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Source: Ichthyology & Herpetology, 111(3) : 467-485

Published By: The American Society of Ichthyologists and Herpetologists

URL: <https://doi.org/10.1643/i2023005>

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The Systematics of the Ophidiid Genus *Spectrunculus* (Teleostei, Ophidiiformes) Revisited with Description of a New Species and Resurrection of *S. radcliffei*

Franz Uiblein^{1,2}, Peter R. Møller^{3,4}, and Jørgen G. Nielsen³

After a preceding revision based on 87 specimens, the systematics of the abyssal giant cuskeel genus *Spectrunculus* Jordan and Thompson, 1914 has been revisited, based on the examination of 34 additional specimens and new otolith shape data of the holotype of *S. grandis*. From the latter, a clear distinction in otolith ostium width could be found in specimens from the Atlantic, Southern Indian Ocean, and Southwest Pacific, which were formerly identified as *S. grandis*. Consequently, the new species, *S. stenostio*, is described, which has a narrower ostium when related to its length or to sulcus length and differs also in the combination of three body shape characters, three meristic characters, and maximum size from the three other congeners, *S. crassus* (Atlantic, East Pacific), *S. grandis* (Pacific), and the previously synonymized *S. radcliffei* (Pacific, Southern Indian Ocean, Southeast Atlantic). The latter species is here resurrected based on a rather short pre-anal length and additional morphometric as well as meristic and maximum size differences. An identification key for the four species of *Spectrunculus* is provided.

THE ophidiid deep-sea fish genus *Spectrunculus* Jordan and Thompson, 1914 belongs to the subfamily Neobythitinae, a rather diverse group of cuskeels found in a large variety of habitats mostly close to the bottom, from the shelf to more than 4000 meters depth (Cohen and Nielsen, 1978; Nielsen et al., 1999). This group is still the subject of intense taxonomic studies with new taxa being described and systematic information updated (e.g., Nielsen et al., 2015; Ohashi, 2018; Uiblein and Nielsen, 2018, 2019, 2021, 2023; Schwarzhans and Møller, 2021; Nielsen and Uiblein, 2022; Schwarzhans et al., 2022).

The giant cuskeel genus *Spectrunculus*—with a maximum size of 130 cm SL (ca. 140 cm TL)—is among the largest deep-sea fishes known. Uiblein et al. (2008) revised the genus based on 87 specimens from the Atlantic and Pacific Oceans, resurrecting the species *S. crassus* (Vaillant, 1888) that had been synonymized by Nielsen and Hureau (1980).

Since our last revision, comparative data of 34 additional specimens of *Spectrunculus* have been collected and analyzed together with earlier published as well as previously not considered or newly generated data. This allows for a more refined and detailed distinction among different forms occurring in various areas of the three major oceans. For instance, new otolith shape data of the holotype of *Spectrunculus grandis* (type locality Japan, NW Pacific) became available suggesting a clear distinction from specimens of the Atlantic, previously considered conspecific in our former revision (Uiblein et al., 2008). Furthermore, detailed morphological studies of specimens of *Spectrunculus* from the South Atlantic, Southern Indian Ocean, and Pacific (including three recently obtained specimens from Japan) indicated the need to reconsider the formerly synonymized *S. radcliffei* as a valid species.

Thus, in the present study, we describe *S. stenostio*, new species, and resurrect *S. radcliffei*, considering also intraspecific regional and sex- or size-related morphological and color variation in the now four valid species. In addition to diagnostic, descriptive, and distribution information for each species, an identification key is provided.

MATERIALS AND METHODS

Morphometric, meristic, and color data of 121 specimens of *Spectrunculus* available from Uiblein et al. (2008) or collected during the present study were compiled and analyzed following the methods described by Cohen and Nielsen (1978), Nielsen et al. (1999), and Uiblein et al. (2008). For the descriptions, the following additional morphometric characters that had not been considered previously were collected from a few selected specimens: pectoral-fin width, i.e., the distance between dorsal and ventral pectoral-fin origins; pectoral-fin depth, i.e., the distance between dorsal pectoral-fin and dorsal-fin origins; head depth through eye; and tail length, i.e., the distance between anal-fin origin and posterior end of the vertebrae column.

In addition to radiographs used for obtaining unpaired fin-ray and vertebrae counts, CT scans were used of a few selected, recently collected specimens as well as for obtaining otolith measurements of the holotype of *S. grandis*. Because otoliths are rather difficult to extract, requiring considerable experience, and may deteriorate with long-term preservation, the identification key is primarily based on non-otolith characters.

One large specimen of *Spectrunculus* (127 cm SL; CAS-ICH 25724), of which only the right otolith and the posterior-most part of the tail had been retained, had been studied in

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Submitted: 20 January 2023. Accepted: 27 May 2023. Associate Editor: M. T. Craig.

© 2023 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/i2023005 Published online: 31 October 2023

detail by Hubbs and Follett (1978) when still intact and hence the published meristic and morphometric data were used, while the otolith could be investigated by us. For another large specimen (128 cm SL; CAS-ICH 90121), a hand-written sheet with unpublished morphometric and meristic data from D. J. Long, taken shortly after collection of the specimen, was used.

To consider allometric change, the morphometric data including otolith shape and measurements were separated into two size groups: larger-sized fish (≥ 200 cm SL; i.e., subadults or adults) and small-sized fish (< 200 cm SL; i.e., juveniles).

Following Uiblein et al. (2008), four categories of body and head color patterns were identified: pale—body and head white-creamy, gray-whitish, or nearly white, only unpaired fins sometimes brown or dark brown; dark—body, head, and fins brown to dark brown; light brown—intermediate between the two former categories; speckled—body more or less covered by dark irregular spots of varying size on pale background. In the interpretation of color differences, we tried to consider the possible effects of fixation and preservation on color loss (“bleaching”).

Morphometric data were rounded to two decimal places in numbers < 4 , to one decimal place in numbers < 10 , and to whole numbers in higher values except for one decimal place in averages provided in tables. Institutional abbreviations follow Sabaj (2020). Other abbreviations are: HT = holotype; PT = paratype; SL = standard length; TL = total length; HL = head length; Min = Minimum; Max = Maximum; n = number (count); N = North; S = South; E = East; W = West.

RESULTS

Spectrunculus Jordan and Thompson, 1914 Giant Cuskeel

Spectrunculus Jordan and Thompson, 1914: 301 (type species by monotypy *S. radcliffei* Jordan and Thompson, 1914).

Parabassogigas Nybelin, 1957: 298 (type species by original designation *Siremba grandis* Günther, 1877).

Diagnosis.—The genus *Spectrunculus* differs from all other ophiidiid genera in the combination of the following characters: dorsal-fin rays 121–148; anal-fin rays 91–112; total vertebrae 72–88; pectoral-fin rays 24–31; head short, 4.2 to 5.9 times in SL and 1.75 to 2.89 times in preanal distance; head robust with rounded snout and with several pores above and below eyes, mouth subterminal, upper jaw extending well behind eye. Teeth minute, blunt and robust, vomer roughly triangular or rhombic shaped. Anterior nostril with a thick, fleshy raised rim, posterior nostril larger, a mere hole or slit close to eye. Opercular spine strong. Head and body completely covered by small oval scales. Eyes shorter than snout, 5.5 or more times in HL; long rakers on anterior gill arch 7–10; two median basibranchial tooth patches; pelvic fins placed below preopercle; otolith ostium and sulcus well developed; color of head and body uniformly pale creamy or whitish, light or dark brown (rarely pale with dark speckles or rings); unpaired fins often dark when fresh or recently collected; dark pigmentation may not be retained with longer-term preservation.

Remarks.—Four valid species with maximum sizes of 60 to 130 cm SL (= ca. 65 to 140 cm TL) distributed in various parts of the major oceans (for details see species accounts below). Larger juveniles, subadults, and adults occur at or close to deep bathyal and abyssal bottoms (depth range ca. 1000 to at least 4255 m), mostly caught by bottom longlining or trawling or photographed in baited landers; larvae and small juveniles are pelagic (Ambrose, 1996). Considering their large size and relatively common occurrence in distinct areas, species of *Spectrunculus* may play an important ecological role in deep-sea ecosystems (Uiblein et al., 2008). No reported commercial value.

Spectrunculus stenostio, new species

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Figures 1–4, Tables 1–3

Spectrunculus grandis (Günther, 1877); Duhamel et al., 2005; in part: Nielsen and Hureau, 1980; Uiblein et al., 2008.

Holotype.—ZMUB 18493 (ZMUB-MAR-ECO 20149), female, 825 mm SL (pale), N Atlantic, 42°25.49'N, 29°48.14'W to 42°25.49'N, 29°46.13'W, M/S LORAN, sta. 13, bottom longline, 2018–2429 m depth, 8 July 2004.

Paratypes.—All North Atlantic ($n = 22$): ZMUB 18477 (ZMUB-MAR-ECO 12291), male, 650 mm SL (pale), 42°48.6'N, 29°38.36'W to 42°46.64'N, 29°38.59'W, R/V G.O. SARS, sta. 42-368, bottom trawl, 2063–2107 m depth, 8 July 2004; ZMUB 18478 (ZMUB-MAR-ECO 13347), female, 825 mm SL (pale), 42°46.2'N, 29°16.2'W, R/V G.O. SARS, sta. 46-372, bottom trawl, 3005–3050 m depth, 11 July 2004; ZMUB 18479 (ZMUB-MAR-ECO 2617), male, 830 mm SL (pale), 43°2.07'N, 28°33.11'W to 43°0.88'N, 28°34'W, R/V G.O. SARS, sta. 50-373, bottom trawl, 2593–2607 m depth, 12 July 2004; ZMUB 18480 (ZMUB-MAR-ECO 13977), male, 670 mm SL, female, 840 mm SL (both pale), 42°55.32'N, 28°8.35'W to 42°53.05'N, 28°8.33'W, R/V G.O. SARS, sta. 52-374, bottom trawl, 2973–2979 m depth, 13 July 2004; ZMUB 18481 (ZMUB-MAR-ECO 13821), male, 680 mm SL (pale), 53°7.8'N, 34°45.6'W, R/V G.O. SARS, sta. 68-384, bottom trawl, 2306–2374 m depth, 25 July 2004; ZMUB 18482 (ZMUB-MAR-ECO 16013), male, 725 mm SL, ZMUB 18483 (ZMUB-MAR-ECO 16027), male, 975 mm SL, ZMUB 18484 (ZMUB-MAR-ECO 16041), female, 858 mm SL, ZMUB 18485 (ZMUB-MAR-ECO 16055), female, 765 mm SL (all pale), 42°34.91'N, 28°2.64'W to 42°33.91'N, 28°5.84'W, M/S LORAN, sta. 1, bottom longline, 2925–2827 m depth, 5 July 2004; ZMUB 18486 (ZMUB-MAR-ECO 17105), female, 950 mm SL, ZMUB 18487 (ZMUB-MAR-ECO 20065), female, 742 mm SL, ZMUB 18488 (ZMUB-MAR-ECO 20079), male, 625 mm SL, ZMUB 18489 (ZMUB-MAR-ECO 20093), female, 825 mm SL, ZMUB 18490 (ZMUB-MAR-ECO 20107), male, 685 mm SL, ZMUB 18492 (ZMUB-MAR-ECO 20135), female, 925 mm SL, ZMUB 18494 (ZMUB-MAR-ECO 20163), female, 885 mm SL (all pale), ZMUB 18491 (ZMUB-MAR-ECO 20121), female, 895 mm SL (pale with several large brown rings on body), same station data as HT; ZMUC P77793, 960 mm SL, ZMUC P77794 800 mm SL, ZMUC P77795, male, 960 mm SL, ZMUC P77796, 730 mm SL (all pale), 43°39.3'N, 22°37.8'W, R/V WALTHER HERWIG, sta. 82-352, beam trawl, 1900–2080 m depth, 8 June 1982.

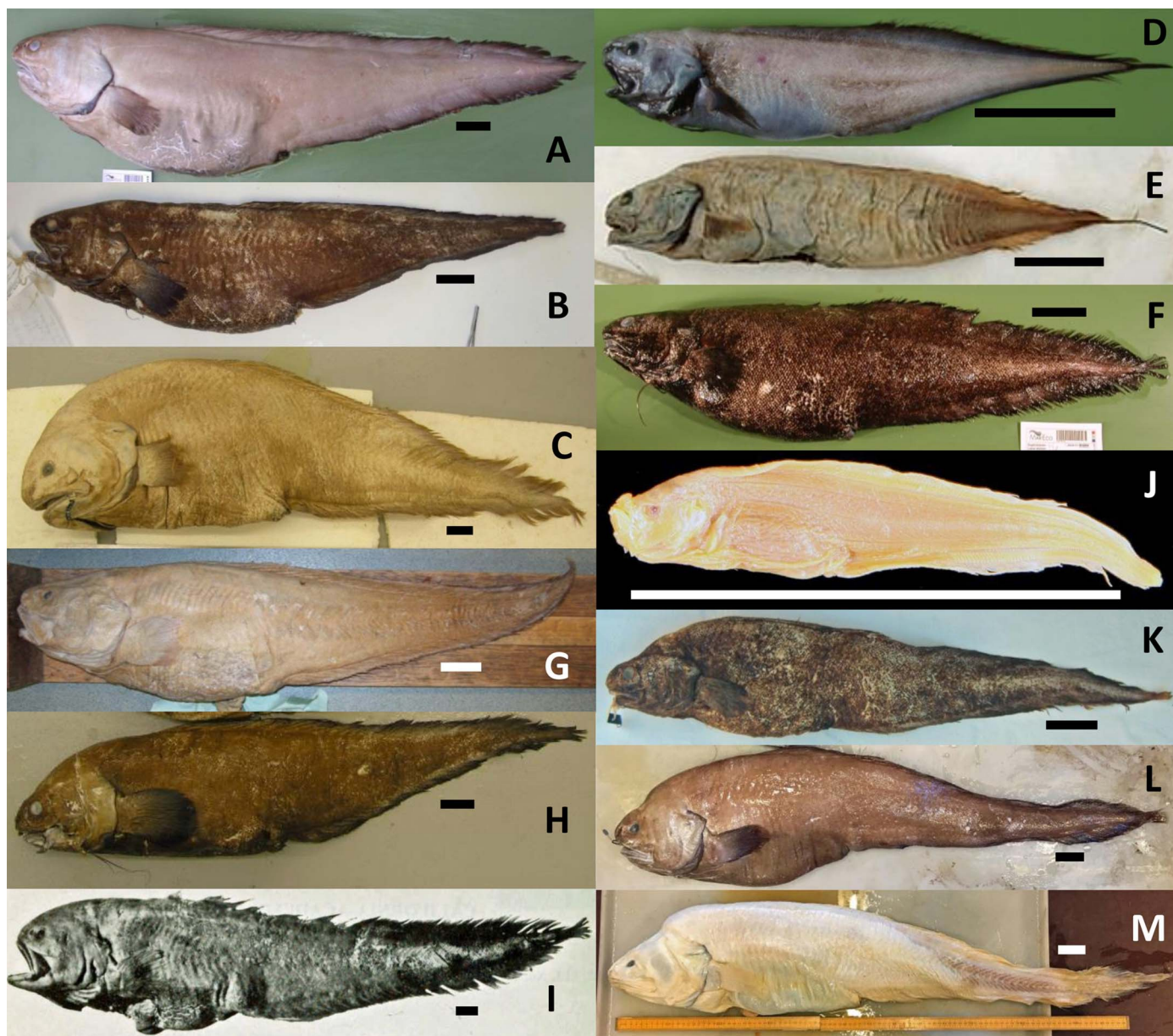


Fig. 1. (A–C) *Spectrunculus stenostio*: (A) HT, ZMUB 18493, 825 mm SL, N Atlantic (F. Uiblein); (B) SAIAB 11892, 706 mm SL, S Indian Ocean (F. Uiblein); (C) NMNZ P.033111, 1030 mm SL, SW Pacific (P. R. Møller). (D–F) *S. crassus*: (D) ZMUB 18355, 187 mm SL, N Atlantic (MAR-ECO cruise); (E) HT, MNHN 1886-0552, 284 mm SL, N Atlantic (J. Pfliger); (F) ZMUB 18463, 500 mm SL, N Atlantic (MAR-ECO cruise); (G–I) *S. grandis*: (G) HT, BMNH 1887, 675 mm SL (F. Uiblein); (H) NMNZ P.041204, 840 mm SL, SW Pacific (P. R. Møller); (I) CAS 25724, 1270 mm SL, NE Pacific (Moulin Studios, San Francisco, used with permission); (J–M) *S. radcliffei*: (J) HT (postlarva), FMNH 57123, 56 mm SL, NW Pacific (FMNH Zoological Collections, used with permission); (K) SAM 47240, 541 mm SL, S Atlantic (F. Uiblein); (L) ZMUC P2397445, 945 mm SL, NW Pacific (M. A. Krag); (M) ZMUC P2397724, 1020 mm SL, NW Pacific (M. A. Krag). Length of black or white scale bars is 5 cm.

Non-type material.—S Indian Ocean E ($n = 4$): MNHN 2003-0598, 754 mm SL (dark), MNHN 2003-0599, 962 mm SL (light brown), Kerguelen, 50°50.3'S, 69°44.1'E, F/V *Ile Bourbon*, longline, 1768 m depth, 11 October 2002; SAIAB 118942, 2, 706 mm SL (dark) and 1001 mm SL (light brown), near Lena Tablemount, 53°30'S, 48°31.5'E, F/V *SHINSEI MARU*, nr. 3, longline, 2112 m depth, 19 May 2010.

SW Pacific ($n = 5$): CSIRO H-5304.01, female, 1060 mm SL (light brown when fresh, pale after preservation), 38°34'S, 149°28'E to 38°36'S, 149°33'E, 1954–1979 m depth, 19 April 2000; CSIRO H-6036.02, female, 510 mm SL (light brown when fresh, pale after preservation),

32°3'S, 159°52'E to 32°2'S, 159°51'E, NORFANZ cruise, R/V *TANGAROA*, station 0308/071, 1920–1934 m depth, 24 May 2003; NMNZ P.031193, female, 610 mm SL (pale), 42°55.59'S, 172°39.21'E, R/V *TANGAROA*, sta. TAN 9406/226, 1694–1707 m depth, 22 June 1994; NMNZ P.033111, female, 1030 mm SL (pale), ~37°30'S, ~176°30'E; USNM 215295, 248 mm SL (pale), 42°11'S, 175°11'E, 2602–2619 m depth, 20 September 1966.

Diagnosis.—Number of dorsal-fin rays 137–148, anal-fin rays 102–112, total vertebrae 80–88, pre-anal length 47–55% in SL, pelvic- to anal-fin origin 34–44% in SL, orbit

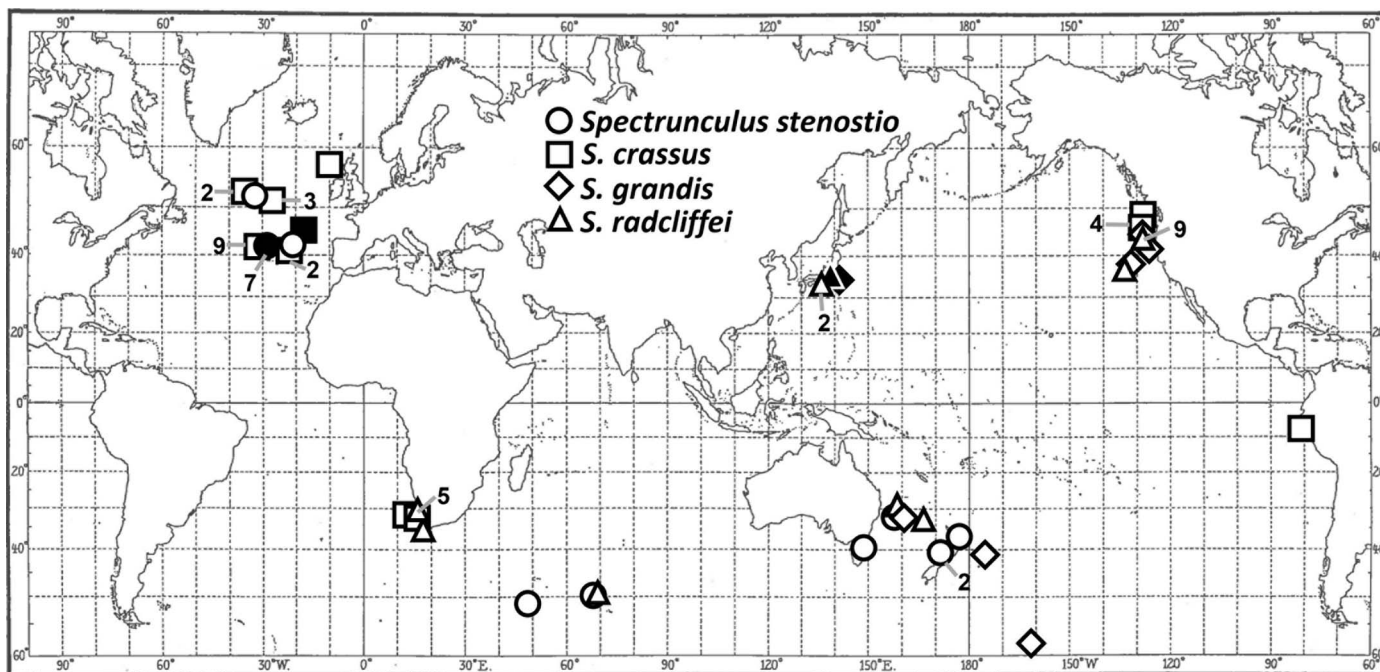


Fig. 2. Distribution map showing the occurrence of studied specimens of the genus *Spectrunculus*. For areas with multiple occurrences, numbers are added to the respective symbols. Type localities are indicated by filled symbols.

length 9.9–12 in % HL, otolith ostium width 15–21 in % sulcus length and 19–29 in % ostium length; maximum size to 110 cm SL.

Description.—The most important meristic and morphometric characters as well as the otolith characters are shown in Tables 1–3. Body elongate, laterally compressed, tapering towards tail. Pectoral-fin depth 5.7–7.9 times in SL, tail length 1.76–1.90 times in SL and preanal length 1.01–1.15 times in tail length. Head length 4.7–5.6 in SL and 2.23–2.75 in preanal length; head depth through eye 7.8–9.5 times in SL. Orbit circular, shorter than snout, 2.09–2.80 in snout length. Anterior gill arch with 8–10 long and 10–13 rudimentary rakers. Pseudobranchial filaments 0–2.

Origin of dorsal fin above vertebra 9–11, well in front of distal tip of pectoral fin. Pelvic fins with two rays each reaching about 1/3 from its base to anal-fin origin. Pectoral fins on lower half of body, rather short, 10–14 times in SL, and moderately wide at fin base, the width 19–21 times in SL.

Otolith (Fig. 3A) mostly elongate, length to height ratio 1.41–2.25, with pointed posterior tip. Anterior tip rounded. Dorsal surface concave. Sulcus long, 54–81% of otolith length with separated colliculi and located at the center of inner face. Ostium narrow, its width 15–21% of sulcus length and 19–29% of ostium length.

Coloration.—Freshly or recently caught specimens with pale creamy body and head, unpaired fins dark brown along distal margins or more entirely, as observed in the 19 type specimens collected by the MAR-ECO cruise, North Atlantic, in 2004. One of those specimens showed in addition several large brown rings on body. Of four specimens collected in the Southern Indian Ocean, the two smaller ones (706–754 mm SL) were dark brown and the two larger ones (962–1001 mm SL) light brown. In three of those specimens, the unpaired fins were dark brown.

Etymology.—The new species name is composed of the Greek word for narrow “stenós” and the otolith structure “ostium.” The ablative of the combined term is “stenostio,” meaning “with a narrow ostium.”

Distribution.—This species is distributed in the North Atlantic and Southern Indian Ocean to the Southwest Pacific (1694 to 3050 m depth). There are no records from the South Atlantic.

Remarks.—Among the studied specimens that could be sexed were 9 males and 15 females. No sexual dimorphism could be found in any meristic and morphometric characters including otolith characters. A clear negative allometry in otolith length, but not in ostium and sulcus shape, was detected (Fig. 4). Apart from a slight decrease in relative orbit length with size (Fig. 4), no other allometric changes in body shape were encountered in *Spectrunculus stenostio*. A slight shift towards a lower number of total vertebrae was found in the Indo-Pacific population, while dorsal- and anal-fin ray number do not follow this trend (Table 2). Small-sized specimens (< 200 mm SL) not known; the smallest specimen studied is 248 mm SL.

***Spectrunculus crassus* (Vaillant, 1888)**

Figures 1–4, Tables 2–5

Bythites crassus Vaillant, 1888: 279 (type locality NE Atlantic, 44°20'N, 17°11'W).

Bassogigas coheni Mayer and Nalbant, 1972: 163 (type locality SE Pacific, 8°23'S, 80°25'W).

Spectrunculus grandis non (Günther, 1877) in part: Nielsen and Hureau, 1980.

Spectrunculus crassus Uiblein et al., 2008; Hanke et al., 2015.

Holotype.—MNHN 1986-0552, 284 mm SL (light brown; described as dark brown in original description by Vaillant,

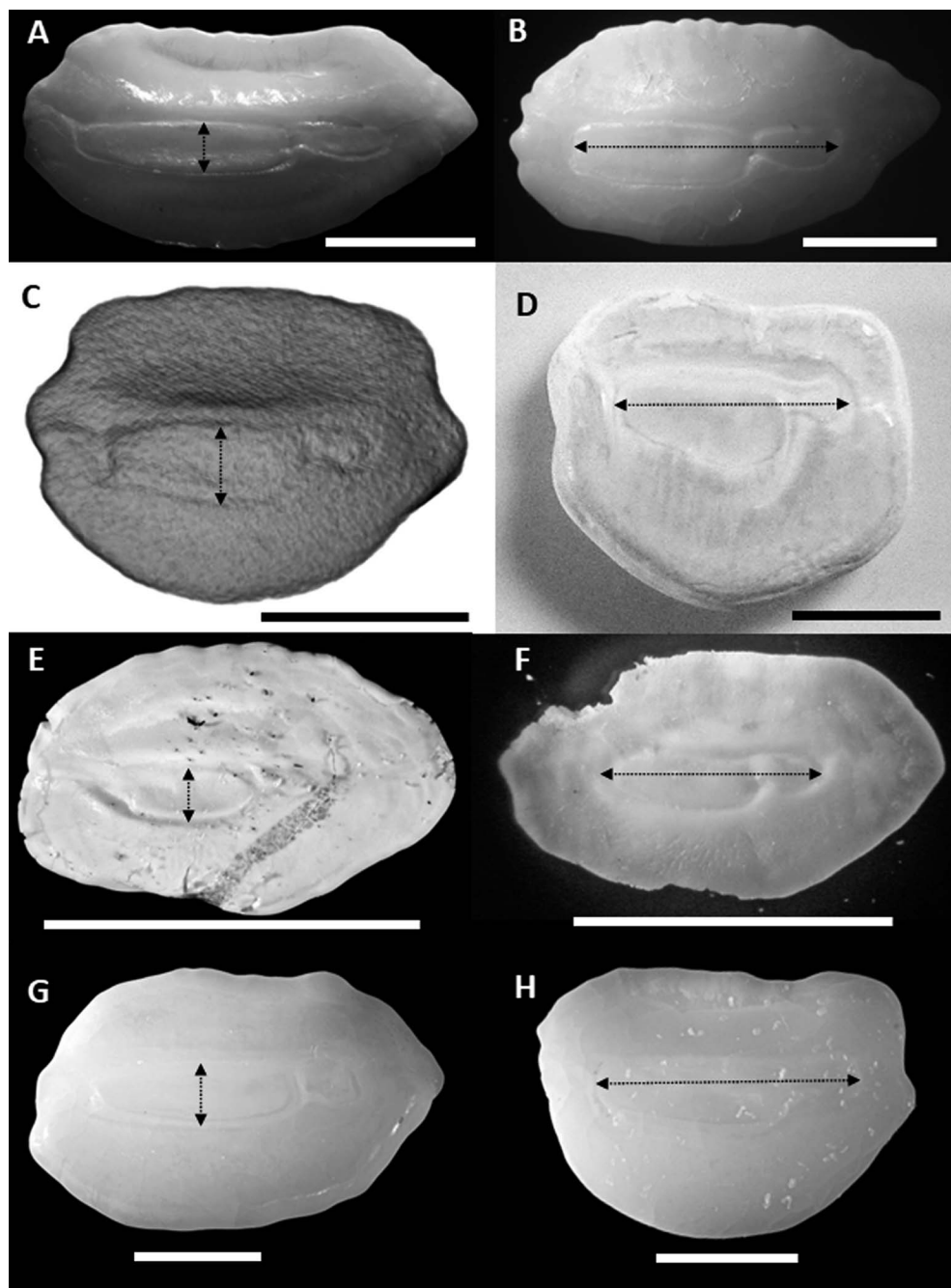


Fig. 3. Images of otoliths of *Spectrunculus*. (A) *S. stenostio*, ZMUB 18480, 670 mm SL, N Atlantic (F. Uiblein); (B) *S. crasus*, ZMUB 18464, 575 mm SL, N Atlantic (F. Uiblein); (C–E) *S. grandis*: (C) HT, BMNH 1887, 675 mm SL, NW Pacific (CT scan, B. Clark); (D) CAS 25724, 1270 mm SL, NE Pacific (F. Uiblein); (E) LACM 43564, 200 mm SL, SW Pacific (M. A. Krag); (F–H) *S. radcliffei*: (F) ZMUC P77704, 192 mm, S Atlantic (M. A. Krag); (G) ZMUC P2397445, 945 mm SL, NW Pacific (from left head side, shown side-reversed; M. A. Krag); (H) ZMUC P2397724, 1020 mm SL, NW Pacific (M. A. Krag). All otoliths from right side of head if not otherwise indicated. Dotted lines with arrows indicate the approximate measurement positions for ostium width (left side of figure) and sulcus length (right side of figure). Length of black or white scale bars is 5 mm.

1888), NE Atlantic, 44°20'N, 17°11'W, R/V *TALISMAN*, sta. 136, 4255 m depth, 26 August 1883.

Non-type material.—N Atlantic ($n = 49$): MNHN 1979-0221, 329 mm SL (pale), 56°38'N, 11°6'W, R/V *J. CHARCOT*, sta. 2721, 2466 m depth, 17 July 1976; MNHN 1979-0222, 142 mm SL (light brown), 56°38'N, 11°6'W, R/V *J. CHARCOT*, sta. 2721, 2466 m depth, 17 July 1976; MNHN 1979-0223, 280 mm SL (light brown), 56°33'N, 11°11'W, R/V *J. CHARCOT*, sta. 2721, 2483–2513 m depth, 17 July 1976; MNHN 1979-0224, 400 mm SL (dark), 56°33'0"N, 11°10'58.8"W, *J. CHARCOT*, sta. Cp04, 2483–2513 m, 17 July 1976; MNHN 1999-0708, 327 mm SL (light brown), 56°15'N, 10°16'W, R/V *N.O. THALASSA*, 2020 m depth, 27 April 1999; ZMUB 18351 (ZMUB-MAR-ECO 8081), female, 250 mm SL (dark), ZMUB 18352 (ZMUB-MAR-ECO 8067), male,

253 mm SL (light brown), 42°54.91'N, 30°20.37'W to 42°53.11'N, 30°20.92'W, R/V *G.O. SARS*, sta. 40-367, bottom trawl, 2660–2670 m depth, 7 July 2004; ZMUB 18353 (ZMUB-MAR-ECO 13053), male, 216 mm SL (light brown), ZMUB 18354 (ZMUB-MAR-ECO 2679), 2 females, 240–282 mm SL, male, 260 mm SL (all dark), ZMUB 18355 (ZMUB-MAR-ECO 12419), female, 187 mm SL (light brown), 42°55.32'N, 28°8.35'W to 42°53.05'N, 28°8.33'W, R/V *G.O. SARS*, sta. 52-374, bottom trawl, 2973–2979 m depth, 13 July 2004; ZMUB 18356 (ZMUB-MAR-ECO 11582), male, 220 mm SL (light brown), 53°16.8'N, 35°31.8'W, R/V *G.O. SARS*, sta. 72-386, bottom trawl, 2522–2567 m depth, 27 July 2004; ZMUB 18463 (ZMUB-MAR-ECO 12291), 3 males, 482–522 mm SL, 1 unsexed specimen, 522 mm SL (all dark), 42°48.6'N, 29°38.36'W to 42°46.64'N, 29°38.59'W, R/V *G.O. SARS*, sta. 42-368, bottom trawl, 2063–2107 m

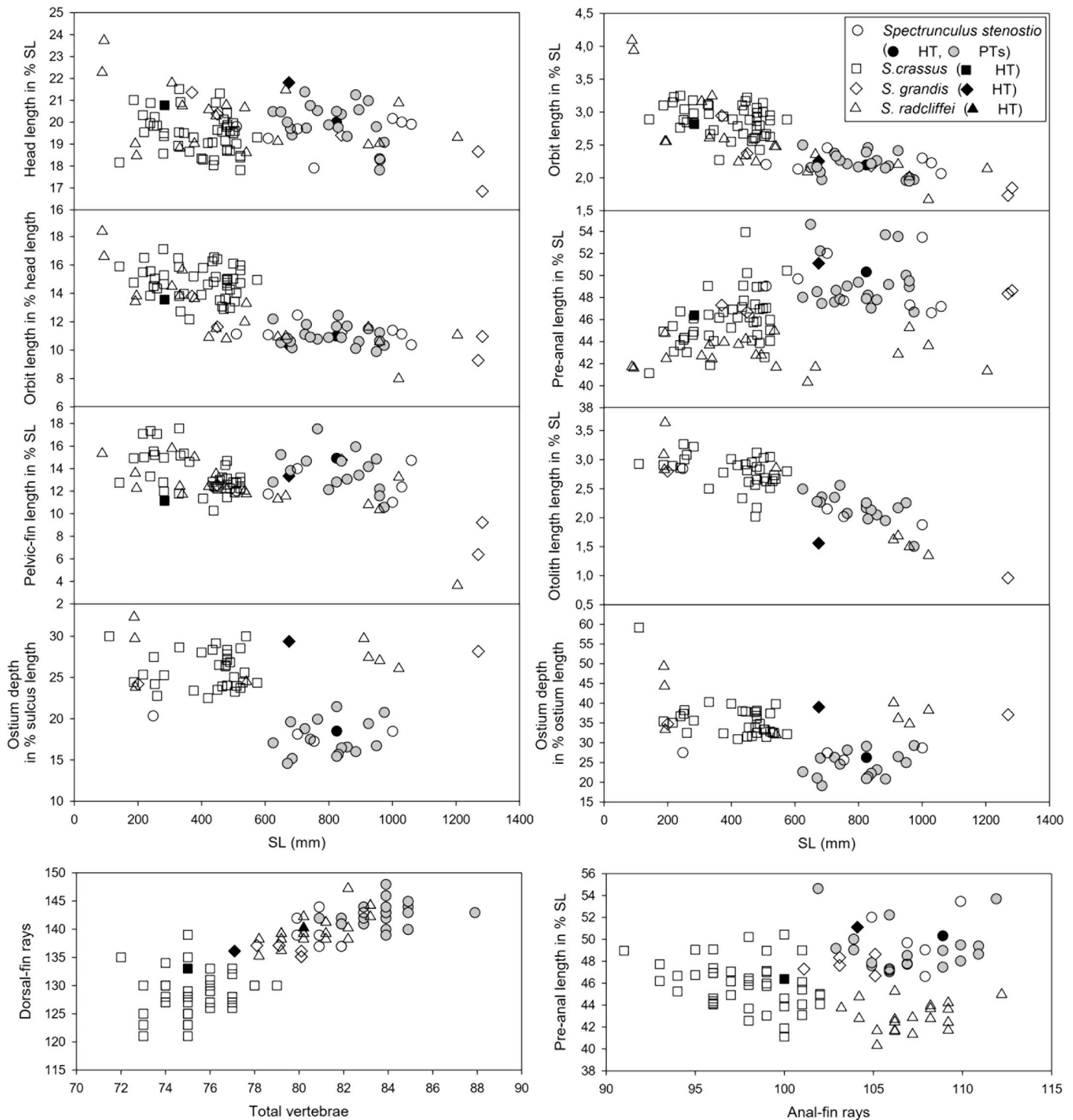


Fig. 4. Relationships between morphological characters in the four species of *Spectrunculus*.

depth, 8 July 2004; ZMUB 18464 (ZMUB-MAR-ECO 10891), 3 females, 435–575 mm SL (all dark), 51°55.08'N, 30°25.02'W to 51°56.14'N, 30°24.44'W, R/V G.O. SARS, sta. 62-380, bottom trawl, 1872–1959 m depth, 20 July 2004; ZMUB 18465 (ZMUB-MAR-ECO 13807), female, 445 mm SL (light-brown speckled), ZMUB 18466 (ZMUB-MAR-ECO 13821), male, 420 mm SL, 7 females, 375–480 mm SL, 1 unsexed specimen, 405 mm SL (all dark), 53°7.8'N, 34°45.6'W, R/V G.O. SARS, sta. 68-384, bottom trawl, 2306–

2374 m depth, 25 July 2004; ZMUB 18467 (ZMUB-MAR-ECO 20275), female, 490 mm SL, ZMUB 18468 (ZMUB-MAR-ECO 20261), female, 465 mm SL, ZMUB 18469 (ZMUB-MAR-ECO 20247), female, 480 mm SL (all dark), 42°25.49'N, 29°48.14'W to 42°25.49'N, 29°46.13'W, M/S LORAN, sta. 13, bottom longline, 2429–2018 m depth, 8 July 2004; ZMUB 18470 (ZMUB-MAR-ECO 17133), female, 510 mm SL (dark), 42°23.26'N, 29°59.71'W to 42°24.88'N, 30°0'W, M/S LORAN, sta. 15, bottom longline, 2650–2675 m

Table 1. *Spectrunculus stenostio*, types and areas separated.

	HT			PTs, N Atlantic			S Indian Ocean			SW Pacific		
	N Atlantic	Min	Max	n	Mean	Max	Min	Mean	Max	n	Mean	Max
SL (mm)	825	625	975	22	809.1	975	702	854.8	1001	4	691.6	1060
Meristic characters												
Dorsal-fin rays	143	139	148	20	142.5	148	137	140.0	143	4	139.8	144
Caudal-fin rays	8	8	9	19	8.2	9	8	8.3	9	4	8.0	8
Anal-fin rays	109	102	112	17	107.1	112	105	107.0	110	4	107.0	108
Precaudal vertebrae	24	23	26	20	24.4	26	22	23.5	25	4	23.6	24
Total vertebrae	84	81	88	20	83.9	88	81	82.0	83	4	80.8	82
First dorsal-fin ray above vertebra nr.	10	9	11	20	9.8	11	9	9.8	10	4	9.4	10
Dorsal-fin ray above anal-fin ray nr.	41	35	41	14	38.8	41	34	34.3	35	3	38.6	42
First anal-fin rays below vertebra nr.	30	26	30	14	28.2	30	26	27.0	28	3	28.2	31
Pectoral-fin rays	28	27	28	3	27.7	28	24	26.3	28	4	26.8	29
Developed gill rakers	10	9	10	4	9.5	10	9	9.0	9	2	9.0	10
Total gill rakers	20	19	21	4	20.3	21	20	20.5	21	2	20.8	22
Morphometric characters in % SL												
Head length	20	18	21	21	20.0	21	18	19.0	20	4	19.7	20
Body depth at anus	17	16	20	21	17.5	20	18	19.8	22	2	19.6	25
Snout length	4.6	4.6	5.9	21	5.3	5.9	5.1	5.2	5.4	2	5.6	5.9
Upper jaw length	9.6	8.9	11	21	9.9	11	9.9	9.9	10	2	10.1	11
Head width at postmaxilla	8.4	8.1	10.1	19	9.3	10.1	8.3	8.8	9.4	2	10.6	13
Depth of postmaxilla	2.61	2.24	3.19	21	2.67	3.19	2.13	2.29	2.44	2	2.04	2.43
Orbit length	2.19	1.95	2.20	21	2.20	2.50	2.30	2.37	2.45	2	2.06	2.23
Interorbital length	5.9	5.2	6.9	21	6.1	6.9	6.0	6.2	6.3	2	6.4	7.2
Postorbital length	14	12	15	21	13.8	15	13	13.7	14	2	13.6	15
Preal distance	50	47	55	21	49.3	55	47	50.1	53	4	48.1	50
Predorsal distance	27	26	33	21	29.0	33	25	25.5	26	2	28.0	31
Distance between pelvic- and anal-fin origin	41	34	44	21	38.0	44	39	38.8	39	2	36.1	37
Pelvic-fin length	15	11	18	16	13.7	18	11	12.5	14	2	12.7	15
In % head length												
Upper jaw length	48	47	53	21	49.7	53	49	49.9	50	2	51.1	54
Orbit length	11	9.9	12	21	11.0	12	11	11.9	12	2	10.9	11
Otolith characters in % SL												
Otolith length	2.21	1.50	2.17	16	2.17	2.55	1.88	2.01	2.15	3	2.84	
Otolith height	1.19	1.06	1.22	16	1.22	1.35	1.14	1.17	1.18	3	1.70	
Sulcus length	1.41	1.19	1.49	16	1.49	1.73	1.38	1.40	1.44	3	1.55	
Ostium length	1.00	0.84	1.09	16	1.09	1.22	0.89	0.93	0.95	3	1.15	
Ostium width	0.26	0.20	0.26	16	0.26	0.31	0.24	0.25	0.26	3	0.31	

Table 1. Continued.

	HT			PTs, N Atlantic			S Indian Ocean			SW Pacific			
	N Atlantic	Min	Max	Mean	Max	n	Min	Mean	Max	Min	Mean	Max	n
In % otolith length													
Otolith height	54	44	71	56.6	71	16	55	58.1	61	3	60		1
Sulcus length	64	60	81	69.0	81	16	67	69.9	74	3	54		1
Ostium length	45	45	58	50.2	58	16	44	46.1	47	3	40		1
Ostium width	12	9	16	12.1	16	16	12	12.5	14	3	11		1
Ostium width in % of:													
Otolith height	22	15	25	21.5	25	16	20	21.6	22	3	18		1
Sulcus length	71	67	79	73.0	79	16	64	66.0	67	3	74		1
Ostium length	26	19	29	24.1	29	16	26	27.2	29	3	27		1

depth, 9 July 2004; ZMUB 18471 (ZMUB-MAR-ECO 16433), 470 mm SL, ZMUB 18472 (ZMUB-MAR-ECO 16419), 510 mm SL, ZMUB 18473 (ZMUB-MAR-ECO 16405), female, 475 mm SL (dark), 42°37.77'N, 28°22.18'W to 42°37.58'N, 28°19.16'W, M/S LORAN, sta. 5, bottom longline, 2125–2436 m depth, 6 July 2004; ZMUB 18474 (ZMUB-MAR-ECO 17119), female, 480 mm SL (dark), 42°25.49'N, 29°48.14'W to 42°25.49'N, 29°46.13'W, M/S LORAN, sta. 13, bottom longline, 2429–2018 m depth, 8 July 2004; ZMUB 18475 (ZMUB-MAR-ECO 17189), female, 330 mm SL (dark), 42°36.14'N, 29°20.05'W to 42°37.82'N, 29°19.51'W, M/S LORAN, sta. 16, bottom longline, 3366–3280 m depth, 9 July 2004; ZMUB 18476 (ZMUB-MAR-ECO 17393), female, 522 mm SL (dark), 42°25.33'N, 29°38.2'W to 42°25.37'N, 29°40.42'W, M/S LORAN, sta. 12, bottom longline, 1580–1964 m depth, 8 July 2004; ZMUB 19505 (ZMUB MAR-ECO 9757), 5 females, 455–540 mm SL, 2 unsexed specimens, 476–530 mm SL (all dark), 51°27.02'N, 29°19.73'W to 51°28.02'N, 29°19.54'W, R/V G.O. SARS, st. 56-378, bottom trawl, 1872–1950 m depth, 17 July 2004; ZMUC P77797, 500 mm SL (dark), 43°39.3'N, 22°37.8'W, R/V WALTHER HERWIG, sta. 82-352, beam trawl, 1900–2080 m depth, 8 June 1982; ZMUC P77805, female, 490 mm SL (dark), 43°33.6'N, 22°33.4'W, R/V WALTHER HERWIG, sta. 82-350, beam trawl, 1800–1970 m depth, 8 June 1982.

S Atlantic ($n = 2$): MNHN 1979-0227, 282 mm SL (light brown), 32°29'S, 13°26'E, R/V J. CHARCOT, sta. 4736, 3677 m depth, 13 January 1979; SAM MB-F042004, 128 mm SL (light brown), 33°49'S, 16°30'E, ca. 2743 m depth.

NE Pacific, off Oregon ($n = 5$): CAS-ICH 36991, female (?), 458 mm SL (dark), 44°37'24"N, 125°39'54"W to 44°37'18"N, 125°41'6"W, 2816 m depth, beam trawl, 13 April 1976; CAS-ICH 40222, male, 334 mm SL (dark), Cascadia Abyssal Plain, 45°9'18"N, 125°38'18"W to 45°10'30"N, 125°38'0"W, 2669 m depth, beam trawl; CAS-ICH 62977, male, 362 mm SL (dark), Cascadia Abyssal Plain, 47°50'30"N, 127°2'36"W, 2519 m depth, beam trawl; OSUO 11743, 345 mm SL (light brown), 44°40'N, 126°0'W, 2800 m depth, 21 August 1965; OSUO 11775, 239 mm SL (light brown), 45°31.7'N, 127°28.4'W, 2800 m depth, 4 February 1973.

SE Pacific: NHMB 191, HT of *Spectrunculus coheni*, 106 mm SL (dark), 8°23'S, 80°25'W, R/V ANTON BRUUN, beam trawl, 2945–2966 m depth, 31 October 1965.

Diagnosis.—Number of dorsal-fin rays 121–131, anal-fin rays 91–102, total vertebrae 72–79, pre-anal length 42–54% in SL, pelvic- to anal-fin origin 29–41% in SL, orbit length 12–17 in % HL, otolith ostium width 22–30 in % sulcus length and 31–40 in % ostium length; dark-brown body, head, and fins in larger, fresh, or recently collected fish; juveniles lighter colored with dark unpaired fins; longer-preserved specimens mostly light brown, paler than when fresh; maximum size to 60 cm SL.

Description.—The most important meristic and morphometric characters as well as the otolith characters are shown in Tables 2–5. Body elongate, laterally compressed, tapering towards tail. Pectoral-fin depth 6.9–8.3 times in SL, tail length 1.78–1.86 times in SL, and preanal length 1.16–1.33 times in tail length. Head length 4.6–5.6 in SL and 2.00–2.72 in preanal length; head depth through eye 8.2–11 times in SL. Orbit circular, shorter than snout, 1.56–2.26 times in snout length. Anterior gill arch with 8–10 long and 8–12 rudimentary rakers. Pseudobranchial filaments 0–2.

Table 2. Three meristic characters for the four species of *Spectrunculus* (entire size range considered), with counts for the holotype of each species marked with an asterisk. The counts for the HT of *S. coheni* (Mayer and Nalbant, 1972) are emphasized in bold italics.

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	
<i>S. stenostio</i> , N Atlantic																			1	3	3	4	4*	3	1	1	1	1	
<i>S. stenostio</i> , S Indian Ocean																	1		1		1		1						
<i>S. stenostio</i> , SW Pacific																2		2	1			1							
<i>S. crassus</i> , Atlantic	1	2		6	2	5	6	3	9	1	1	4*	1	2					1										
<i>S. crassus</i> , E Pacific	1	1																											
<i>S. grandis</i> , W Pacific														1	2*	1													
<i>S. grandis</i> , NE Pacific														1	1	2													
<i>S. radcliffei</i> , S Atlantic															1			1	2	1	1								
<i>S. radcliffei</i> , W Pacific															1			2	2	1*									
<i>S. radcliffei</i> , NE Pacific																		2	3		1	2	2					1	
Anal-fin rays	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112							
<i>S. stenostio</i> , N Atlantic												1	1	2	2	2	2	2	3*	2	2	1							
<i>S. stenostio</i> , S Indian Ocean															1	1	1	1											
<i>S. stenostio</i> , SW Pacific																2	1	2											
<i>S. crassus</i> , Atlantic	1	2	2	2	7	3	5	7	7*	5	3																		
<i>S. crassus</i> , E Pacific					1	1	2		1		1																		
<i>S. grandis</i> , W Pacific														1	1*	2													
<i>S. grandis</i> , NE Pacific														1	1	1													
<i>S. radcliffei</i> , S Atlantic															1	2	1		1	1		1							
<i>S. radcliffei</i> , W Pacific														1	1*	1	1	1	1										
<i>S. radcliffei</i> , NE Pacific														1	1	3	1	1	3									1	
Total vertebrae	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88												
<i>S. stenostio</i> , N Atlantic										1	2	4	8*	5															
<i>S. stenostio</i> , S Indian Ocean										1	2	1																	
<i>S. stenostio</i> , SW Pacific										2	2	1																	
<i>S. crassus</i> , Atlantic	1	3	5	17*	6	7	2	1																					
<i>S. crassus</i> , E Pacific			1	3	1	1																							
<i>S. grandis</i> , W Pacific						1*		1	2																				
<i>S. grandis</i> , NE Pacific																													
<i>S. radcliffei</i> , S Atlantic																													
<i>S. radcliffei</i> , W Pacific							2	3	1*																				
<i>S. radcliffei</i> , NE Pacific								1	3	2	2	3																	

Table 3. Larger-sized (≥ 200 mm SL) specimens of *Spectrunculus* compared.

	<i>S. stenostio</i>				<i>S. crassus</i>				<i>S. grandis</i>				<i>S. radcliffei</i>			
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
SL (mm)	248	796.9	1060	32	216	416.1	575	54	200	726.9	1283	7	307	623.6	1205	17
Meristic characters																
Dorsal-fin rays	137	141.7	148	30	121	128.3	139	44	135	136.1	137	7	135	139.3	144	16
Caudal-fin rays	8	8.2	9	28	7	8.0	10	31	8	8.0	8	5	7	8.2	10	16
Anal-fin rays	102	107.1	112	27	91	97.9	102	44	101	103.7	105	7	103	107.0	112	16
Precaudal vertebrae	22	24.1	26	30	20	21.3	22	47	22	22.6	23	7	20	22.8	24	16
Total vertebrae	80	83.1	88	30	72	75.3	79	44	77	79.0	80	7	78	80.2	83	16
First dorsal-fin ray above vertebra nr.	9	9.7	11	30	7	8.4	10	44	9	9.2	10	5	7	9.3	11	16
Dorsal-fin ray above anal-fin ray nr.	34	38.3	42	23	27	32.8	38	43	35	38.0	41	5	32	35.6	38	16
First anal-fin rays below vertebra nr.	25	28.1	31	23	22	24.4	27	44	26	27.2	28	5	24	25.9	28	16
Total vertebrae	80	83.1	88	30	72	75.3	79	44	77	79.0	80	7	78	80.2	83	16
Pectoral-fin rays	24	26.9	29	12	25	25.9	27	14	26	28.2	31	5	25	26.9	29	16
Developed gill rakers	8	9.3	10	11	8	8.9	10	15	7	7.8	10	5	8	8.5	9	15
Total gill rakers	19	20.5	22	11	17	19.2	22	14	19	22.6	26	5	17	19.2	21	15
Morphometric characters in % SL																
Head length	18	19.8	21	30	18	19.5	22	45	17	19.7	22	6	19	20.0	22	15
Body depth at anus	15	17.9	25	28	15	18.3	22	45	17	19.4	22	5	14	16.5	19	15
Snout length	4.6	5.3	5.9	28	4.7	5.4	6.1	45	5.0	5.5	6.1	5	4.9	5.4	6.0	15
Upper jaw length	8.9	9.9	11	28	8.1	9.1	10.5	44	8.7	10.4	11	6	8.4	10.2	12	15
Head width at postmaxilla	8.1	9.4	13	26	6.3	8.4	12	43	9.1	11.0	12	4	7.5	9.8	13	15
Depth of postmaxilla	2.04	2.60	3.19	26	1.93	2.50	3.02	43	2.20	2.78	3.29	5	2.18	2.65	3.31	14
Orbit length	1.95	2.20	2.50	28	2.27	2.87	3.25	45	1.73	2.22	2.95	6	1.67	2.39	3.24	15
Interorbital length	5.2	6.2	7.2	28	3.9	6.0	7.4	45	6.8	7.2	7.6	6	4.9	6.1	7.1	15
Postorbital length	12	13.8	15	28	11	12.4	13	45	13	13.6	15	4	12	13.3	15	15
Preanal distance	47	49.3	55	30	42	46.2	54	44	47	48.3	51	6	40	43.0	45	16
Predorsal distance	25	28.5	33	28	24	26.8	32	45	25	27.4	30	6	24	27.2	31	15
Distance between pelvic- and anal-fin origin	34	37.9	44	28	29	34.1	41	44	32	34.6	36	5	28	30.2	33	15
Pelvic-fin length	11	13.5	18	23	10	13.5	18	36	6.4	11.2	15	5	3.6	11.8	16	15
In % head length																
Upper jaw length	47	49.8	54	28	43	46.8	52	44	51	52.9	55	6	45	51.0	57	15
Orbit length	9.9	11.0	12	28	12	14.8	17	45	9.3	11.2	14	6	8.0	11.9	16	15
Otolith characters in % SL																
Otolith length	1.50	2.19	2.84	21	2.02	2.78	3.27	31	0.96	1.77	2.80	3	1.35	1.80	2.85	5
Otolith height	1.06	1.23	1.70	21	1.30	1.65	2.16	31	0.80	1.23	1.68	3	0.96	1.19	1.83	5
Sulcus length	1.19	1.48	1.73	21	1.23	1.70	2.17	30	0.57	0.97	1.39	3	1.00	1.18	1.75	5
Ostium length	0.84	1.06	1.22	21	0.92	1.25	1.63	31	0.44	0.70	0.97	3	0.68	0.88	1.34	5
Ostium width	0.20	0.26	0.31	21	0.35	0.44	0.58	31	0.16	0.26	0.34	3	0.26	0.31	0.43	5

Table 4. *Spectrunculus crassus*, larger-sized (≥ 200 mm SL) specimens, type and areas separated.

	<i>S. crassus</i> HT N Atlantic	N Atlantic				SE Atlantic	NE Pacific			
		Min	Mean	Max	<i>n</i>		Min	Mean	Max	<i>n</i>
SL (mm)	284	216	429.1	575	47	282	239	347.6	458	5
Meristic characters										
Dorsal-fin rays	133	121	128.3	139	37	135	121	125.6	129	5
Caudal-fin rays	10	7	8.0	9	27		8	8.0	8	3
Anal-fin rays	100	91	97.7	102	37	102	96	97.8	100	5
Precaudal vertebrae	20	20	21.3	22	40	22	20	21.2	22	5
Total vertebrae	75	73	75.5	79	37	72	73	74.4	76	5
First dorsal-fin ray above vertebra nr.	8	7	8.4	10	37	8	8	9.0	10	5
Dorsal-fin ray above anal-fin ray nr.	31	30	33.2	38	36	35	27	30.0	31	5
First anal-fin rays below vertebra nr.	23	22	24.5	27	37	25	22	23.8	25	5
Total vertebrae	75	73	75.5	79	37	72	73	74.4	76	5
Pectoral-fin rays	26	25	25.9	27	7	25	25	26.0	27	5
Developed gill rakers	8	8	8.9	9	8	9	8	9.0	10	5
Total gill rakers		17	19.0	21	8	18	18	19.8	22	5
Morphometric characters in % SL										
Head length	21	18	19.4	22	38	19	18.7	20.1	21.3	5
Body depth at anus	22	16	18.3	21	38	17	15.4	17.2	19.1	5
Snout length	5.3	4.7	5.4	6.0	38	5.2	5.0	5.5	6.1	5
Upper jaw length		8.1	9.0	10	38	8.8	9.0	9.6	10.5	5
Head width at postmaxilla		6.3	8.2	12	37	11	6.9	9.4	10.8	5
Depth of postmaxilla	2.89	1.93	2.46	2.98	37	2.20	2.61	2.86	3.02	5
Orbit length	2.82	2.42	2.90	3.25	38	2.84	2.27	2.66	2.88	5
Interorbital length	7.4	4.9	6.0	7.0	38	6.2	3.9	5.9	7.2	5
Postorbital length	13.2	11	12.4	13	38	12	11.5	12.7	13.3	5
Preanal distance	46.4	43	46.4	54	37	45	41.9	44.4	46.2	5
Predorsal distance	26.9	24	26.9	32	38	24	25.5	27.0	29.9	5
Distance between pelvic- and anal-fin origin	32.0	29	34.5	41	37	30	30.3	32.0	34.7	5
Pelvic-fin length	11.1	10	13.6	18	29	12	13.0	14.3	15.3	5
In % head length										
Upper jaw length		43	46.7	51	38	45	45.5	47.7	51.8	5
Orbit length	14	13	15.0	17	38	15	12.2	13.2	14.0	5
Otolith characters in % SL										
Otolith length		2.02	2.78	3.27	31					
Otolith height		1.30	1.65	2.16	31					
Sulcus length		1.23	1.70	2.17	30					
Ostium length		0.92	1.25	1.63	31					
Ostium width		0.35	0.44	0.58	31					
In % otolith length										
Otolith height		48	59.7	75	31					
Sulcus length		47	61.4	72	30					
Ostium length		34	45.2	54	31					
Ostium width		12	15.8	20	31					
Ostium width in % of:										
Otolith height		21	26.5	33	31					
Sulcus length		22	25.8	30	30					
Ostium length		31	35.1	40	31					

September 1966; NMNZ P.041204, female, 840 mm SL (dark), 58°36'S, 161°23'E, 1496–1638 m depth, 19 August 2004.

NE Pacific (*n* = 3): CAS-ICH 25724, male, 1270 mm SL (light brown), California, 40 miles west southwest of the Farallon Islands, ~37°30'N, ~132°4'W, surface, above ca. 3000 m depth; CAS-ICH 90121, 1283 mm SL (dark), California, off Trinidad Head, 41°50'N, 125°10'W, surface, above ca. 2500 m depth, 16 September 1996; OSUO 11789, 370

mm SL (light brown), 44°41.8'N, 127°22.7'W, 3021 m depth, 12 June 1974.

Diagnosis.—Number of dorsal-fin rays 135–137, anal-fin rays 101–105, total vertebrae 77–80, pre-anal length 47–55% in SL, pelvic- to anal-fin origin 32–36% in SL, orbit length 9.3–14 in % HL, otolith ostium width 24–29 in % sulcus length and 35–39 in % ostium length; maximum size to 130 cm SL.

Table 5. Small-sized (< 200 mm SL) specimens of two species of *Spectrunculus*.

	<i>S. crassus</i>				<i>S. radcliffei</i>			
	Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>
SL (mm)	106	136.3	187	4	56	143.4	196	7
Meristic characters								
Dorsal-fin rays	129	130.8	134	4	138	140.9	147	7
Caudal-fin rays	8	8.0	8	2	8	8.3	9	3
Anal-fin rays	97	99.5	101	4	104	106.3	110	7
Precaudal vertebrae	20	21.3	22	4	22	23.0	24	7
Total vertebrae	74	75.3	78	4	80	81.0	83	7
First dorsal-fin ray above vertebra nr.	7	7.5	8	2	8	9.0	10	4
Dorsal-fin ray above anal-fin ray nr.	33	33.5	34	2	34	36.0	37	4
First anal-fin rays below vertebra nr.	24	24.0	24	2	25	26.3	27	4
Total vertebrae	74	75.3	78	4	80	81.0	83	7
Pectoral-fin rays	25	26.0	27	2	27	27.7	28	3
Developed gill rakers		9		1	9	9.0	9	2
Total gill rakers		18		1	20	20.5	21	2
Morphometric characters in % SL								
Head length	18	19.6	21	2	18	20.9	24	4
Body depth at anus	16	17.3	19	2	14	15.5	17	4
Snout length	5.2	5.4	5.6	2	4.6	5.2	5.8	4
Upper jaw length	7.7	8.9	10	2	7.9	9.5	10	4
Head width at postmaxilla	7.1	7.8	8.6	2	7.7	8.4	9.3	4
Depth of postmaxilla	2.32	2.53	2.73	2	2.40	2.86	3.30	4
Orbit length	2.89	2.99	3.10	2	2.55	3.28	4.09	4
Interorbital length	4.2	4.3	4.4	2	4.5	4.8	5.3	4
Postorbital length	11	12.1	13	2	11	12.8	15	4
Preanal distance	41	43.0	45	2	42	42.6	45	4
Predorsal distance	24	25.5	27	2	24	24.3	26	4
Distance between pelvic- and anal-fin origin	29	30.1	31	2	29	30.9	32	4
Pelvic-fin length	13	13.8	15	2	12	13.7	15	3
In % head length								
Upper jaw length	43	45.2	48	2	41	45.9	54	4
Orbit length	15	15.3	16	2	13	15.5	18	4
Otolith characters in % SL								
Otolith length	2.91	2.92	2.93	2	2.83	3.18	3.63	3
Otolith height	1.76	1.87	1.97	2	1.61	1.82	2.06	3
Sulcus length	1.27	1.33	1.38	2	1.45	1.74	2.06	3
Ostium length	0.65	0.80	0.95	2	0.97	1.19	1.47	3
Ostium width	0.34	0.36	0.38	2	0.43	0.49	0.55	3
In % otolith length								
Otolith height	60	64.0	68	2	57	57.3	58	3
Sulcus length	43	45.5	47	2	51	54.5	57	3
Ostium length	22	27.4	33	2	34	37.1	40	3
Ostium width	12	12.3	13	2	13	15.6	18	3
Ostium width in % of:								
Otolith height	17	19.4	22	2	24	27.1	31	3
Sulcus length	24	27.2	30	2	24	28.6	32	3
Ostium length	35	47.3	59	2	33	42.3	49	3

Description.—The most important meristic and morphometric characters as well as the otolith characters are shown in Tables 2, 3, and 6. Body elongate, laterally compressed, tapering towards tail. Pectoral-fin depth in HT 7.2 times in SL, tail length 1.80–1.88 times in SL, and preanal length 1.04–1.14 times in tail length in HT and two non-types. Head length 4.9–5.9 in SL and 2.22–2.89 in preanal length; head depth through eye 8.57 times in SL. Orbit circular, shorter than snout, 1.98–3.27 times in snout length. Anterior

gill arch with 7–10 long and 11–19 rudimentary rakers. Pseudobranchial filaments 1–2.

Origin of dorsal fin above vertebrae 9–10, well in front of distal tip of pectoral fin. Pelvic fins with two rays in each reaching about 1/4 to 1/3 from its base to anal-fin origin. Pectoral fins on lower half of body, rather short, 10–12 times in SL, and moderately wide at fin base, the width 17–19 times in SL.

Otolith (Fig. 3C–E) oval to slightly elongated (length to height ratio 1.20–1.67), posteriorly flattened or with only a

Table 6. *Spectrunculus grandis*, type and areas separated.

	HT NW Pacific	SW Pacific				NE Pacific			
		Min	Mean	Max	<i>n</i>	Min	Mean	Max	<i>n</i>
SL (mm)	675	200	496.7	840	3	370	974.3	1283	3
Meristic characters									
Dorsal-fin rays	136	135	136.0	137	3	135	136.3	137	3
Caudal-fin rays	8	8	8.0	8	2	8	8.0	8	2
Anal-fin rays	104	103	104.3	105	3	101	103.0	105	3
Precaudal vertebrae	22	22	22.7	23	3	22	22.7	23	3
Total vertebrae	77	79	79.7	80	3	78	79.0	80	3
First dorsal-fin ray above vertebra nr.	9	9	9.0	9	2	9	9.5	10	2
Dorsal-fin ray above anal-fin ray nr.	38	39	40.0	41	2	35	36.0	37	2
First anal-fin rays below vertebra nr.	27	28	28.0	28	2	26	26.5	27	2
Total vertebrae	77	79	79.7	80	3	78	79.0	80	3
Pectoral-fin rays	29	26	28.5	31	2	27	27.5	28	2
Developed gill rakers	7	8	9.0	10	2	7	7.0	7	2
Total gill rakers	19	21	21.5	22	2	25	25.5	26	2
Morphometric characters in % SL									
Head length	22	19	19.9	20	2	17	19.0	21	3
Body depth at anus	22	17	18.7	20	2	18	18.6	19	2
Snout length	6.1	5.0	5.0	5.1	2	5.7	5.8	6.0	2
Upper jaw length	11	10.5	10.6	11	2	8.7	10.1	11	3
Head width at postmaxilla	11	9.1	10.3	11	2		12		1
Depth of postmaxilla	3.29		2.72		1	2.20	2.63	2.92	3
Orbit length	2.25	2.18	2.27	2.37	2	1.73	2.18	2.95	3
Interorbital length	7.1	6.8	7.1	7.4	2	7.0	7.3	7.6	3
Postorbital length	15	13	12.9	13	2	14	14.1	14	1
Preal distance	51	47	47.1	48	2	47	48.1	49	3
Predorsal distance	27	26	28.1	30	2	25	27.1	28	3
Distance between pelvic- and anal-fin origin	36	35	35.3	36	2	32	33.1	35	2
Pelvic-fin length	13	13	13.6	15	2	6.4	7.8	9.2	2
In % head length									
Upper jaw length	51	51.6	53.5	55	2	52	53.0	55	3
Orbit length	10	11	11.4	12	2	9.3	11.3	14	3
Otolith characters in % SL									
Otolith length	1.56		2.80		1		0.96		1
Otolith height	1.22		1.68		1		0.80		1
Sulcus length	0.95		1.39		1		0.57		1
Ostium length	0.71		0.97		1		0.44		1
Ostium width	0.28		0.34		1		0.16		1
In % otolith length									
Otolith height	78		60		1		83		1
Sulcus length	61		49		1		60		1
Ostium length	46		34		1		45		1
Ostium width	18		12		1		17		1
Ostium width in % of:									
Otolith height	23		20		1		20		1
Sulcus length	29		24		1		28		1
Ostium length	39		35		1		37		1

weakly pointed tip. Variably formed anteriorly, no pointed tip. Sulcus long, 49–61% of otolith length with separate colliculi and located at the center or slightly dorsally of inner face. Ostium width 24–29% of sulcus length and 35–39% of ostium length.

Coloration.—Two specimens collected in the Southwest Pacific in 2000 and 2003 (510–1060 mm SL) both showed light brown body and head color when fresh (the smaller

specimen slightly paler and pale grayish from below eye to belly) and were found to be pale after preservation, the unpaired fins still being slightly darker. A large Northeast Pacific specimen (1270 mm SL) had pinkish orange color when fresh (Hubbs and Follett, 1978). The largest specimen studied from the same area collected drifting at the surface in 1996 was still entirely dark brown when studied in 2019. Long-term preserved HT (collected in 1877) is pale, creamy whitish (Fig. 1).

Distribution.—This species is distributed in the West to Northeast Pacific (1496 to 3431 m depth).

Remarks.—Otolith length appears to follow the negative allometric trend as in the other three species of *Spectrunculus*, and the two largest *S. grandis* have particularly short pelvic fins (Fig. 4). However, too few specimens were available for study to allow us to investigate intraspecific variation (sex-, size-, or population-related) more closely. Small-sized specimens (< 200 mm SL) not known; the smallest specimen studied is 200 mm SL.

***Spectrunculus radcliffei* Jordan and Thompson, 1914**

Figures 1–4, Tables 2, 3, 5, 7

Spectrunculus radcliffei Jordan and Thompson, 1914 (type locality: NW Pacific, Japan, 35°10'N, 139°37'E).

Spectrunculus grandis non (Günther, 1877), in part: Nielsen and Hureau, 1980; Uiblein et al., 2008.

Holotype.—FMNH 57123, postlarva (pale; described as translucent in original description by Jordan and Thompson, 1914), 56 mm SL, NW Pacific, Japan, Misaki, 35°10'N, 139°37'E.

Non-type material.—S Atlantic ($n = 6$): CAS-ICH 40233, female, 378 mm SL (light brown), off Cape of Good Hope, 35°07'S, 18°25.6'E, ca. 1000 m depth; SAIAB 47240, 541 mm SL (dark), off Cape Columbine, Western Cape, 32°22'S, 16°09'E, 1150 m depth, trawl, 14 January 1995; SAM F023413, 188 mm SL (pale), 33°52'S 16°51'E, RV *Africana II*, 2440 m depth, 9 December 1959; SAM F027093, 190 mm SL (pale), 33°49'S, 16°30'E, RV *Africana II*, 2743 m depth, 27 August 1959; ZMUC P77702, 196 mm SL (light brown), 33°36'S, 16°15'E, R/V *AFRICANA II*, sta. 191, 3080 m depth, beam trawl, 24 August 1959; ZMUC P77704, 192 mm SL (light brown), 34°46'S, 16°42'E, R/V *AFRICANA II*, sta. 316, 3360 m depth, beam trawl, 8 December 1959.

S Indian Ocean: MNHN OTO 354-49 (only otolith and photo of freshly collected fish retained), 910 mm SL (light brown), Kerguelen, 50°50'S, 69°53.8'E, 1769 m depth, F/V *Albius*, longline, 20 September 2012.

NW Pacific ($n = 3$): ZMUC P2397424, male, 1020 mm SL (pale), 2500 m depth, ZMUC P2397444, female, 950 mm SL (light brown), ZMUC P2397445, male, 945 mm SL (light brown), 2000 m depth, Suruga Bay, Central Japan, 34°N, 138°E, caught in 2020.

SW Pacific ($n = 2$): NMNZ P.041951, male, 332 mm SL (pale), 34°31.5'S, 166°21'E, 2930 m depth, September 1982; NMV A25135.002, female, 423 mm SL (pale), 32°3.98'S, 159°52.8'E to 32°2.26'S, 159°51.11'E, NORFANZ cruise, R/V *TANGAROA*, sta. TAN 0308/071, 1920–1934 m depth, 24 May 2003.

NE Pacific ($n = 11$): OSUO 11722, 88 mm SL (dark), off Oregon Coast, 44°48.8'N, 125°36.5'W, ca. 2800 m depth, 8 March 1972; OSUO 11738, 94 mm SL (light brown), 45°56.4'N, 127°39.1'W, 2763 m depth, 13 March 1973; CAS-ICH 246805, male, 478 mm SL (light brown), 45°18'42"N, 126°34'24"W, R/V *YAQUINA*, beam trawl, 2750 m depth, 2 December 1974; CAS-ICH 32364, male, 495 mm SL (light brown), off Oregon, 44°57'18"N, 126°37'18"W to 44°58'0"N, 126°42'42"W, 2850 m depth, beam trawl; CAS-ICH 33083, male, 665 mm SL (light brown), female, 536 mm SL (dark), off Oregon, near

Cascadia Channel, 45°22'24"N, 127°27'48"W to 45°23'54"N, 127°28'36"W, 2788 m depth, beam trawl; CAS-ICH 39821, male, 640 mm SL (light brown), off Oregon, 45°21'30"N, 127°33'0"W to 45°21'42"N, 127°38'30"W, 2800 m depth, beam trawl; CAS-ICH 40234, male, 446 mm SL (pale), off Oregon, Cascadia Abyssal Plain, 45°27'48"N, 126°17'24"W to 45°27'0"N, 126°21'0"W, 2606 m depth, beam trawl; CAS-ICH 40235, 307 mm SL (light brown), off Oregon, Cascadia Abyssal Plain, 45°27'48"N, 126°17'24"W to 45°27'0"N, 126°21'0"W, 2606 m depth, beam trawl; CAS-ICH 62566, 340 mm SL (light brown), off Oregon, Cascadia Abyssal Plain, 44°5'18"N, 125°23'35"W to 44°7'6"N, 125°21'48"W, 2940 m depth, beam trawl; LACM 45789, 1205 mm SL (light brown), ca. 37°N 123°W, ca. 3000 m depth.

Diagnosis.—Number of dorsal-fin rays 135–147, anal-fin rays 103–112, total vertebrae 78–83, pre-anal length 40–45% in SL, pelvic- to anal-fin origin 28–33% in SL, orbit length 8.0–16 in % HL, otolith ostium width 24–30 in % sulcus length and 32–40 in % ostium length; maximum size to 130 cm SL.

Description.—The most important meristic and morphometric characters as well as the otolith characters are shown in Tables 2, 3, 5, and 7. Body moderately elongate, laterally compressed, tapering towards tail. Pectoral-fin depth 6.1–10 times in SL, tail length 1.67–1.81 times in SL, and preanal length 1.24–1.43 times in tail length. Head length 4.2–5.4 in SL and 1.75–2.38 in preanal length; head depth through eye 6.8–12 times in SL. Orbit circular, shorter than snout, 1.27–3.18 times in snout length, slightly larger in small specimens. Anterior gill arch with 8–9 long and 9–13 rudimentary rakers. Pseudobranchial filaments 0–3.

Origin of dorsal fin above vertebra 7–11, well in front of distal tip of pectoral fin. Pelvic fins with two rays each reaching about 1/3 from its base to anal-fin origin. Pectoral fins on lower half of body, rather short, 8.8–12 times in SL, and moderately wide at fin base in most specimens, the width 18–24 times in SL.

Otolith (Fig. 3F–H) oval in large-sized fish (length to height ratio 1.40–1.58) and more elongate in small-sized fish (length to height ratio 1.72–1.76), with slightly pointed posterior tip, anteriorly rather blunt. Sulcus long in large-sized specimens (61–74% of otolith length) and shorter in small-sized fish (51–57% of otolith length), with separate colliculi and located at the center of inner face. Ostium width 24–30% of sulcus length and 32–40% of ostium length in fish of 192 mm SL and larger; ostium width 44–49% of ostium length in two 188 and 190 mm SL juveniles.

Coloration.—Two freshly collected specimens from Japan, Northwest Pacific (ZMUC P2397444 and P2397445; 945–950 mm SL) with light brown body and head, unpaired fins slightly darker, especially posteriorly in tail region. A slightly larger fresh specimen (ZMUC P2397724) from same area (1020 mm SL) is entirely whitish. Long-term preserved specimens, including HT (larva), pale creamy or pale yellowish.

Distribution.—This species is distributed in the Pacific and Southeast Atlantic (ca. 1000 to 3360 m depth). There are no records from the Indian Ocean.

Remarks.—Among the studied specimens, the four females and eight males showed no sex-related differences in morphological or color characters. Head, orbit, and ostium

Table 7. Larger-sized *Spectrunculus radcliffei*, areas separated, with small-sized HT.

	HT, NE Pacific (small)			NW Pacific			SW Pacific			NE Pacific			S Indian Ocean		SE Atlantic	
	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
SL (mm)	56	968.3	1020	3	423	332	307	568.0	1205	9	910	541	378			
Meristic characters																
Dorsal-fin rays	140	138.3	139	3	135	139	138	140.4	144	9	140	136	140			
Caudal-fin rays	8	8.0	8	3	8	10	7	8.1	9	9	8	8	8			
Anal-fin rays	104	107.3	109	3	103	108	104	107.3	112	9	108	105	108			
Precaudal vertebrae	23	22.7	23	3	23	20	22	23.2	24	9	23	22	23			
Total vertebrae	80	78.7	79	3	78	79	79	81.0	83	9	82	79	82			
First dorsal-fin ray above vertebra nr.		8.7	10	3	9	7	9	9.8	11	9	10	9	10			
Dorsal-fin ray above anal-fin ray nr.		36.3	38	3	37	35	32	35.2	38	9	37	35	37			
First anal-fin rays below vertebra nr.		27.7	28	3	26	24	24	25.6	27	9	27	25	27			
Pectoral-fin rays	28	26.3	27	3	27	25	25	27.6	29	9	26	26	26			
Developed gill rakers		8.0	8	3	9	9	8	8.6	9	8	9	8	9			
Total gill rakers		20.3	21	3	18	21	18	19.1	21	8	17	17	18			
Morphometric characters in % SL																
Head length		19.6	21	3	21	19	19	20.5	22	8	19	19	19			
Body depth at anus		14	15.2	16	3	17	14	16.3	19	8	19	19	19			
Snout length		4.9	5.1	5.3	3	5.7	5.1	5.5	6.0	8	4.9	4.9	5.6			
Upper jaw length		9.6	10.1	11	3	10	9.0	10.7	12	8	8.4	8.4	9.6			
Head width at postmaxilla		7.5	8.2	9.2	3	9.6	8.5	10.3	12	8	8.5	8.5	8.9			
Depth of postmaxilla		2.29	2.37	2.42	3	2.50	2.62	2.88	3.31	8	2.18	2.18	2.30			
Orbit length		1.67	1.96	2.20	3	2.24	2.09	2.50	3.24	8	2.47	2.47	2.59			
Interorbital length		5.1	5.4	5.7	3	6.8	4.9	6.3	7.1	8	5.4	5.4	5.7			
Postorbital length		13	13.6	15	3	14	12	13.4	15	8	13	13	13			
Preal distance		43	43.9	45	3	44	40	42.6	45	9	44	42	44			
Predorsal distance		29	30.0	31	3	26	26	26.9	29	8	27	27	26			
Distance between pelvic- and anal-fin origin		31	31.8	33	3	33	28	29.1	31	8	31	31	31			
Pelvic-fin length		10	11.5	13	3	12	3.6	11.5	16	8	12	12	15			
Morphometric characters in % head length																
Upper jaw length		51	51.3	52	3	50	48	52.1	57	8	45	45	51			
Orbit length		8.0	10.1	12	3	11	11	12.2	16	8	13	13	14			
Otolith characters in % SL																
Otolith length		1.35	1.51	1.68	3						1.62	2.85				
Otolith height		0.96	1.03	1.07	3						1.04	1.83				
Sulcus length		1.00	1.04	1.07	3						1.04	1.75				
Ostium length		0.68	0.77	0.81	3						0.77	1.34				
Ostium width		0.26	0.28	0.29	3						0.31	0.43				
Otolith characters in % otolith length																
Otolith height		63	68.5	72	3						64	64				
Sulcus length		63	69.1	74	3						65	61				

Table 7. Continued.

	HT, NE Pacific (small)			NW Pacific			SW Pacific			NE Pacific			S Indian Ocean		SE Atlantic	
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	n	Min	Max	n
Ostium length	48	51.0	54	48	51.0	54	48	51.0	54	48	51.0	54	3	48	47	47
Ostium width	17	18.5	19	17	18.5	19	17	18.5	19	17	18.5	19	3	19	15	15
Ostium width in % of:																
Otolith height	27	27.0	28	27	27.0	28	27	27.0	28	27	27.0	28	3	30	23	23
Sulcus length	26	26.8	27	26	26.8	27	26	26.8	27	26	26.8	27	3	30	24	24
Ostium length	35	36.3	38	35	36.3	38	35	36.3	38	35	36.3	38	3	40	32	32

length show negative allometry when the entire size range (i.e., small-sized juveniles to largest-sized adults) is considered (Fig. 4). No such pattern was found for pre-anal and pelvic-fin length and ostium width. Two of the three smallest specimens (size range 188–190 mm SL) showed a relatively wide ostium compared to all other conspecifics (including the 192 mm SL specimen shown in Figs. 3F, 4), possibly indicating early life-history modification in otolith form. Like in *Spectrunculus grandis*, the largest specimen of *S. radcliffei* showed a clearly shorter pelvic fin (Fig. 4).

Specimens from the South Atlantic show slightly shorter heads, narrower interorbitals, and deeper bodies than in the other areas of occurrence. However, data are insufficient for detailed quantitative population comparisons.

Distinction of each of the four species of *Spectrunculus*.—(Table 8) *Spectrunculus stenostio* differs from the other three species by the clearly narrower ostium and by the mostly higher number of total vertebrae; *S. crassus* differs from the other three species in the combination of low dorsal-fin, anal-fin, and vertebrae counts, mostly larger eyes and lower maximum size; *S. radcliffei* differs from the other three species in the combination of a mostly shorter preanal length, shorter pelvic- to anal-fin origin distance, and by higher anal-fin ray counts; *S. grandis* differs from the other three species in the combination of all nine characters.

Color patterns have no significance in species distinction except for fresh or recently collected specimens of the two North Atlantic species, with body and head color in *S. crassus* being mostly darker than in *S. stenostio* (see also Uiblein et al., 2008).

KEY TO THE SPECIES OF *SPECTRUNCULUS*

The key below is prepared to allow identification among the four species of *Spectrunculus* without necessary extraction of otoliths (see also Materials and Methods section). Consequently, distinction in otolith shape is indicated in parentheses.

- 1a. Dorsal-fin rays 135–148, anal-fin rays 101–112, total vertebrae 77–88, eye diameter in subadult or adult specimens 6.4–13 times in HL, maximum size to 100 cm SL or larger, body and head color in freshly caught or recently fixed and/or preserved specimens pale gray or pale whitish, light brown or dark brown, all major oceans..... 2
- 1b. Dorsal-fin rays 121–139, anal-fin rays 91–102, total vertebrae 72–79, eye diameter in subadult or adult specimens 5.8–8.2 times in HL, maximum size 60 cm SL, body and head color in freshly caught or recently fixed and/or preserved specimens light brown in juveniles or subadults and dark gray or dark brown (rarely speckled) in larger specimens, Atlantic and E Pacific..... ***Spectrunculus crassus***
- 2a. Pre-anal length 1.83–2.15 times in SL and 1.01–1.15 in tail length (= subequal or only slightly shorter), distance between pelvic- and anal-fin origins 2.28–3.17 times in SL, total vertebrae 80–88, all major oceans..... 3
- 2b. Pre-anal length 2.22–2.48 times in SL and 1.24–1.43 in tail length, distance between pelvic- and

Table 8. Ranges of major characters separating the four species of *Spectrunculus* (morphometric data referring to specimens ≥ 200 mm SL). The most important distinguishing characters (singly or in combination) from the three other species, respectively, are emphasized in bold italics (see the previous tables for numbers of specimens studied).

	<i>S. stenostio</i>	<i>S. crassus</i>	<i>S. grandis</i>	<i>S. radcliffei</i>
Maximum standard length	<110 cm	<60 cm	<130 cm	<130 cm
Dorsal-fin rays	137–148	121–139	135–137	135–147
Anal-fin rays	102–112	91–102	101–105	103–112
Vertebrae	80–88	72–79	77–80	78–83
Preanal length in % SL	47–55	42–54	47–51	40–45
Base of pelvic fin to anal-fin origin in % SL	34–44	29–41	32–36	28–33
Orbit length in % head length	9.9–12	12–17	9.3–14	8.0–16
Otolith ostium width in % sulcus length	15–21	22–30	24–29	24–30
Otolith ostium width in % ostium length	19–29	31–40	35–39	32–40

- anal-fin origins 3.02–3.58 times in SL, total vertebrae 78–83, Pacific and S Atlantic ***S. radcliffei***
- 3a. Dorsal-fin rays 135–137, anal-fin rays 101–105, total vertebrae 77–80, maximum size 130 cm SL (otolith ostium width 2.56–2.86 in its length and 4.2–4.4 times in sulcus length), Pacific..... ***S. grandis***
- 3b. Dorsal-fin rays 137–148, anal-fin rays 102–112 (106–108 in the SW Pacific population [co-occurrence with *S. grandis*]), total vertebrae 80–88, maximum size 110 cm SL (otolith ostium width 3.45–5.3 in its length and 4.8–6.7 times in sulcus length), N Atlantic, S Indian Ocean, and SW Pacific..... ***S. stenostio***

DATA ACCESSIBILITY

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ACKNOWLEDGMENTS

For arranging collection visits, providing material, loans, or other collection-related assistance, we thank A. Kuwamoto (Blue Corner), J. Maclaine (BMNH), D. Catania, J. Fong, and T. Iwamoto (CAS), A. Graham (CSIRO), N. Camacho, R. Feeney, and C. Thacker (LACM), A. Williston (MCZ), G. Duhamel, Z. Gabsi, J. Pfliger, and P. Pruvost (MNHN), P. Konstantinidis (OS/OSUO), G. Hanke (RBCM), O. Gon, R. Bills, N. Mazungala, and the SAIAB collection staff (SAIAB), M. Lisher and M. Bougaardt (SAM), N. Straube and B. R. Olsson (ZMUB), and M. A. Krag (ZMUC). For photos, radiographs, or CT scans, we thank H. Lauridsen and C. Carøe Ejlskov Pedersen (Aarhus University), B. Clark (BMNH), J. Fong, A. Graham, M. A. Krag, M. Lisher, and J. Pfliger. For providing information on additional specimens of *Spectrunculus* from Japan which could not be included in this study, we thank Y. Fujiwara and K. Mita (JAMSTEC). Additional thanks go to all supporting colleagues acknowledged in our first revision of the genus *Spectrunculus* (Uiblein et al., 2008). The first author thanks the Institute of Marine Research, Norway, for sabbatical travel support.

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