ869228; HUMZ 33542, 1 (597 mm female), Aleutian Islands, 52.05°N, 179.8333°W, 7 September 1963; HUMZ 67241, 1 (503 mm female), 52.45°N, 179.65°W, 22 June 1977; HUMZ 67423, 1 (249 mm male), 52.1667°N, 179.8333°W, 22 June 1977; HUMZ 68338, 1 (340 mm male), 51.6333°N, 175.7167°E; HUMZ 88952, 1 (654 mm male), 52.4435°N, 174.3162°E, 247 m depth, 16 August 1980, RV *Hatsue Maru No. 62*, cruise 1980-01, haul 95; HUMZ 88950, 1 (776 mm female), 52.4435°N, 174.3162°E, 247 m depth, 16 August 1980, RV *Hatsue Maru No. 62*, cruise 1980-01, haul 95; UW 113477, 1 (413 mm female), tissue, 52.3866°N, 175.9298°E, 51 m depth, 25 July 2004, FV *Sea Storm*, cruise 2004-01, haul 195, Genbank FJ869227; UW 119267, 1 (1080 mm male), claspers only, off Buldir I., 52.2764° N, 176.0590° E, 126 m depth, 16 July 2002, J. W. Orr, FV *Sea Storm*, cruise 2002-01, haul 136; UF 174177, 1 (425 mm male), 51.8965°N, 178.2418°E, 221 m depth, 20 September 1991, W. Raschi, FV *Green Hope*, cruise 1991–01, haul 160; UF 174178, 1 (210 mm male), 53.1075°N, 170.9687°E, 112 m depth, 16 September 1991, W. Raschi, FV *Green Hope*, cruise 1991–01, haul 150.

Egg capsules. A total of 12 egg capsules, 106–134 mm CL. **Western Aleutian Islands:** TCWC 12056.02, 10 (106–134 mm CL), 52.5979°N, 172.9151°E, 151 m depth, 17 July 2000, J. D. McEachran, FV *Dominator*, cruise 2000-01, haul 218; UW 119288, 2 (113–131 mm CL), 52.3078°N, 175.8071°E, 253 m depth, 13 July 2006, W. C. Flerx, FV *Gladiator*, cruise 2006-01, haul 133.

Tissues with photo vouchers only. A total of 70 tissues. **Western Aleutian Islands:** UW 116981, 2 (190–1050 mm females), 53.1232°N, 170.8807°E, 109 m depth, 8 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 129; UW 116979, 1 (1200 mm female), 52.9835°N, 170.9324°E, 135 m depth, 8 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 126; UW 116983, 1 (1150 mm female), 52.5492°N, 173.5101°E, 138 m depth, 13 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 147; UW 116982, 1 (1040 mm female), 52.3438°N, 173.5329°E, 87 m depth, 12 July 2006, E. Jorgensen, FV *Sea Storm*, cruise 2006-01, haul 145; UW 116985, 2 (220–1070 mm, 1 male, 1 female), 51.6958°N, 175.5452°E, 190 m depth, 15 July 2006, P.Munro, FV *Sea Storm*, cruise 2006-01, haul 162; UW 116987, 1 (330 mm female), 51.8564°N, 175.892°E, 87 m depth, 16 July 2006, FV *Sea Storm*, cruise 2006-01, haul 166; UW 116899, 1 (250 mm female), 52.3166°N, 175.9024°E, 96 m depth, 5 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 110; UW 116988, 5 (110–1150 mm, 3 males, 2 females), 51.7766°N, 175.9152°E, 86 m depth, 17 July 2006, FV *Sea Storm*, cruise 2006-01, haul 167; UW 116977, 2 (1180 mm male, 1200 mm female), 52.2977°N, 176.0453°E, 147 m depth, 5 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 112; UW 116978, 2 (830–1150 mm males), 52.2776°N, 176.0584°E, 140 m depth, 5 July 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 113; UW 116989, 7 (4 males 940–1170 mm, 3 females 970–1100 mm), 52.1233°N, 176.2380°E, 229 m depth, 17 July 2006, FV *Sea Storm*, cruise 2006-01, haul 169; UW 116990, 1 (sex and length unknown), 52.1390°N, 176.2432°E, 123 m depth, 17 July 2006, FV *Sea Storm*, cruise 2006-01, haul 170; UW 116898, 3 (1 male, 2 females, length unknown), 51.9287°N, 176.6561°E, 176 m depth, 4 July 2006, E. Jorgensen, FV *Sea Storm*, cruise 2006-01, haul 107; UW 116994, 1 (1140 mm male), 51.8243°N, 177.2470°E, 74 m depth, 23 July 2006, D. Carrison-Stone, FV *Sea Storm*, cruise 2006-01, haul 188; UW 116895, 2 (1100–1270 mm females), 52.0478°N, 177.4402°E, 123 m depth, 4 July 2006, FV *Sea Storm*, cruise 2006-01, haul 104; UW 116896, 1 (1230 mm male), 52.0732°N, 177.3509°E, 162 m depth, 4 July 2006, E. Jorgensen, FV *Sea Storm*, cruise 2006-01, haul 105; UW 116897, 1 (450 mm male), 51.9995°N, 177.4242°E, 87 m depth, 4 July 2006, E. Jorgensen, FV *Sea Storm*, cruise 2006-01, haul 106; UW 116995, 2 (1130–1180 mm females), 51.9957°N, 177.6525°E, 84 m depth, 28 July 2006, D. Carrison-Stone, FV *Sea Storm*, cruise 2006-01, haul 201; UW 116996, 1 (590 mm male), 52.0947°N, 177.711°E, 94 m depth, 28 July 2006, D. Carrison-Stone, FV *Sea Storm*, cruise 2006-01, haul 203; UW 116997, 1 (1170 mm male), 52.0343°N, 178.0327°E, 203 m depth, 28 July 2006, D. Carrison-Stone, FV *Sea Storm*, cruise 2006-01, haul 205; UW 116998, 1 (1090 mm female), 51.8814°N, 177.7093°E, 97 m depth, 28 July 2006, D. Carrison-Stone, FV *Sea Storm*, cruise 2006-01, haul 207; UW 116999, 1 (1130 mm female), 51.8785°N, 177.6962°E, 94 m depth, 29 July 2006, D. Carrison-Stone, FV *Sea Storm*, cruise 2006-01, haul 208; UW 116991, 2 (1120–1150 mm males), 51.9905°N, 178.2126°E, 90 m depth, 18 July 2006, FV *Sea Storm*, cruise 2006-01, haul 171; UW 116992, 1 (1130 mm male), 51.8647°N, 178.2483°E, 95 m depth, 18 July 2006, FV *Sea Storm*, cruise 2006-01, haul 176; UW 116993, 6 (690–1060 mm males), 51.2542°N, 179.2757°E, 162 m depth, 22 July 2006, P. Von Szalay, FV *Sea Storm*, cruise 2006-01, haul 180; UW 116894, 2 (1120–1170 mm females), 52.4457°N, 179.8854°E, 175 m depth, 30 June 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 90; UW 116893, 3 (1020–1130 mm males), 52.5411°N, 179.5742°W, 94 m depth, 29 June 2006, B. Knoth, FV *Sea Storm*, cruise

2006-01, haul 87; UW 116892, 8 (760–1190 mm, 1 male, 7 females), 52.5192°N, 179.5092°W, 142 m depth, 29 June 2006, E. Jorgensen, FV *Sea Storm*, cruise 2006-01, haul 86; UW 116863, 8 (670–1080 mm, 3 males, 5 females), 52.67438°N, 179.3521°W, 147 m depth, 29 June 2006, B. Knoth, FV *Sea Storm*, cruise 2006-01, haul 85.

Diagnosis. A species of *Arctoraja* distinguished from all other members of the subgenus by its body coloration of light greenish brown, with vermiculated and round black spots and yellow blotches; distal tip of ventral marginal sinusoidal; accessory terminal 2 elongate and broad, with long spike; distal tip of axial cartilage pointed; and unique COI haplotype (Spies et al., 2011).

Bathyraja panthera is further distinguished from *B. parmifera* by its higher total thorn count (31–42 vs. 19–36 in *B. parmifera*), higher tail thorn count (19–28 vs. 15–23), internal carotid foramina in a single median pit (vs. foramina widely separated), distal portion of ventral marginal cartilage sinusoidal (vs. straight), accessory terminal 2 elongate with long spike (vs. broadly triangular with short spike), distal tip of axial cartilage pointed (vs. bluntly rounded), anterior portion of body longer and wider (vs. shorter and narrower), and tail longer (vs. shorter).

It is further distinguished from *B. simoterus* by interdorsal space wide (1.4–3.1% TL vs. 0.5–1.0% TL in *B. simoterus*); anterior portion of body longer and wider (vs. shorter and narrower); tail longer (vs. shorter); posterior fontanelle pear-shaped (vs. narrowly elongate); internal carotid foramina in a single median pit (vs. widely separated foramina), anterior postdorsal foramen of scapulocoracoid large, others much smaller (vs. all large), and ventral terminal tear-drop shaped (vs. lanceolate).

It is distinguished further from *B. smirnovi* by its complete series of dorsal thorns (vs. interrupted series between nuchal and tail thorns in *B. smirnovi*), wider interdorsal length (1.4–3.1% TL vs. 0.1–1.4% TL), anterior portion of body longer and wider (vs. shorter and narrower); tail longer (vs. shorter); separate anterior and posterior fontanelles (vs. single fontanelle), ventral terminal tear-drop shaped (vs. lanceolate), and dorsal and ventral marginals extending to about a quarter length of dorsal terminal 2 (vs. extending farther distally to distal tip of dorsal terminal 3).

Description. Body moderately large (maximum length examined 111 cm TL, maximum length observed 139 cm TL; Stevenson et al., 2007). Disc 1.3 (range 1.2–1.3) times as broad as long. Anterior lobe of pelvic fin moderately long, length 0.60 (0.45–0.80) times posterior lobe. Tail long, length of tail from posterior margin of cloaca to tip 1.06 (0.77–1.16) times distance from tip of snout to posterior margin of cloaca.

Snout short, preorbital snout length 3.27 (2.19–4.89) times orbital length and 2.97 (2.60–3.72) times interorbital width; preoral snout length 1.70 (1.39–2.33) times internarial distance. Interorbital space narrow, distance 1.10 (0.64–1.34) times orbit length; orbit length 1.47 (0.90–2.24) times spiracle length. Mouth width 15.6% (12.5–17.5%) of disc width.

Distance between first gill slits 2.42 (2.19–2.88) times internarial distance; length of first gill slits 1.39 (1.15–2.38) times length of fifth gill slits. Distance between dorsal fins 54% of base of first dorsal fin in holotype, varying in paratypes from 30–100% of first dorsal-fin base.

Disc with 4 (2–5) nuchal thorns, 7 (6–10) mid-dorsal thorns, 2 (1–2) scapular thorns. Tail thorns 22 (19–28), interdorsal thorns 1 (1–2). Total thorns on the mid-dorsal line from posterior to the orbits to the tip of tail 34 (31–42). Denticles on tail small, aligned in poorly defined rows.

Neurocranium (Figs. 11–13, Table 8) with separate anterior and posterior fontanelles: anterior fontanelle egg-shaped, larger end posterior; posterior fontanelle pear-shaped, larger end anterior. Cranial nerve IV foramen dorsal to cranial nerve II foramen. Internal carotid foramina in single median pit.

Scapulocoracoid (Fig. 14, Table 8) with rounded rear corner. Anterodorsal and anteroventral fenestrae subcircular, approximately equal in size, separated by a robust anterior bridge. Mesocondyle elongate. Postdorsal foramina 5, anteriormost 10 times larger than more posterior foramina; postventral foramina 6, posteriormost about twice the size of more anterior foramina. Pectoral radials 82–90.

Pelvic girdle (Fig. 15, Table 8) with two closely spaced obturator foramina on each side, a third present anteriorly on one side. Pelvic radials I, 22–27. Predorsal vertebrae 118–129: trunk vertebrae 35–40, predorsal caudal vertebrae 81–94.

Clasper robust (Figs. 16 and 17), 64% (48.3–72.6%) tail length in mature males. Projection present. Small denticles present externally at distal tip. Distal tip of axial cartilage pointed in lateral profile; dorsal marginal cartilage short, constricted distally to a narrow distal tip, extending for about half the length of dorsal terminal 2; ventral marginal cartilage extending distally beyond dorsal marginal for about three-quarters of the length of dorsal terminal 2, distolateral extension thick and sinusoidal, forming component projection. Dorsal terminal 1 entire proximally, strongly notched distally; dorsal terminal 2 about twice as large as dorsal terminal 3; accessory terminal 2 broadly elliptical in ventral view, with pointed spike distoventrally, two-thirds the length of ventral terminal; ventral terminal cartilage a broad tear-drop shape, distal margin rounded.

Table 9

Proportional morphometric (in percent capsule length) and meristic characters of egg capsules of *Bathyraja panthera* and *B. parmifera*. Range followed by mean ± standard deviation in parentheses.

	B. panthera		*B. parmifera*	
n	12		25	
Capsule length (mm)	106–134	(118 ± 8.5)	113–152	(125 ± 9.1)
Ventral case ribs per cm	32–55	(42 ± 4.9)	40–53	(48 ± 4.0)
Percent capsule length				
Capsule width (with keel)	67–87	(75 ± 5.3)	56–79	(73 ± 5.2)
Capsule width (without keel)	57–70	(63 ± 4.2)	45–69	(60 ± 5.3)
Capsule keel width (mean)	4–9	(6 ± 1.3)	3–10	(6 ± 1.4)
Anterior horn width (with keel, left)	6–10	(8 ± 1.0)	7–14	(11 ± 1.7)
Anterior horn width (without keel, left)	5–7	(6 ± 0.4)	5–8	(7 ± 0.9)
Anterior horn keel width (left)	6–10	(8 ± 1.0)	7–14	(11 ± 1.7)
Posterior horn width (with keel, left)	9–14	(11 ± 1.4)	9–14	(11 ± 1.4)
Posterior horn keel width (left)	1–3	(2 ± 0.7)	0–4	(2 ± 0.9)
Posterior horn width (without keel, left)	8–11	(9 ± 0.9)	7–10	(9 ± 1.0)
Byssal thread attachment from anterior margin	–43–2	(–23 ± 9.3)	–7–10	(2 ± 4.9)
Total keel width (sum of 4-horns and both sides of capsule)	14–29	(19 ± 4.1)	13–33	(25 ± 4.4)

Coloration. In life (Fig. 6), background color of dorsal surface light greenish brown, with vermiculated and round black spots and yellow blotches. Typically, anteroposteriorly elongate yellow blotches located lateral to orbits, smaller round yellow blotches just posterior and lateral to scapular spines; large yellow blotches at base of pectoral fins at midbody. Most prominent yellow blotches surrounded by a rosette of black spots, some connected to form elongate blotches. Tail with four more or less distinct yellow bands bordered by dark spots, anterior bands more distinct than posterior. Ventral surface predominantly creamy white, with dark gray blotching often around cloaca and along midline of tail.

After storage in 70% ethanol, dorsal background color medium brown, with black spots and blotches and irregular light-brown to yellow blotches on disc and tail, large yellowish blotches usually present on posteromedial surface of each pectoral fin; ventral background color on disc uniformly light, and usually some dark pigment surrounding cloaca; ventral surface of tail light at margins and tip, dark blotches along midline of tail.

Egg capsule. Byssal threads attached at the base of the anterior horns at the anterior margin of egg capsule (Fig. 10A, Table 9). Longitudinal ridges with domed apices (Fig. 10A). Additional description as for subgenus. Egg capsules of *B. panthera* were taken only among the western Aleutian Islands, west of Attu Island on Stalemate Bank (TCWC 12056.02) and south of Kiska Island (UW 119288).

Distribution. All specimens were collected among the western Aleutian Islands or on Petrel Bank between longitudes 170° E and 179° W, at depths ranging from 51 to 258 m (Fig. 18). Among species of *Arctoraja*, only *B. panthera* has been recorded west of 180° longitude in the Aleutian Islands, and the depth range in survey records of all skates recorded as "*B. parmifera*" west of 180° longitude is 51–294 m (NMFS, AFSC, RACE survey database, 2009).

Etymology. The specific epithet *panthera* is taken from the generic name for the leopard (Felidae), recognizing the distinctive dorsal coloration of the species, often characterized by rosettes of black spots surrounding yellow blotches.

Comparative remarks. Among the 25 species of *Bathyraja* in the North Pacific, only two other species of *Arctoraja*, *B. simoterus* and *B. parmifera*, are likely to be misidentified as *B. panthera* but are readily distinguished by characters given in the diagnosis. All examined specimens of *B. smirnovi* lacked a middorsal series of thorns and all specimens of *B. panthera* were fully thorned, with a complete middorsal series.

In addition to the differences noted in the subgenus comparisons above, *B. panthera* is readily distinguished from both *B. aleutica* and *B. interrupta* by its background dorsal color of greenish brown and color pattern of black spots and yellow blotches. Both *B. aleutica* and *B. interrupta* are relatively uniform in color: *B. aleutica* is overall gray, rarely with scattered faint white spots; *B. interrupta* is overall brown, occasionally with scattered dark spots.

Bathyraja (Arctoraja) parmifera (Bean, 1881)
Alaska skate

(Figures 2–5, 7, 10–19, 21; Tables 1–9)

Raia parmifera Bean, 1881:157 (original description, two specimens, partially disintegrated: lectotype, herein designated, USNM 27651, female, 975 mm TL, Alaska, Unalaska, Iliuliuk, 12 October 1880, U.S. Coast Survey schooner *Yukon*; paralectotype, USNM 28098, male, length unknown ["portions only"], Alaska, St. Michaels, U.S. Coast Survey schooner *Yukon*, collected by L. Turner).

Raia obtusa Gill and Townsend, 1897:231 (original description, one specimen, poor condition: holotype, USNM 48763, immature male, ca. 305 mm TL, Alaska, Bering Sea, RV *Albatross*, "field number 1298").

Raja parmifera: Jordan and Evermann, 1898:74 (new combination, redescription).

Breviraja parmifera: Ishiyama, 1952:1 (new combination, key, Hokkaido).

Breviraja (Arctoraja) parmifera: Ishiyama, 1958a:146 (new subgenus, key, Hokkaido).

Bathyraja parmifera: Ishiyama and Ishihara, 1977 (new combination, *Bathyraja* first proposed for North Pacific *Breviraja* by Ishiyama and Hubbs, 1968, comparison).

Rhinoraja obtusa: Compagno 1999:489 (new combination, checklist).

Material examined. A total of 81 specimens, 210–1150 mm TL, including the type specimens listed above. **Commander Islands:** HUMZ 55522, 1 (784 mm male), off Bering Island, 54.4667°N, 167.0667°E, 17 May 1976; HUMZ 54991, 1 (618 mm female), off Bering Island, 54.4667°N, 167.0667°E, 17 May 1976. **Aleutian Islands:** UW 116015, 1 (1035 mm male), tissue, 52.2378°N, 173.4039°W, 109 m depth, 18 June 2004, J. W. Orr, FV *Sea Storm*, cruise 2004-01, haul 57; UW 113474, 1 (940 mm male), tissue, 51.5140°N, 178.6179°W, 162 m depth, 3 July 2004, N. W. Raring, FV *Sea Storm*, cruise 2004-01, haul 106, Genbank GQ469972; UW 112327, 1 (995 mm female), tissue, 51.9603°N, 173.6338°W, 99 m depth, 27 June 2004, J. W. Orr, FV *Sea Storm*, cruise 2004-01, haul 74, Genbank FJ869214; UW 46417, 1 (455 mm female), 52.3468°N, 173.9485°W, 87 m depth, 1 June 2000, J. W. Orr, FV *Dominator*, cruise 2000-01, haul 57; UW 46420, 2 (547 mm female, 615 mm male), 52.2198°N, 174.0388°W, 81 m depth, 24 June 1997, FV *Vesteraalen*, cruise 1997-01, haul 67; UW 117310, 1 (959 mm female), tissue, 51.7113°N, 178.2883°W, 148 m depth, 27 August 2005, G. R. Hoff, FV *Sea Fisher*, cruise 2005-01, haul 3; UW 117311, 3 (1005 mm male, 1025 mm female, 1150 mm male), tissue, 51.8317°N, 178.2967°W, 90 m depth, 27 August 2005, G. R. Hoff, FV *Sea Fisher*, cruise 2005-01, haul 4; UW 116010, 1 (1070 mm female), tissue, 53.6157°N, 167.4712°W, 94 m depth, 10 June 2004, J. W. Orr, FV *Sea Storm*, cruise 2004-01, haul 18; UW 116028, 1 (1060 mm male), 51.9105°N, 173.7785°W, 125 m depth, 19 June 2006, J. W. Orr, FV *Gladiator*, cruise 2006-01, haul 46, Genbank FJ869198; UW 116013, 1 (815 mm male), 54.15230°N, 166.3376°W, 152 m depth, 8 June 2004, J. W. Orr, FV *Sea Storm*, cruise 2004-01, haul 9; UW 112325, 1 (970 mm male), tissue, 53.1931°N, 167.7287°W, 82 m depth, 26 May 2003, J. W. Orr, FV *Northwest Explorer*, cruise 2003-01, haul 13, Genbank FJ869207; UW 48083, 1 (880 mm male), tissue, Aleutian Islands, 51.4092°N, 178.1637°W, 106 m depth, 10 October 2002, G. R. Hoff, FV *Sea Fisher*, cruise 2002-02, haul 49, Genbank DQ104922, FJ869194. **Bering Sea:** BCPM 985-242, 1 (234 mm male), 56.003°N, 168.23°W, 15 July 1984; MTUF 21942, 1 (430 mm male), 57.9667°N, 171.15°W, 92 m depth; MTUF 21939, 1 (530 mm male), 57.9667°N, 171.15°W, 92 m depth; UW 22336, 1 (1002 mm male), 56°N, 168.3°W, 160 m depth, 5 October 1980, M. Levenson, FV *Ekvator*, cruise 1980–01, haul 67; UW 22337, 1 (534 mm male), 55.665°N, 168.6833°W, 165 m depth, 5 October 1980, M. Levenson, FV *Ekvator*, cruise 1980–01, haul 66; HUMZ 33546, 1 (828 mm male), 58.5333°N, 167.4167°W, 1 July 1964; HUMZ 33543, 1 (702 mm female), 57.4167°N, 166.55°W, 2 July 1964; UW 48753, 1 (540 mm male), 60.012°N, 169.3298°W, 45 m depth, 24 June 2002, E. Acuna, FV *Arcturus*, cruise 2002-01, haul 100; UW 48751, 1 (510 mm male), 58.6545°N, 167.8613°W, 46 m depth, 23 June 2002, E. Acuna, FV *Arcturus*, cruise 2002-01, haul 92; MTUF 21921, 1 (965 mm male), 58.5°N, 175.1667°W; MTUF 21936, 1 (867 mm male), 58.5°N, 175.1667°W; UW 48755, 3 (329 mm male, 340 mm female, 348 mm female), 60.6626°N, 176.2187°W, 118 m depth, 16 July 2003, D. E. Stevenson, FV *Aldebaran*, cruise 2003-01, haul 173; UW 22338, 2 (520–645 mm females), dissected, Bering Sea, 54.7–62.0°N, 165.0–174.0°W, 2 January 1981, M. Levenson, RV *Ekvator*, cruise 198001; BCPM 985-241, 1 (248 mm female), 56.996°N, 170.705°W, 99 m depth, 14 July 1984; FAKU 122436, 1 (903 mm female), no data; FAKU-S 2671–2672, 2 (818 mm male, 923 mm female), no data; UW 48605, 1 (303 mm male), tissue, 59.33°N, 174.85°W, 121 m depth, 13 August 2002, FV *American Triumph*, cruise 7790, haul 376, Genbank FJ869195, FJ869212; UW 46421, 1 (655 mm female), 56.2467°N, 162.2417°W, 77 m depth, 10 July 1994, C. D. Wilson, RV *Miller Freeman*, cruise 199407, haul 2; UW 46418, 1 (485 mm male), 59.3447°N, 177.0561°W, 154 m depth, 29 July 1998, G. R. Hoff, FV *Aldebaran*, cruise 1998-01, haul 183; UW 48752, 2 (415–615 mm females), 59.0097°N, 169.1872°W, 54 m depth, 25 June 2002, FV *Arcturus*, cruise 2002-01, haul 103; UW 46423, 1 (475 mm male), tissue, 59.8480°N, 172.9079°W, 79 m depth, 4 July 2000, E. Acuna, FV *Aldebaran*, cruise 2000-01, haul 135, Genbank GQ469973; UW 119808, 3 (210 mm female, 227 mm female, 240 mm male), 54.9162°N, 165.3657°W, 122 m depth, 27 July 2003, D. E. Stevenson, FV *Arcturus*, cruise 2003-02, haul 171; UW 119806, 1 (235 mm), female, 54.9484°N, 165.3445°W, 120 m depth, 27 July 2003, FV *Arcturus*, cruise 200302, haul 180; UW 119807, 3 (225 mm male, 237 mm male, 260 mm female), 56.6760°N, 167.6731°W, 102 m depth, 26 June 2003, FV *Aldebaran*, cruise 2003-01, haul 94; UW 119811, 1 (200 mm male), 55.9983°N, 168.2241°W, 152 m depth, 26 June 2003, D. E. Stevenson, FV *Aldebaran*, cruise 2003-01, haul 98; UW 119628, 2 (220–240 mm), 56.3379°N, 167.6536°W, 129 m depth, 26 June 2003, D. E. Stevenson, FV *Aldebaran*, cruise 2003-01, haul 95; MTUF 21946, 1 (794 mm male), 58.9333°N, 178.0833°W, 310 m depth; UW 47200, 1 (310 mm male), tissue, 60.1667°N, 176.8833°W, 141 m depth, 26 August 2002, J. Miles, FV *American Triumph*, cruise 7790, haul 408, Genbank FJ869208; MTUF 21937, 1 (811 mm male), 61.1167°N, 179.1667°W; UW 112315, 1 (657 mm), tissue, Bering Sea, 25 March 2004; UW uncataloged, 6 (207 mm male, 212 mm female, 222 mm female, 222 mm female, 232 mm female, 272 mm male), 54.7672°N, 165.9174°W, 203 m depth, 7 August 2004, FV *Northwest Explorer*, cruise 2004-01, haul 233; MTUF 21932, 1 (957 mm female), 60°N, 174.45°W, 110 m depth; MTUF 21954, 1 (480 mm female), 60°N, 174.45°W, 110 m depth; UW 150018, 1 (1050 mm male, claspers only), Bering Sea, 61.6567°N, 176.4650°W, 103 m depth, 16 July 2003, G. R. Hoff, FV *Aldebaran*, cruise 2003-01, haul 176; UW 119269, 1 (1000 mm male, claspers and tissues only), Bering Sea, 56.5573°N, 172.0973°W, 272 m depth, 26 July 2004, FV *Northwest Explorer*, cruise 2004-01, haul 176, Genbank FJ869197; MTUF 21965, 1 (800 mm male), Bering Sea; UW 118932, 1 (1010 mm male), macerated, tissue, Bering Sea, 59.38°N, 177.61°W, 257 m depth, 1 August 2006, G. R. Hoff, FV *Northwest Explorer*, cruise 2006-02, hauls 17–22; UW 118933, 1 (1070 mm female), macerated, tissue, Bering Sea, 59.3854°N, 177.5912°W, 242 m depth, 1 August 2006, G. R. Hoff, FV *Northwest Explorer*, cruise 2006-02, haul 21; MTUF 21969, 1 (680 mm female), western Bering Sea, Ozernoy Bay, 57.1167°N, 163.3167°E, 450 m depth. **Gulf of Alaska:** BCPM 980-591, 1 (369 mm male), 59.7812°N, 141.7342°W, 62 m depth, 4 July 1981, FV *Ocean Harvester*, cruise 198101, haul 87; UW 112322, 1 (955 mm female), 54.7849°N, 163.2544°W, 41 m depth, 4 June 2003, J. W. Orr, FV *Northwest Explorer*, cruise 2003-01, haul 52; UW 113475, 1 (1023 mm male), 56.6266°N, 153.0948°W, 152 m depth, 3 August 2005, FV *Northwest Explorer*, cruise 2005-01, haul 310; UW 112326, 1 (710 mm female), 54.5250°N, 164.2417°W, 65 m depth, 1 June 2003, J. W. Orr, FV *Northwest Explorer*, cruise 2003-01, haul 35; UMMZ 129014, 1 (227 mm female), southeast Alaska, Frederick Sound between Frederick Pt. and Coney I., S of Petersburg, C. Hubbs; UW 119628, 1 (1120 mm male, claspers only), 52.2057°N, 172.8249°W, 161 m depth, 22 June 2004, J. W. Orr, FV *Sea Storm*, cruise 2004-01, haul 70. **No locality data:** HUMZ 34828, 1 (241 mm female); FAKU-S 2448, 1 (655 mm female).

Egg capsules. A total of 26 egg capsules (113–145 mm CL). **Bering Sea:** UW 119315, 12 (113–145 mm CL), Bering Sea, 56.9288°N, 173.3718°W, 213 m depth, 14 July 2004, FV *Northwest Explorer*, cruise 2004-01, haul 170; UW 119286, 9 (118–152 mm CL), Bering Sea, 54.8532°N, 165.6818°W, 145 m depth, 17 November 2004, G. R. Hoff, FV *Great Pacific*, cruise 2004-01, haul 2. **Gulf of Alaska:** UW 119287, 5 (117–131 mm CL), 53.8026°N, 165.1343°W, 150 m depth, 5 June 2007, J. W. Orr, FV *Vesteraalen*, cruise 2007–01, haul 19.

Tissues with photo vouchers only. A total of 45 tissues. **Aleutian Islands:** UW 117014, 16 (380–1290 mm), 51.1991°N, 179.0975°W, 93 m depth, 2 August 2006, P. Von Szalay, FV *Sea Storm*, cruise 2006-01, haul 229; UW 117015, 1 (1110 mm male), 51.6112°N, 178.1702°W, 126 m depth, P. Von Szalay, 2 August 2006, FV *Sea Storm*, cruise 2006-01, haul 231; UW 116848, 1 (975 mm male), 51.7659°N, 177.5172°W, 82 m depth, 26 June 2006, FV *Sea Storm*, cruise 2006-01, haul 70; UW 116847, 1 (sex and length unknown), 51.8007°N, 175.7054°W, 179 m depth, 23 June 2006, FV *Sea Storm*, cruise 2006-01, haul 68; UW 117301, 1 (750 mm male), 52.2839°N, 174.754°W, 162 m depth, 24 June 2006, J. W. Orr, FV *Gladiator*, cruise 2006-01, haul 64, Genbank FJ869200; UW 117303, 1 (975 mm male), 52.2629°N, 172.8827°W, 165 m depth, 21 June 2006, J. W. Orr, FV *Gladiator*, cruise 2006-01, haul 52, Genbank FJ869191; UW 117305, 1 (1085 mm male), 53.7772°N, 167.2704°W, 163 m depth, 8 June 2006, J. W. Orr, FV *Gladiator*, cruise 2006-01, haul 10; UW 117306, 1 (1060 mm female), 53.8017°N, 167.1223°W, 46 m depth, 8 June 2006, J. W. Orr, FV *Gladiator*, cruise 2006-01, haul 9; UW 117302, 1 (790 mm male), 54.0329°N, 166.6522°W, 76 m depth, 8 June 2006, J.W. Orr, FV *Gladiator*, cruise 2006-01, haul 8, Genbank FJ869205; UW 119647, 7 (790–1070 mm, 5 males, 2 females), 52.1415°N, 175.1125°W, 112 m depth, 24 June 2006, FV *Gladiator*, cruise 2006-01, haul 65, Genbank FJ869199, FJ869201, FJ869203, FJ869206, FJ869202; UW 119645, 1 (950 mm female), 58.0295°N, 153.2973°W, 133 m depth, 27 June 2003, FV *Gladiator*, cruise 2003-01, haul 131, Genbank FJ869216; UW 150058, 1 (1110 mm female), 52.2607°N, 173.6796°W, 145 m depth, 18 June 2004, J. W. Orr, FV *Sea Storm*, cruise 2004-01, haul 55, Genbank GQ469972. **Bering Sea:** UW 117945, 3 (780–863 mm, 2 males, 1 female), 59.5231°N, 178.0787°W, 200 m depth, 25 June 2002, G. R. Hoff, FV *Morning Star*, cruise 2002-02, haul 71, Genbank FJ869219, FJ869209; UW 117688, 2 (1010–1040 mm females), 55.1243°N, 167.5251°W, 199 m depth, 30 July 2004, FV *Northwest Explorer*, cruise 2004-01, haul

197, Genbank FJ869210, FJ869213. **Gulf of Alaska:** UW 117689, 4 (sex and length unknown), 55.7383°N, 156.7308°W, 204 m depth, 17 July 2003, D. E. Stevenson, FV *Northwest Explorer*, cruise 2003-01, haul 110, Genbank GQ469974, FJ869218, DQ104920, FJ869196.

Diagnosis. A species of *Arctoraja* distinguished from all other members of the subgenus by a complete or, uncommonly, an incomplete row of dorsal thorns extending from the nuchal region to the interdorsal; dorsum nearly uniform brown, often with vague dark spotting and a yellowish blotch at pectoral-fin base; and two unique COI haplotypes (Spies et al., 2011).

Bathyraja parmifera is distinguished from *B. panthera* by having fewer total thorns (19–36 vs. 31–42 in *B. panthera*), fewer tail thorns (15–23 vs. 19–28), internal carotid foramina widely separated (vs. foramina in a single median pit), distal portion of ventral marginal cartilage distolaterally directed and straight (vs. sinusoidal), accessory terminal 2 broadly triangular with short spike (vs. elongate with long spike), distal tip of axial cartilage bluntly rounded (vs. pointed), anterior portion of body short and narrow (vs. longer and wider); and tail short (vs. longer).

Bathyraja parmifera is distinguished from *B. simoterus* by its wider interdorsal space (1.0–3.9% TL vs. 0.5–1.0% TL in *B. simoterus*), fewer precaudal and caudal vertebrae (32–40 and 82–89 vs. 41 and 90), fewer tail thorns (15–23 vs. 22–28), larger orbit (4.3–5.3% TL vs. 2.6–4.8% TL), anterior- and posterior-most postdorsal and postventral foramina of the scapulacoracoid larger than three intervening foramina (vs. three postdorsal foramina slightly smaller posteriorly, posteriormost postventral foramina four times larger than preceding six foramina), distal projection of the ventral marginal directed distolaterally (vs. distally), ventral terminal tear-drop shaped (vs. lanceolate), and dorsal and ventral marginals extend to about a quarter the length of dorsal terminal 2 (vs. extending farther distally to distal tip of dorsal terminal 3).

Bathyraja parmifera is distinguished from *B. smirnovi* by its typically complete dorsal row of thorns (vs. always broadly interrupted between the nuchal and tail thorns in *B. smirnovi*), wider interdorsal space (1.0–3.9% TL vs. 0.1–1.4% TL in *B. smirnovi*), distal projection of the ventral marginal projecting distolaterally (vs. distally), ventral terminal tear-drop shaped (vs. lanceolate), and dorsal and ventral marginals extending to about a quarter the length of dorsal terminal 2 (vs. extending farther distally to distal tip of dorsal terminal 3).

Description. Maximum body size moderately large (maximum length examined 115 cm TL, maximum length observed 135 cm TL, Stevenson et al., 2007). Disc 1.1–1.3 times as broad as long. Anterior lobe of pelvic fin moderately long, length 0.39–0.82 times posterior lobe. Tail long, length of tail from posterior margin of cloaca to tip 0.76–1.15 times distance from tip of snout to posterior margin of cloaca.

Snout short; preorbital snout length 2.8–5.9 times orbital length and 2.7–4.1 times interorbital width; preoral snout length 1.5–2.4 times internarial distance. Interorbital space narrow, distance 0.58–1.14 times orbit length; orbit length 0.89–2.23 times spiracle length. Mouth width 11.0–15.6% of disc width.

Distance between first gill slits 2.1–2.8 times internarial distance; length of first gill slits 1.0–2.4 times length of fifth gill slits. Distance between dorsal fins variable, from 26–98% of base of first dorsal fin.

Disc with 1–4 nuchal thorns, 0–10 mid-dorsal thorns, 1–3 scapular thorns. Tail thorns 15–23, interdorsal thorns 1–3. Total thorns on the mid-dorsal line from posterior to the orbits to the tip of tail 19–36. Denticles on tail large, aligned in well-defined rows.

Neurocranium (Figs. 11–13, Table 8) with single large, elongate pear-shaped fontanelle in one dissected specimen (1002 mm). In other specimens (1010 and 1070 mm), two fontanelles are present: anterior oval; posterior long, rectangular. Cranial nerve IV foramen directly dorsal to foramen for cranial nerve II. Internal carotid foramina in separate pits, separated by a distance about equal to least width of rostral cartilage.

Scapulocoracoid (Fig. 14, Table 8) with markedly produced rear corner. Anterodorsal and anteroventral fenestrae subcircular, approximately equal in size, separated by a robust anterior bridge. Mesocondyle rounded. Postdorsal foramina 4, anteriormost and posteriormost about five times as large as others. Postventral foramina 5, anteriormost and posteriormost about three times as large as others. Pectoral radials 81–89.

Pelvic girdle (Fig. 15, Table 8) with a single large obturator foramen on left side, two present on right side, anterior on right side three times as large as posterior. Pelvic radials I, 21–29. Predorsal vertebral count 118–128: trunk vertebrae 32–40, predorsal caudal vertebrae 82–89.

Clasper robust (Figs. 16 and 17), 43.4–70.6% tail length in mature males. Projection present. Small denticles present externally at distal tip. Distal tip of axial cartilage blunt in lateral profile; dorsal marginal cartilage short, constricted distally to a narrow distal tip, extending for about half length of dorsal terminal 2; ventral marginal cartilage extending distally beyond dorsal marginal to about three-quarters length of dorsal terminal 2, distolateral extension thick and directed straight laterally, forming component projection. Dorsal terminal 1 notched proximally, strongly notched distally; dorsal terminal 2 about twice as large as dorsal terminal 3; accessory terminal 2 triangular in ventral view, with rounded distoventral protuberance, about half the length of ventral terminal; ventral terminal cartilage a broad tear-drop shape, ventral margin rounded.

Coloration. Dorsum nearly uniform brown in life, often with vague dark spots and pale yellow blotches at pectoral-fin bases and on anterior part of tail (Fig. 7). Ventrum creamy white, with few scattered dark blotches on disc, especially around the snout, mouth, and gill slits; cloaca often with dark margin; tail with irregular dark blotches along the ventral midline. Specimens from the central and eastern Aleutian Islands typically more heavily spotted, with larger pale blotches.

After storage in alcohol, dorsal background color grayish brown, often with a distinct white spot on posterior portion of each pectoral fin and scattered dark spots on dorsal disc and tail; ventral background color on disc uniformly light, and usually some dark pigment surrounding cloaca; ventral surface of tail light at margins and tip, dark blotches along midline of tail.

Egg capsule. Byssal threads attached on anterior horns (Fig. 10B, Table 9). Longitudinal ridges with domed apices (Fig. 10B). Additional description as for subgenus. Egg capsules of *B. parmifera* have been examined from as far west as 178°W at the eastern margin of Amchitka Pass and farther east in the Aleutian Islands, throughout the eastern Bering Sea, including the northern Bering Sea upper continental slope in Zhemchug Canyon, and in the Gulf of Alaska south of Unimak Pass.

Distribution. North Pacific from the Bering Sea to southeastern Alaska, abundant in the eastern Bering Sea, central and eastern Aleutian Islands, and common in the northern Gulf of Alaska (Fig. 18). Common among the Commander Islands and the western Bering Sea (Sheiko and Fedorov, 2000), but apparently absent from the western Aleutian Islands west of Amchitka Pass and Petral Bank. The northernmost specimen examined was the paralectotype taken in Norton Sound at about 63°N; the northernmost record in the RACE survey database is from Norton Sound, 63.98°N, 166.03°W, among several other survey records nearby. A single dried specimen was found washed up on a beach near Kivalina, Alaska, in the Chukchi Sea (Mecklenburg[1]). The eastern- and southern-most specimen examined was taken in Frederick Sound in southeast Alaska (UMMZ 129014).

Ecology and life history. *Bathyraja parmifera* is found at depths from 19 to 392 m (Stevenson et al., 2008) over soft bottoms. Egg cases are deposited seasonally in distinct nursery sites along the upper slope of the eastern Bering Sea; embryos may develop more than three years before emergence (Hoff, 2008). Males live to at least 15 years and females to 17 years (Matta and Gunderson, 2007). The smallest mature male and female were 85 and 87 cm, the largest immature male and female were 98 and 101 cm, respectively. Lengths at 50% maturity were 91.75 cm at 8.97 years in males and 93.28 cm at 9.71 years in females. A hermaphroditic *B. parmifera* has been recorded from the eastern Bering Sea (Matta, 2006).

The trypanorhynch cestode *Grillotia borealis* was described from host species *B. parmifera* and *B. smirnovi*, as well as *B. aleutica*, *B. interrupta*, and *B. minispinosa* (Kenney and Campbell, 2001). In the eastern Bering Sea, *B. parmifera* and its egg capsules have been found in the stomach contents of larger fishes, such as *Hippoglossus stenolepis*, *Gadus macrocephalus*, and other skates (Lang et al., 2005; Hoff, 2007, 2010), and its egg capsules are preyed upon by drilling gastropods, which consume the yolk within (Hoff, 2009).

In summer in the Aleutian Islands, large *B. parmifera* feed primarily on *Pleurogrammus monopterygius* and miscellaneous other fishes, while smaller *B. parmifera* feed on crabs and amphipods (Yang, 2007). In the eastern Bering Sea, mature *B. parmifera* feed primarily on *Theragra chalcogramma*, miscellaneous fishes, and *Chionocetes* crabs (Hoff, 2008).

Bathyraja parmifera constitutes more than 95% of the skate biomass on the eastern Bering Sea shelf (Lauth and Acuna, 2009). Population estimates suggest that the biomass of *B. parmifera* increased dramatically during the 1980s and has maintained a relatively high biomass for more than 15 years (Hoff, 2006). It is encountered frequently as bycatch in bottom trawl and longline fisheries in Alaskan waters and is occasionally landed for consumption (Lauth and Acuna, 2009).

Etymology. The name *parmifera* is taken from the Latin "*parma*," meaning "shield," and "*fero*," meaning "to bear" (Jordan and Evermann, 1898), likely in reference to the strong thorns along the midline.

Remarks and comparisons. Of the two syntypes on which Bean (1881) based *Raia parmifera*, we hereby designate USNM 27651 as the lectotype and USNM 28098 as the paralectoype. The lectotype is a female from Iliuliuk, Unalaska, for which Bean (1881) provided a more detailed description, including morphometric and meristic data. The previously unpublished illustration of the lectotype possibly prepared by A. H. Baldwin is provided here (Fig. 19). The paralectoype is a male taken in Norton Sound for which Bean (1881) provided only counts of thorns and a brief description of the claspers. Only the lectotype is now extant, but

[1] Mecklenburg, C. W. 2010. Personal commun. Point Stephens Research, 18881 Trail End Drive, Juneau, AK 99801.

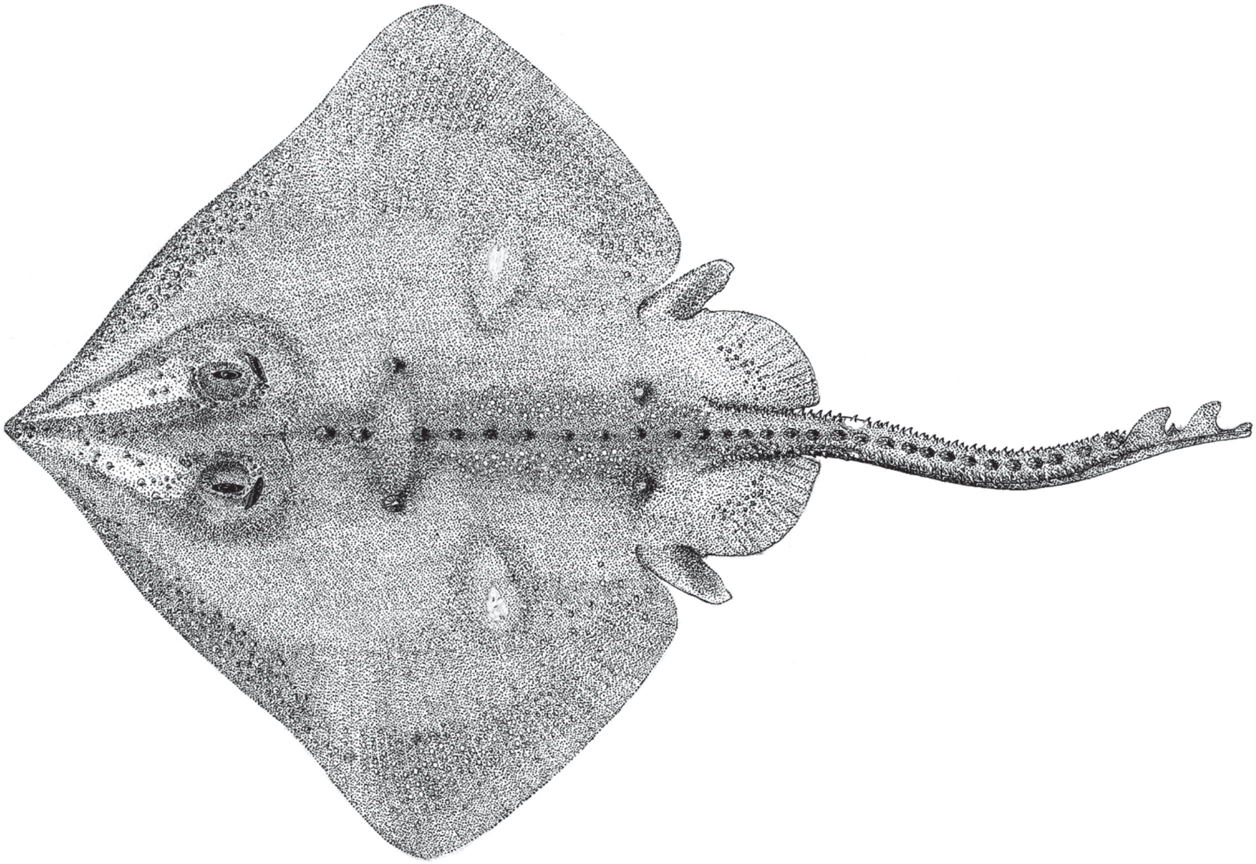

Figure 19

Raia parmifera, lectotype, 975 mm TL, USNM 27651. USNM Illustration P06693, possibly prepared by A. Baldwin. Courtesy of Lisa Palmer, Smithsonian Institution, NMNH, Division of Fishes.

it is badly deteriorated and cannot be used to confirm Bean's (1881) description.

We consider *Raia obtusa* Gill and Townsend (1897) to be a junior synonym of *B. parmifera*. Stehmann (1986) also placed the species in the synonymy of *B. parmifera* but without discussion. Unfortunately the original description of *R. obtusa* is uninformative, an illustration of the specimen was not provided, and no comparative comments were made. The holotype and only type specimen (USNM 48763) is badly deteriorated. However, vertebral counts of 35 + 80 (R. Ishiyama, unpubl. data[2]) are within the range of species of *Arctoraja*. *Raja obtusa* was described as having the orbital thornlets characteristic of adults of *Arctoraja*, and at least nine thornlets were present when examined by Ishiyama[2]. In addition, the numbers of tooth rows (27) in the upper jaw are also within the range of species of *Arctoraja*. The presence of a complete row of uninterrupted thorns along the midline and two scapular thorns are also characteristic of *B. parmifera*.

Gill and Townsend (1897) described *R. obtusa*, along with two other species, *Raia rosispinis* and *R. interrupta,* all from the Bering Sea. Now placed in *Bathyraja*, *B. interrupta* is presently recognized as a valid and common species (or species complex; Stevenson et al., 2007; Spies et al., 2011) found throughout the eastern North Pacific (Stevenson et al., 2007). *Raia rosispinis* has been considered a synonym of *B. parmifera* (Stehman, 1986; Mecklenberg et al., 2002); however, the absence of several characters and the presence of features in a previously unpublished illustration of the holotype (USNM 48762; Fig. 20) suggest that *R. rosispinis* is either a valid species or synonymous with *B. interrupta*. The holotype and only type specimen is disintegrated; however, a radiograph is available. The illustration is of an immature male about 350 mm disc length, uniformly covered with denticles, some enlarged, with no orbital thorns. Denticles are present at the base of the tail thorns, unlike the condition in all species of *Arctoraja*. Although an or-

[2] Ishiyama, R. 1962. Unpubl. data. Shimonoseki College of Fisheries, Yoshimi, Japan.

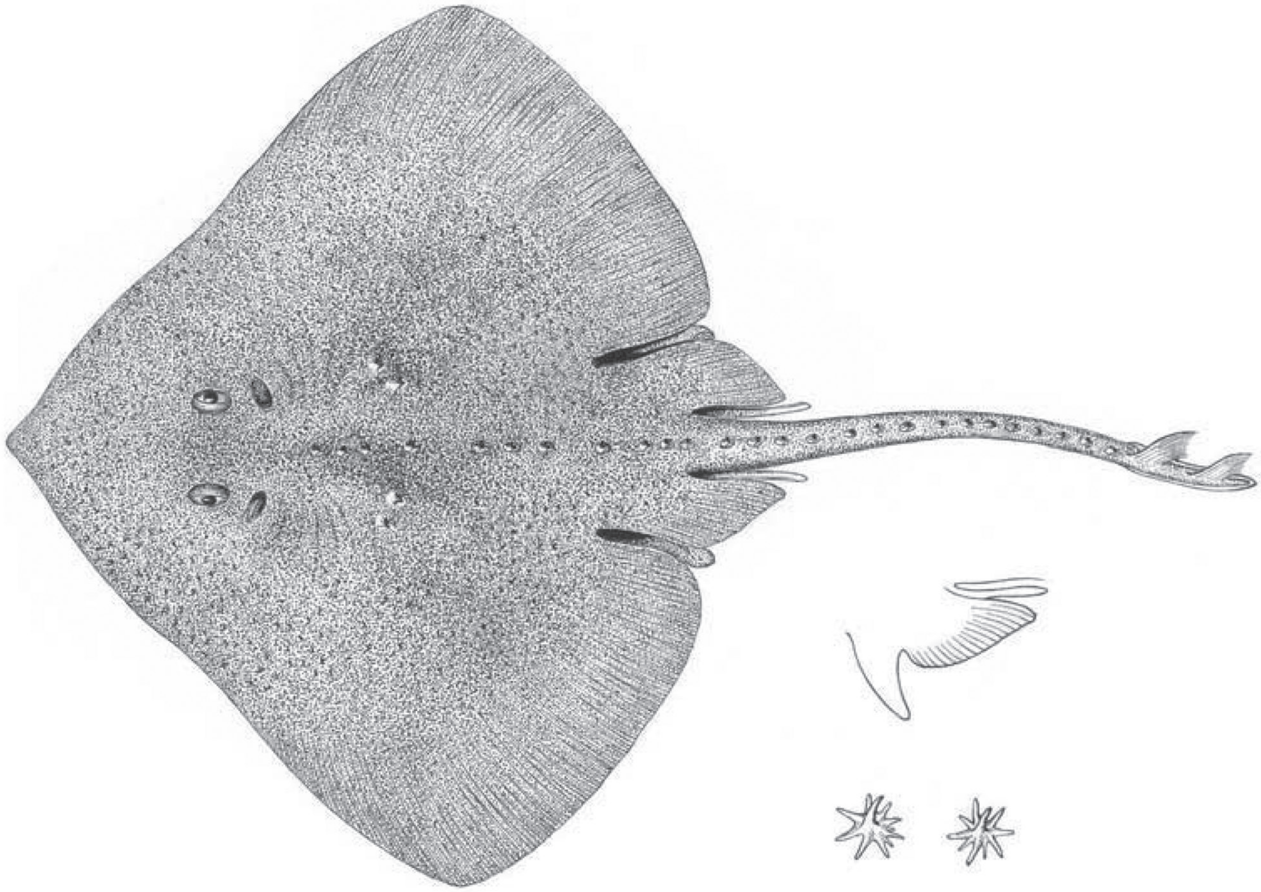

Figure 20

Raia rosispinis, holotype, ca. 350 mm disc length, USNM 48762. USNM Illustration P06700, possibly prepared by A. Baldwin. Courtesy of Lisa Palmer, Smithsonian Institution, NMNH, Division of Fishes.

bital series of thorns is noted in the original description ("antocular," "postocular," and "another behind it"), neither the illustration, radiograph, nor data of Ishiyama [2] indicate the presence of these thorns. Although Sheiko and Federov (2000) synonymized *R. rosispinis* with *Amblyraja hyperborea*, likely on the basis of Gill and Townsend's (1897) description of thorns, the vertebral counts of the holotype are much higher than those found in the eastern North Pacific species of *Amblyraja* (*A. badia*; Stevenson and Orr, 2005).

Bathyraja smirnovi is similar to *B. parmifera*. According to Ishiyama (1958a, 1967) it differs from *B. parmifera* in lacking middorsal thorns along the disc posterior to the nuchal thorns, possessing one rather than two nuchal thorns, having a pointed rather than blunt snout, having a relatively broader disc, and lacking the clasper component projection. The thorn characters do not consistently distinguish between the two species, but *B. smirnovi* has a relatively broad disc and although *B. smirnovi* has the clasper projection, it is weak unlike the strong projection in *B. parmifera*, further evidence that the two species are distinct. Some specimens of *B. parmifera* lack thorns in the middorsal region. That these individuals are indeed *B. parmifera* and not *B. smirnovi* is supported by genetic as well as morphological data. Seven specimens with tissues available had a wide naked area in the middorsal region, similar to *B. smirnovi*, but had the more common of the two *B. parmifera* COI haplotypes and lacked the additional differences at six other positions characterizing *B. smirnovi*.

Two COI haplotypes (Bparm1 and Bparm2) were found in genetic samples of *B. parmifera* (Spies et al., 2011). The rarer of the two (Bparm2) was found only in samples taken from specimens unavailable for morphological examination (i.e., the specimen was released at sea). Of more than 75 specimens examined morphologically, 13 also had tissues taken for genetic sampling. All of these specimens exhibited the com-

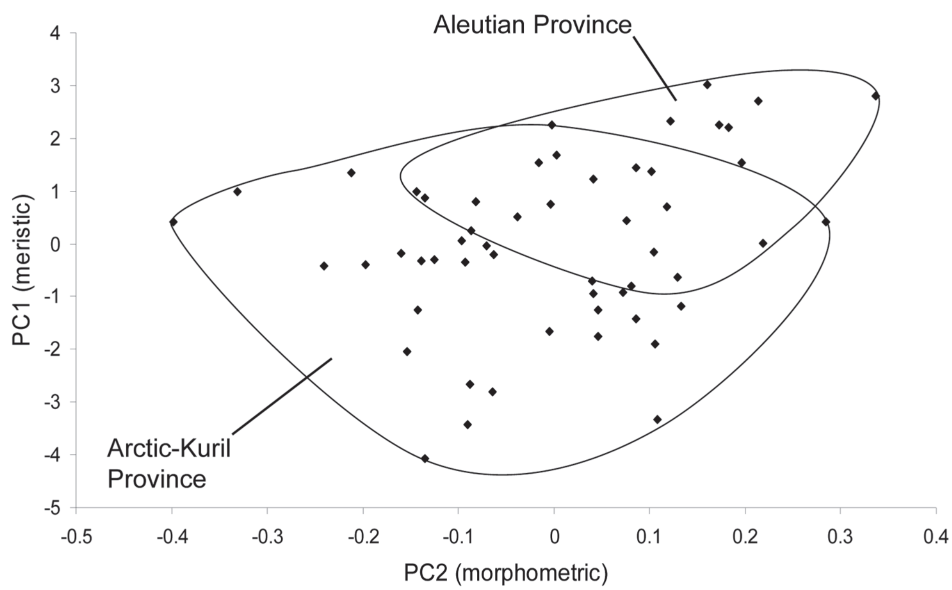

Figure 21

Plots of principal component scores (PC) for morphometric and meristic characters of *Bathyraja parmifera*.

mon haplotype Bparm1. Among the 86 specimens sampled for tissue only, 13 of these exhibited the less common haplotype of Bparm2. No morphological differences are evident in photos serving as vouchers, although most notably, both haplotypes were found among photographed specimens that had a complete mid-dorsal row of thorns and those that lacked mid-dorsal thorns. Both Bparm1 and Bparm2 were found broadly overlapping in distribution in the Bering Sea, Gulf of Alaska, and east of Samalga Pass in the eastern Aleutian Islands (Fig. 18). Only Bparm1 was found in the 20 tissues sampled across the 725 km of the central Aleutian Islands between Amchitka Pass and Samalga Pass, two deep-water zoogeographic barriers (Fig. 18; Logerwell et al., 2005; Spies et al., 2011), perhaps evidence of species-level separation rather than incomplete lineage sorting (i.e., a retained ancestral haplotype). A standard PCA of only *B. parmifera* suggests the presence of two populations slightly differentiated morphologically: a population primarily located in the Aleutian Province and a population located in the western and northeastern Bering Sea of the Arctic-Kuril Province (Fig. 21). Distinct, geographically separated nursery areas of *B. parmifera* have been recently discovered in the Eastern Bering Sea (Hoff, 2009), suggesting a possible mechanism for reproductive segregation of populations. Our laboratory will be collecting the additional samples necessary to conduct further work to establish the status of the two haplotypes.

Bathyraja (Arctoraja) smirnovi (Soldatov and Pavlenko, 1915) golden skate, Dobu-kasube

(Figures 2–5, 8, 10–18, 22; Tables 1–8)

Raja smirnovi Soldatov and Pavlenko, 1915:162 (original description, two specimens: holotype, apparently lost, male, 1077 mm, Russia, Peter the Great Bay; paratype, ZIN 19051, female, 525 mm TL, Sea of Okhotsk, 58.63°N, 152.75 °E, 126 m ["69 fms."], collected by Derbek).

Breviraja (Arctoraja) smirnovi: Ishiyama, 1952:6–9 (new combination, key).

Breviraja (Arctoraja) smirnovi smirnovi Ishiyama, 1958a:149 (new subspecies, key).

Breviraja (Arctoraja) smirnovi ankasube Ishiyama, 1958a:151 (original description, 25 specimens: holotype, apparently lost, "930 mm, Wakasa Bay, off Maizuru, Kyoto Prefecture; Oct. 13, 1953; paratypes, apparently lost, 24 specimens, 223–983 m, Akita, Sado Island, Niigata Prefecture, Maizuru; Oki Island, Shimane Prefecture").

Bathyraja smirnovi: Kato, 1971 (new combination, *Bathyraja* first proposed for North Pacific *Breviraja* by Ishiyama and Hubbs, 1968).

Material examined. A total of 82 specimens, 237–1094 mm TL, including one paratype listed above. **Sea of Okhotsk:** MTUF 21927, 1 (1015 mm male), 55.2667ºN, 154.8333ºE, 80 m depth; MTUF 21941, 1 (720 mm male), 55.2667ºN, 154.8333ºE, 80 m depth; MTUF

21960, 1 (653 mm male), 55.2667°N, 154.8333°E, 80 m depth; MTUF 21961, 1 (710 mm male), 55.2667°N, 154.8333°E, 80 m depth; MTUF 21970, 1 (685 mm female), 55.2667°N, 154.8333°E, 80 m depth; MTUF 21971, 1 (602 mm female), 55.2667°N, 154.8333°E, 80 m depth; HUMZ 58288, 1 (485 mm female), 56.7333°N, 143.5°E, 305 m depth, 16 September 1976; HUMZ 60359, 1 (593 mm male), 58.2°N, 154.1667°E, 275 m depth, 13 September 1976; ZIN 19051, 1 (525 mm female), 58.63°N, 152.75°E, 126 m depth; HUMZ 58182, 1 (377 mm female), 58.4833°N, 153.9667°E, 176 m depth, 13 September 1976; HUMZ 58183, 1 (475 mm male), 58.4833°N, 153.9667°E, 176 m depth, 13 September 1976; HUMZ 58184, 1 (330 mm female), 58.4833°N, 153.9667°E, 176 m depth, 13 September 1976; HUMZ 58185, 1 (541 mm female), 58.4833°N, 153.9667°E, 176 m depth, 13 September 1976; MTUF 21929, 1 (930 mm male), 54.05°N, 154.1667°E; MTUF 21962, 1 (870 mm male), 54.05°N, 154.1667°E; MTUF 21963, 1 (805 mm male), 54.05°N, 154.1667°E; MTUF 21964, 21972, 21930, 21931, 4 (660 mm male, 665 mm female, 915 mm male, 975 mm male), 51.8833°N, 154.7167°E, 290 m depth, 24 July 1963; HUMZ 90682, 1 (440 mm male), off Lake Touhutsu, northeastern Hokkaido, 44°N, 144.8333°E, 50 m depth, 7 May 1981; HUMZ 49053, 1 (249 mm male), coast of Hokkaido, 45.6167°N, 143.8833°E, 480 m depth, 8 October 1975; HUMZ 58997, 1 (393 mm female), East of Sakhalin, 47.7167°N, 144.1667°E, 120 m depth, 30 September 1976; HUMZ 152289, 1 (704 mm male), dissected, off Utoro, Hokkaido, 44.08°N, 144.97°E, 16 December 1996; HUMZ 77655, 1 (331 mm male), Kitami-Yamato Bank, 48.8°N, 144.4333°E, 800 m depth, 21 September 1978; ZIN 35385, 1 (535 mm male), Yuzhno, Sakhalin, Kuril-Sakhalin Expedition, 48.8°N, 143.6°E, August–September 1949; ZIN 35386, 1 (583 mm male), 25 miles SE off Cape Svobodnyy, 46.8°N, 143.5°E, 187 m depth, 4 September 1947; HUMZ 67436, 1 (628 mm female), Okhotsk coast of Hokkaido, 45.1667°N, 143.7°E, 188 m depth, 19 May 1977; HUMZ 143360, 1 (827 mm female), north of Shiretoko Pen., off Shari-Cho, 44.3°N, 145°E, 700 m depth, 17 July 1995; HUMZ 152304, 1 (752 mm female), off Utoro, Hokkaido, 44°N, 144.8°E, 21 April 1997; HUMZ 79671, 1 (628 mm female), Kitami-Yamato Bank, NE Hokkaido, 45.2267°N, 144.6833°E, 950 m depth, 6 September 1978; HUMZ 152282, 1 (887 mm male), off Utoro, Hokkaido, 44.08°N, 144.97°E, 500 m depth, 26 July 1996; HUMZ 143350, 1 (788 mm male), north of Shiretoko Pen., off Shari-Cho, 44.2°N, 145°E, 500 m depth, 20 November 1995; HUMZ 152274, 1 (768 mm female), off Utoro, Hokkaido, 44°N, 144.8°E, 500 m depth, 24 July 1996; HUMZ 152275, 1(587 mm male), off Utoro, Hokkaido, 44°N, 144.8°E, 500 m depth, 24 July 1996; HUMZ 152279, 1 (782 mm male), off Utoro, Hokkaido, 44°N, 144.8°E, 500 m depth, 24 July 1996; UW 114999, 2 (1076–1094 mm males), claspers and tissue only in 95% ethanol, 158 m depth, 4 Dec 2004, T. Yanagimoto, Genbank FJ869230–31. **Pacific Ocean:** HUMZ 192368, 1 (265 mm male), Pacific coast of Hokkaido; HUMZ 192369, 1 (272 mm female), Pacific coast of Hokkaido; HUMZ 192370, 1 (299 mm male), Pacific coast of Hokkaido; HUMZ 192371, 1 (286 mm male), Pacific coast of Hokkaido; HUMZ 58282, 1 (540 mm male), 144 m depth; HUMZ 58283, 1 (413 mm), 144 m depth; HUMZ 58284, 1 (381 mm male), 144 m depth; HUMZ 58286, 1 (489 mm), 144 m depth. NSMT-P 68833, 1 (979 mm male), tissue, off E. Hokkaido, 462 m depth, 5 November 2003; NSMT-P 68834, 1 (1002 mm male), tissue, off E. Hokkaido, 462 m depth, 5 November 2003; ZIN 35387, 1 (558 mm female), Iturup Island, 45°N, 148°E, 124–146 m depth, 26 September 1949. **Sea of Japan:** HUMZ 34897, 1 (225 mm male), Japan, Akita Pref., Honshu, 24 May 1972; HUMZ 53081, 1 (381 mm female), Yamato-tai, 39.2833°N, 135.075°E, 460 m depth, 29 May 1976; HUMZ 53790, 1 (418 mm female), Yamato-tai, 39.2833°N, 135.075°E, 460 m depth, 29 May 1976; HUMZ 66123, 1 (237 mm male), off Ishikawa Pref., 38.0167°N, 137.1167°E, 295 m depth, 28 May 1977; NSMT-P 61660, 2 (393 mm male, 505 mm female), 39.5617°N, 133.76°E; NSMT-P 61664, 1 (391 mm male), 39.5933°N, 135.7183°E, 732 m depth, 27 August 2001; NSMT-P 61686, 1 (497 mm female), Yamato Bank; NSMT-P 61687, 1 (625 mm female), Yamato Bank; NSMT-P 61665, 1 (448 mm male), Yamato Bank; UMMZ 200725, 1 (525 mm male), Sea of Japan, Yamato-tai; UW 119198, 1 (228 mm male), tissue in 95% ethanol, 36.0057°N, 132.5198°E, 359 m depth, 4 July 2009, Y. Kai; UMMZ 200724, 1 (395 mm female), Japan, Toyama Bay near Namerikawa, 36.46°N, 137.2°E, C. Hubbs and K. Sakamoto; HUMZ 68590, 1 (705 mm male), west coast of Hokkaido, north of Shakotan Peninsula, 45.2267°N, 140.6533°E, 444 m depth, 2 July 1997; HUMZ 42465, 1 (497 mm male), off Okushiri Is., SW Hokkaido, 42.0167°N, 139.6167°E, 655 m depth, 6 June 1975; HUMZ 42689, 1 (497 mm male), off Okushiri Is., southwest of Hokkaido, 42.09°N, 139.66°E, 700 m depth, 5 June 1975; HUMZ 42839, 1 (387 mm female), off Okushiri Is., southwest of Hokkaido, 42.09°N, 139.66°E, 700 m depth, 5 June 1975; HUMZ 42690, 1 (400 mm female), off Okushiri Is., southwest of Hokkaido, 42.09°N, 139.66°E, 700 m depth, 5 June 1975; HUMZ 42844, 1 (308 mm female), off Okushiri Is., southwest of Hokkaido, 42.09°N, 139.66°E, 700 m depth, 5 June 1975; HUMZ 42729, 1 (385 mm female), off Okushiri Is., southwest of Hokkaido, 42.09°N, 139.66°E, 700 m depth, 5 June 1975; HUMZ 42840, 1 (420 mm male), off Okushiri Is., southwest of Hokkaido, 42.09°N, 139.66°E, 700 m depth, 5 June 1975; HUMZ 42843, 1 (258 mm male), off Okushiri I., southwest of Hokkaido, 42.09°N, 139.66°E, 700 m depth, 5 June 1975; HUMZ 46650, 1 (383 mm male), off Okushiri I., southwest of Hokkaido, 41.8167°N, 139.5817°E, 720 m depth, 7 June 1975; HUMZ 46616, 1 (348 mm female), off Okushiri I., southwest of Hokkaido, 41.8167°N, 139.5817°E, 720 m depth, 7 June 1975; HUMZ 46619, 1 (475 mm female), off Okushiri I., southwest of Hokkaido, 41.8167°N, 139.5817°E, 720 m depth, 7 June 1975; HUMZ 46649, 1 (470 mm female), off Okushiri I., southwest of Hokkaido, 41.8167°N, 139.5817°E, 720 m depth, 7 June 1975; HUMZ 46647, 1 (467 mm male), off Okushiri I., southwest of Hokkaido, 41.8167°N, 139.5817°E, 720 m depth, 7 June 1975; NSMT-P 65750, 1 (443 mm female), 27 August 2002; NSMT-P 65751, 1 (551 mm female), 27 August 2002. **No locality data:** FAKU 49460, 1 (900 mm male); FAKU 111943, 1 (800 mm female); HUMZ 34859, 1 (482 mm male); NSMT-P 61680, 1 (415 mm male); NSMT-P 76121, 1 (400 mm male), tissue in 95% ethanol; NSMT-P 76122, 1 (478 mm female), tissue in 95% ethanol.

Diagnosis. A species of *Arctoraja* distinguished from all other members of the subgenus by the absence of a complete row of middorsal thorns, and ridge of clasper poorly developed (vs. strongly developed).

Bathyraja smirnovi is further distinguished from *B. parmifera*, which occasionally lacks middorsal thorns, by the following characters: narrow interdorsal space (0.1–1.4% TL vs. 1.0–3.9% TL), distal projection of the ventral marginal projects directly distally (vs. distolaterally), ventral terminal lanceolate (vs. tear-drop shaped), dorsal and ventral marginals extending farther distally to distal tip of dorsal terminal 3 (vs. extending to about a quarter the length of dorsal terminal 2), and COI haplotype (Spies et al., 2011).

It is further distinguished from *B. panthera* by its narrower interdorsal length (0.1–1.4% TL vs. 1.4–3.1% TL); anterior portion of body shorter and narrower (vs. longer and wider); tail shorter (vs. longer); single cranial fontanelle (vs. separate anterior and posterior fontanelles); ventral terminal lanceolate (vs. tear-drop shaped); dorsal and ventral marginals extending farther distally to distal tip of dorsal terminal 3 (vs. extending to about a quarter the length of dorsal terminal 2); and COI haplotype (Spies et al., 2011).

It is further distinguished from *B. simoterus* by having fewer vertebrae (118–127 vs. 131 in *B. simoterus*), fewer precaudal vertebrae (31–38 vs. 41), larger mouth size (8.3–11.6% TL vs. 8.1–9.1% TL), neurocranium with one fontanelle (vs. two), internal carotid foramina close together in a single pit (vs. widely separated), scapulocoracoid with five foramina, anterior- and posteriormost larger than three intermediates (vs. three foramina, more posterior each slightly smaller), and pelvic girdle with two obturator foramina close together (vs. widely spaced).

Description. Maximum body size moderately large (maximum length examined 101.5 cm TL, maximum length reported 116 cm TL; Ishiyama, 1958a). Disc 1.19 (range 1.14–1.37) times as broad as long. Anterior lobe of pelvic fin moderately long, length 0.64 (0.46–0.90) times posterior lobe. Tail long, length of tail from posterior margin of cloaca to tip 0.89 (0.71–1.05) times distance from tip of snout to posterior margin of cloaca.

Preorbital snout length 3.98 (2.83–4.13) times orbital length and 2.61 (2.56–3.72) times interorbital width; preoral snout length 2.08 (1.53–2.36) times internarial distance. Interorbital space narrow, distance 0.66 (0.66–1.13) times orbit length; orbit length 1.63 (1.15–2.1) times spiracle length. Mouth width 15.0 (11.2–16.5)% of disc width.

Distance between first gill slits 2.39 (2.21–2.66) times internarial distance; length of first gill slits 1.16 (1.0–1.71) times length of fifth gill slits. Distance between dorsal fins short, 44 (2–44)% of base of first dorsal fin.

Upper surface of disc and lateral margins of tail sparsely covered with coarse dermal denticles (denticles absent around thorns); orbital thornlets lining the anterior and posterior rims of orbits; denticles with stellate bases and posteriorly directed recurved spines.

Disc with 2 (1–4) nuchal thorns, 0 (0–4) mid-dorsal thorns, and 1 (1–2) scapular thorn. Tail thorns 22 (17–31), interdorsal thorns 1 (0–2). Total thorns on the mid-dorsal line from posterior to the orbits to the tip of tail 25 (20–35). Denticles on tail small, scattered or aligned in poorly defined rows.

Neurocranium (Figs. 11–13, Table 8) with single large, elongate pear-shaped fontanelle. Cranial nerve IV foramen dorsal to foramen for cranial nerve II. Separate intercerebral vein foramen absent. Internal carotid foramina in single median pit.

Scapulocoracoid (Fig. 14, Table 8) with rounded rear corner. Anteroventral fenestrae subcircular, approximately equal in size, separated by a robust anterior bridge. Mesocondyle elongate. Postdorsal foramina are of various sizes in *B. smirnovi*, with the anteriormost largest. Postventral foramina of various sizes in *B. smirnovi*, the anteriormost about twice as large as succeeding foramina, with the exception of the posteriormost, which is about three times the size of the smallest. Pectoral radials 82–92.

Pelvic girdle (Fig. 15, Table 8) with two closely spaced obturator foramina on each side. Pelvic radials I, 21–25. Predorsal vertebral 118–127: trunk vertebrae 31–38, predorsal caudal vertebrae 83–96.

Clasper moderately robust (Figs. 16 and 17), 49.3–75.0% tail length in mature males. Projection absent. Small denticles present externally at distal tip. Distal tip of axial bluntly rounded in lateral profile; dorsal marginal cartilage long, extending for about the entire length of dorsal terminal 2, gradually narrowing to the distal tip; ventral marginal cartilage extending distally

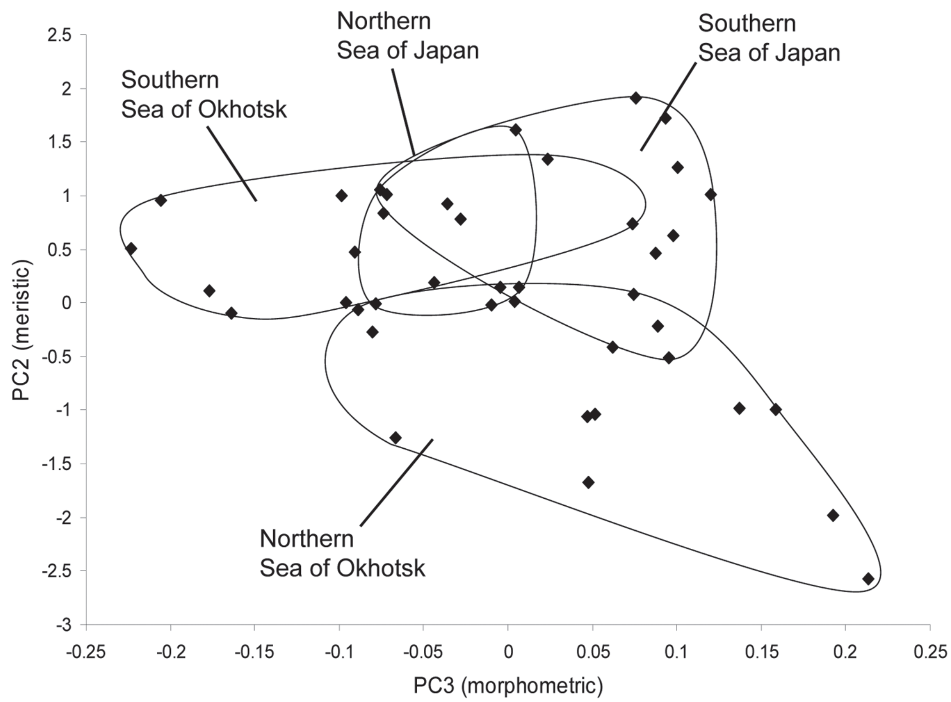

Figure 22

Plots of principal component scores (PC) for morphometric and meristic characters of *Bathyraja smirnovi*.

beyond dorsal marginal to just beyond the distal end of dorsal terminal 2, its distolateral extension slender and oriented distally, embedded deeply in clasper tissue, forming a weak projection. Dorsal terminal 1 strongly notched proximally and distally; dorsal terminal 2 of similar size to dorsal terminal 3; accessory terminal 2 triangular in ventral view, with rounded distoventral protuberance, one-third the length of ventral terminal; ventral terminal cartilage lanceolate, with distal margin slightly crenulate.

Coloration. Dorsum nearly uniform brownish-gray (Fig. 8). After storage in alcohol, dorsal background color grayish brown; ventral background color light with dark markings on tail, cloaca, and possibly on the snout, and around the gill slits.

Egg capsule. Longitudinal ridges with domed apices (Fig. 10C). Additional description as for subgenus (Ishiyama, 1958b, fig. 68, I3–I4; Fig. 10C); photo published by Ishihara et al. (2005).

Distribution. Material examined was collected from the Sea of Okhotsk, Kuril Islands, and the Sea of Japan (Fig. 18).The northernmost record examined is the paratype from the northern Sea of Okhotsk. The southernmost record examined was taken in the southern Sea of Japan at 36°N.

Ecology and life history. The trypanorhynch cestode *Grillotia borealis* was described from host species *B. smirnovi* and *B. parmifera*, as well as *B. aleutica*, *B. interrupta*, and *B. minispinosa* (Kenney and Campbell, 2001). On Yamato Bank in the Sea of Japan, *B. smirnovi* feeds primarily on amphipods, decapods, fishes, euphausids, and squid (Kono et al., 2008).

Etymology. The name *smirnovi* is a patronym in honor of "Mr. Smirnov," Inspector of Fishes, who collected fishes from the Sea of Okhotsk (Soldatov and Pavlenko, 1915).

Remarks. Analyses of both meristic and morphometric variation in *B. smirnovi* suggest that populations of the northern and southern Sea of Okhotsk, as well as the southern Sea of Japan, may be differentiated from one another (Fig. 22). Ishiyama (1958a) erected two subspecies, referring specimens from the southern Sea of Okhotsk off Hokkaido to *B. s. smirnovi* and specimens from the eastern Sea of Japan off Akita and Oki Island to *B. s. ankasube*. He distinguished the subspecies on the basis of clasper morphology and the degree of development of the electric organ, as well as the relative length of the snout (longer in *B. s. smirnovi*) and tail (shorter in *B. s. smirnovi*). We did not examine the electric organ and were able to examine in detail only two sets of mature claspers, both from the southern Sea of Okhotsk, but our data also show that the anterior lobe of the pelvic fin and the tail are shorter and thorns along the dorsal midline are fewer in specimens from the northern Sea of Okhotsk relative to those of specimens from the Sea of Japan and off the Pacific coast of Japan. While thorn counts indicate a latitudinal cline from low counts in the northern Sea of Okhotsk to high counts off northern Japan (a reverse of Jordan's Rule; Jordan, 1892), thorn counts of specimens from the northern Sea of Japan are significantly higher than those in specimens from the southern Sea of Japan (exhibiting the pattern of Jordan's Rule). Counts taken from specimens from the southern Sea of Japan are comparable to those of specimens from the Sea of Okhotsk. Additionally, unlike all other regional groups within *B. smirnovi*, but like all other species of *Arctoraja*, the southern Sea of Okhotsk specimens exhibit a direct relationship between interdorsal length and total length. Primarily because nearly all of our Sea of Japan specimens are small and immature, our data are inadequate to thoroughly examine the status of populations within *B. smirnovi*. Although Kato (1971) examined morphometric variation in *B. smirnovi* and found little evidence of significant morphometric differences other than those related to size and gender, his large sample was restricted to the central Sea of Japan only. Similarly, the five specimens for which we analyzed mitochondrial DNA (Spies et al., 2011) had identical sequences within the COI subunit gene. The two specimens with known locality data came from the same general area off Hokkaido in the southern Sea of Okhotsk.

Bathyraja (Arctoraja) simoterus **(Ishiyama, 1967)** **Hokkaido skate, Tsuno-kasube**

(Figures 2–5, 9–18; Tables 1–8)

Raja parmifera: Ishiyama, 1950 (misidentification, description of egg capsules from Muroran specimen of *B. simoterus*).

Breviraja parmifera: Ishiyama, 1958a (misidentification, new combination; description of holotype and egg capsules of *B. simoterus*).

Breviraja simoterus Ishiyama, 1967:62 (original description, one adult male and two egg capsules, all apparently lost: holotype, FAKU 40136, male, 941 mm TL, "below 300 m near Muroran, Hokkaido," 1938, collected by K. Matsubara; paratypes, two egg capsules, capsule length ca. 120 mm, taken from female collected near Muroran).

Bathyraja simoterus: Nakaya, 1984:14 (new combination, *Bathyraja* first proposed for North Pacific *Breviraja* by Ishiyama and Hubbs, 1968).

Material examined. A total of five specimens, 690–1006 mm TL: **Sea of Okhotsk:** HUMZ 152280, 1 (792 mm male), off Utoro, Hokkaido, 44°N, 144.8°E, 500 m depth, 24 July 1996; HUMZ 143347, 1 (711 mm male), Hokkaido, Shari-gun, Shiretoko Peninsula, along coast of Shari-cho, 44.2°N, 145°E, 540 m depth, 21 October 1995; HUMZ 143369, 1 (690 mm male), dissected, off Utoro, Shari, Hokkaido, 44°N, 144.8°E, Genbank GQ449820; HUMZ 143363, 1 (1006 mm male), north of Shiretoko, off Shari-Cho, 44.2°N, 145°E, 500 m depth, 17 July 1995, Genbank FJ869229. **Pacific Ocean:** HUMZ 21787, 1 (881 mm female), Kushiro, eastern Hokkaido, 42.83°N, 144.65°E, 96 m depth, 26 April 1996.

Diagnosis. A species of *Arctoraja* distinguished from all other members of the subgenus by the combination of a complete row of dorsal thorns, narrow interdorsal space, high count of precaudal vertebrae, and COI haplotype (Spies et al., 2011).

Bathyraja simoterus is further distinguished from *B. parmifera* by its narrower interdorsal space (0.5–1.0% TL vs. 1.0–3.9% TL in *B. parmifera*), greater number of precaudal and caudal vertebrae (41 and 90 vs. 32–40 and 82–89), more tail thorns (22–28 vs. 15–23), larger orbit (4.3–5.3% TL vs. 2.6–4.8% TL), three postdorsal foramina slightly smaller posteriorly, posteriormost postventral foramina four times larger than preceding six foramina (vs. anterior- and posterior-most postdorsal and postventral foramina of the scapulacoracoid larger than three intervening foramina), distal projection of the ventral marginal directed distally (vs. distolaterally), ventral terminal lanceolate (vs. tear-drop shaped), dorsal and ventral marginals extending farther distally to distal tip of dorsal terminal 3 (vs. extending to about a quarter the length of dorsal terminal 2), and COI haplotype (Spies et al., 2011).

Bathyraja simoterus is distinguished from *B. panthera* by its narrow interdorsal space width (0.5–1.0% TL vs. 1.4–3.1% TL in *B. panthera*); anterior portion of body shorter and narrower (vs. longer and wider); tail shorter (vs. longer); posterior fontanelle narrowly elongate (vs. pear-shaped); internal carotid foramina widely separated (vs. foramina in a single median pit), foramen of scapulocoracoid all large (vs. anterior postdorsal foramen large, others much smaller), ventral terminal lanceolate (vs. tear-drop shaped), and COI haplotype (Spies et al., 2011).

It is distinguished from the incompletely thorned *B. smirnovi* by its higher number of vertebrae (131 vs. 118–127 in *B. smirnovi*), more precaudal vertebrae (41 vs. 31–38), smaller mouth size (8.1–9.1% TL vs.

8.3–11.6% TL), neurocranium with two fontanelles (vs. one), internal carotid foramina widely separated (vs. close together in a single pit), scapulocoracoid with three foramina, more posterior each slightly smaller (vs. five foramina, anterior- and posteriormost larger than three intermediates), and pelvic girdle with two obturator foramina widely spaced (vs. close together).

Description. Body moderately large (maximum length recorded and examined 101 cm TL). Disc 1.2–1.4 times as broad as long. Anterior lobe of pelvic fin moderately long, length 0.67–0.86 times posterior lobe. Tail long, length of tail from posterior margin of cloaca to tip 0.84–0.93 times distance from tip of snout to posterior margin of cloaca.

Snout short; preorbital snout length 2.6–3.5 times orbital length and 2.8–3.2 times interorbital width; preoral snout length 1.8–2.2 times internarial distance. Interorbital space narrow, distance 0.90–1.14 times orbit length; orbit length 1.3–1.9 times spiracle length. Mouth width 11.0–12.2% of disc width.

Distance between first gill slits 2.5–2.6 times internarial distance; length of first gill slit 1.2–1.8 times length of fifth gill slit. Distance between dorsal fins small, 14.8–31.0% of base of first dorsal fin.

Disc with 3–4 nuchal thorns, 5–8 mid-dorsal thorns, 1–3 scapular thorns. Tail thorns 22–28, interdorsal thorn 1. Total thorns on the mid-dorsal line from posterior of the orbits to the interdorsal space 33–38. Denticles on tail small, aligned in poorly defined rows.

Neurocranium (Figs. 11–13, Table 8) with separate anterior and posterior fontanelles: anterior fontanelle round; posterior fontanelle elongate, narrow. Cranial nerve IV foramen well anterior to foramen for cranial nerve II. Internal carotid foramina pits widely separated by a distance about twice the least width of rostral cartilage.

Scapulocoracoid (Fig. 14, Table 8) with rounded rear corner. Anteroventral fenestrae subcircular, dorsal fenestra about three times as large as ventral, separated by a robust anterior bridge. Mesocondyle elongate. Postdorsal foramina 3, nearly equal in size, slightly smaller posteriorly; postventral foramina 7, posteriormost about twice the size of more anterior foramina. Pectoral radials 82–90.

Pelvic girdle (Fig. 15, Table 8) with two closely spaced obturator foramina on one side, one present posteriorly on one side. Pelvic radials I, 24. Predorsal vertebral count 131: trunk vertebrae 41, predorsal caudal vertebrae 90.

Clasper robust (Figs. 15 and 16), 70% tail length in sole mature male examined. Projection present. Denticles absent externally at distal tip. Distal tip of axial bluntly rounded in lateral profile; dorsal marginal cartilage long, extending for about the entire length of dorsal terminal 2, gradually narrowing to the distal tip; ventral marginal cartilage extending distally beyond dorsal marginal to well beyond the distal end of dorsal terminal 2, its distolateral extension slender and oriented distally, forming component projection. Dorsal terminal 1 un-notched proximally and strongly notched distally; dorsal terminal 2 of similar size to dorsal terminal 3; accessory terminal 2 triangular in ventral view, with rounded distoventral protuberance, about one-third the length of ventral terminal; ventral terminal cartilage lanceolate, with distal margin slightly crenulate.

Coloration. After storage in alcohol, dorsal background color grayish brown, with vague dark spots and pale yellow blotches at pectoral-fin bases (Fig. 9); ventral background color uniformly light, with dark blotches on tail and around cloaca. Color in life unknown.

Egg capsule. Longitudinal ridges with expanded apices (Fig. 10D). Additional description as for subgenus (Ishiyama, 1967, fig. 19, E and F; Fig. 10D). Described by Ishiyama (1950, 1958b) as an egg capsule of *B. parmifera* and by Ishiyama (1967) as that of *B. simoterus*.

Distribution. Known from off Hokkaido, northern Japan, in the Pacific Ocean, off Muroran (the type locality) and Kushiro, and in the southern Sea of Okhotsk (Fig. 18) at depths of 96–540 m.

Etymology. The specific epithet *simoterus* is likely derived from the comparative tense of the Greek σιμός, meaning "pug-nosed," referring to the rounded snout.

Remarks. Ishiyama (1967) described *B. simoterus* on the basis of the specimen he originally recognized as *B. parmifera* in his earlier review (Ishiyama, 1958a). He distinguished his two specimens of *B. simoterus* from the holotype of *B. parmifera* using three characters that we also found to vary in species of *Arctoraja*: 1) orbit 4.5 times into broad, rounded snout; 2) length of tail from origin of first dorsal much longer than outer spiracle width; and 3) clasper blunt and lacking distal denticles. Ishiyama (1967) gave no indication of whether he thought snout length was longer or shorter than in *B. parmifera*, but orbit length is relatively longer in *B. simoterus* than in all other species of *Arctoraja* (Fig. 2). The distance from origin of the first dorsal fin compared with outer spiracular width is greater than in most individuals of *B. parmifera*, but it does not differ from either *B. panthera* or *B. smirnovi* (Fig. 2). Denticles are present on the clasper in all species except *B. simoterus*, but although the clasper of *B. simoterus* is more robust than in *B. smirnovi*, its external shape is similar to *B. panthera* and *B. parmifera*. We found no differences in one other character listed by Ishiyama (1967): dorsal surface of disc of mature male naked except for denticles along margin and along midline of disc. Unfortunately the states of these characters are not given for *B. parmifera*, and the type specimen of this species is a female that is now disintegrated.

In their key to *Bathyraja* of the North Pacific, Ishihara and Ishiyama (1985) distinguished *B. simoterus* and *B. parmifera* by shape of the snout and coloration: snout tip narrowly projected in *B. parmifera* (vs. wide, not projected in *B. simoterus*), dorsal surface of disc with white spots (vs. white spots absent), and dorsal surface of tail with white cross bars (vs. bars absent). The difference in width of the snout tip may be valid but is highly subjective and, while the greater width is evident in our five specimens of *B. simoterus*, snout width is variable in *B. parmifera*. The color characters are valid for *B. parmifera* from the Bering Sea; however, in the central and eastern Aleutian Islands, *B. parmifera* is more strongly colored and, in particular, light bars on the tail and light spots on the dorsum are present. Although all of the characters used by Ishiyama (1967) and Ishihara and Ishiyama (1985) to distinguish the two species are within the range of variation of the specimens of *B. parmifera* we examined, interdorsal length, among other diagnostic characters listed above, readily distinguishes *B. simoterus* from *B. parmifera*.

Thorn counts are often considered too variable to be useful in distinguishing closely related species of *Bathyraja*. Within *Arctoraja*, however, not only are thorn counts useful diagnostic characters to distinguish *B. panthera* and *B. simoterus* from *B. parmifera* and *B. smirnovi*, they also show significant trends. For example, the total dorsal thorn counts of *B. parmifera* and *B. smirnovi* broadly overlap, despite *B. smirnovi* lacking nearly all thorns in the middorsal region (the few present are either the end of the nuchal series or the beginning of the tail series). The overlap between the two species reflects the higher number of tail thorns in *B. smirnovi*. A slight ontogenetic decrease in total thorns is evident within all three species for which we had an adequate size range of material for examination. Within *B. parmifera*, a reverse latitudinal cline in thorn counts is evident, with generally higher counts in specimens from the Aleutian Islands and Gulf of Alaska than in more northern material from the eastern and western Bering Sea, similar to the situation in *B. smirnovi* from the Sea of Okhotsk.

Ishiyama (1958a, 1967) distinguished *B. simoterus* from *B. smirnovi* in keys to the subgenus *Arctoraja*. Differentiated primarily on the basis of a complete versus incomplete row of middorsal thorns, he also separated the species by the greater disc width, shorter rostral appendices, more precaudal vertebrae (83–91 vs. 82), a poorly developed ridge in the clasper, absence of a clasper projection, and presence of small denticles on the external surface of the clasper in *B. smirnovi*. The projection was present in our material examined of each species, although weaker in *B. smirnovi*. Otherwise, with the exception of rostral appendices, combinations of these characters serve to distinguish *B. simoterus* from *B. smirnovi* in our material examined. The vertebral counts provided by Ishiyama (1958a, 1967) for the holotype of *B. simoterus* are lower than our counts, but he likely dissected the specimen to obtain his data, a method that is less accurate than counts taken by radiograph. However, assuming the counts are accurate, the precaudal vertebral count is higher than that of *B. smirnovi* and both caudal and total counts are within the higher portion of the vertebral ranges of all species.

While no differences were found in COI sequence data between *B. smirnovi* and *B. simoterus*, these results are not particularly surprising given the results found in other North Pacific species of *Bathyraja*. Spies et al. (2006) found low divergence among species of *Bathyraja* and no fixed differences between *B. lindbergi* and *B. maculata*, two species that are commonly captured and readily identifiable in syntopic collections from the upper continental slope of the Bering Sea (Stevenson et al., 2007, 2008). Other batoids with identical COI sequences are known from Australia (Ward et al., 2008). No genetic data are available for these species from any other region of the genome and more comprehensive analyses with fresh material are needed. A more complete discussion of the molecular systematics of *Arctoraja* is provided by Spies et al. (2011).

It might be argued that *B. simoterus* represents only fully thorned specimens of *B. smirnovi*, similar to the situation in *B. parmifera*, in which individuals without middorsal thorns are found among the far more common fully thorned individuals in the Bering Sea. Indeed Dolganov (1999, 2001) and Dolganov and Korolev (2006) argued from observations of this kind of variation that both *B. smirnovi* and *B. simoterus* were synonyms of *B. parmifera*. In this view, the species are populations of *B. parmifera* representative of a gradation in thorn counts from a primitive fully thorned form in the Bering Sea and eastern North Pacific to a form with reduced middorsal thorns in the Sea of Okhotsk and western North Pacific, with the notable exception of waters around the eastern part of Hokkaido, Japan (see unnumbered figure in Dolganov, 2001). The distribution of thorns they describe matches closely the geographical distribution of the four species we recognize, including the otherwise anomalous thorn distribution around Hokkaido representing *B. simoterus*. Although *B. simoterus* is clearly closely related to *B. smirnovi* and requires additional fresh material for more conclusive morphological and genetic analysis, our material can be differentiated from *B. smirnovi* by vertebral counts and characters of the neurocranium, scapulocoracoid, pelvic girdle, and clasper, and therefore deserves recognition at the species level.

Acknowledgments

We thank T. Pietsch and K. Maslenikov (UW); T. Nakabo, Y. Kai, and S. Suzuki (FAKU); M. Yabe, K. Nakaya, and M. Shimazaki (HUMZ); H. Kohno, M. Moteki, and T. Yokoo (MTUF); K. Matsuura, G. Shinohara, Y. Takata, and K. Hoshino (NSMT); T. Saruwatari (ORIT); A. Balushkin (ZIN); J. Williams and S. Raredon (USNM); H. J. Walker (SIO); and G. Burgess, R. Robins, and M. Phillips (UF) for providing access to or loans of specimens, and H. Ishihara (W&I Associates Corporation), C. –H. Joong (Inha University, Korea), A. Orlov (All-Russian Federal Research Institute of Marine Fisheries and Oceanography), and B. Sheiko (ZIN) for helpful discussions. Our examination of western Pacific material was immeasurably aided by the hospitality of T. Nakabo and Y. Kai in inviting the senior author for a lengthy stay in Japan. We also thank the crews of the FV *Morning Star*, FV *Sea Storm*, FV *Northwest Explorer*, FV *Gladiator*, FV *Dominator*, FV *Vesteraalen*, and FV *Sea Fisher* for assistance at sea, and the scientific crews, especially collectors W. Flerx, B. Knoth, P. Von Szalay, D. Cooper, E. Logerwell, N. Raring, E. Acuna, S. Kotwicki, D. Carrison-Stone, and E. Jorgensen, of the NMFS-AFSC surveys on which the specimens were collected. T. Yanagimoto, Hokkaido National Fisheries Research Institute, and Y. Kai, Maizuru Fisheries Research Station of Kyoto University, graciously provided fresh material of *B. smirnovi*. Discussions with H. Ishihara were critical for assessing the status of North Pacific species of *Bathyraja*. We were able to obtain radiographs and CT scans of type material only with the generous assistance from the staff of the Veterinary Specialty Center of Seattle, including T. Gannon, T. McKlveen, and C. Peck. T. Pietsch and M. Wilkins provided helpful comments on an early draft of the manuscript.

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Title page should include authors' full names and mailing addresses and the senior author's telephone, fax number, and e-mail address.

Abstract should not exceed one double-spaced typed page. It should state the main scope of the research but emphasize its conclusions and relevant findings. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely.

Text must be typed double-spaced throughout. A brief introduction should portray the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods, Results, Discussion**, **Conclusions**, and **Acknowledgments**. Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e. there can be no subdivision without at least two items). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow the *U.S. Government Printing Office Style Manual* (2000 ed.) and the *CSE Manual for Authors, Editors, and Publishers* (7th ed.) for editorial style, and the most current issue of the *American Fisheries Society's Common and Scientific Names of Fishes from the United States, Canada, and Mexico* for fish nomenclature. Dates should be written as follows: 11 November 2010. Measurements should be expressed in metric units, e.g., metric tons as (t); if other units of measurement are used, please make this fact explicit to the reader. The numeral one (1) should be typed as a one, not as a lower-case el (l). Write out the numbers zero through nine unless they form part of measurement units (e.g., nine fish but 9 mm). Refrain from using the shorthand slash (/), an ambiguous symbol, in the general text.

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- Use a comma in numbers of five digits or more (e.g. 13,000 but 3000).
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