

TITLE PAGE

Manuscript title: **THE SYSTEMATICS OF THE OPHIDIID GENUS
SPECTRUNCULUS (TELEOSTEI, OPHIDIIFORMES) REVISITED WITH
DESCRIPTION OF A NEW SPECIES AND RESURRECTION OF *S. RADCLIFFEI***

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Running head: Systematics of *Spectrunculus* revisited

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1 **The Systematics of the ophidiid genus *Spectrunculus* (Teleostei, Ophidiiformes)**

2 **revisited with description of a new species and resurrection of *S. radcliffei***

3

4 **ABSTRACT**

5 After a preceding revision based on 87 specimens, the systematics of the abyssal Giant
6 Cuskeel genus *Spectrunculus* has been revisited, based on the examination of additional 34
7 specimens and new otolith shape data of the holotype of *S. grandis*. From the latter a clear
8 distinction in otolith ostium width could be found in specimens from the Atlantic, Southern
9 Indian Ocean and Southwest Pacific which were formerly identified as *S. grandis*.

10 Consequently, the new species *S. stenostio* is described which has a narrower ostium when
11 related to its length or to sulcus length and differs also in the combination of three body shape
12 characters, three meristic characters and maximum size from the three other congeners, *S.*
13 *crassus* (Atlantic, East Pacific), *S. grandis* (Pacific) and the previously synonymized *S.*
14 *radcliffei* (Pacific, Southern Indian Ocean, Southeast Atlantic). The latter species is here
15 resurrected based on a rather short pre-anal length and additional morphometric as well as
16 meristic and maximum size differences. An identification key for the four *Spectrunculus*
17 species is provided.

18

19

20 Key words: Ophidiidae, Neobythitinae, Giant Cuskeel, deep-sea fishes, distribution,
21 morphology, color, otoliths

22

23 INTRODUCTION

24 The ophidiid deep-sea fish genus *Spectrunculus* belongs to the subfamily Neobythitinae,
25 a rather diverse group of cuskeels found in a large variety of habitats mostly close to the
26 bottom from the shelf to more than 4000 meters depth (Cohen & Nielsen 1978; Nielsen et al.
27 1999). This group is still subject of intense taxonomic studies with new taxa being described
28 and systematic information updated (e.g. Nielsen et al. 2015; Ohashi 2018; Uiblein & Nielsen
29 2018, 2019, 2021; Schwarzhans & Møller 2021; Nielsen & Uiblein 2022; Schwarzhans et al.
30 2022).

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

35 Since our last revision comparative data of 34 additional *Spectrunculus* specimens has
36 been collected and analyzed together with earlier published as well as previously not
37 considered or newly generated data. This allows for a more refined and detailed distinction
38 among different forms occurring in various areas of the three major oceans. For instance, new
39 otolith shape data of the holotype of *Spectrunculus grandis* (Günther, 1877) (type locality
40 Japan, NW Pacific) became available suggesting a clear distinction from specimens of the
41 Atlantic, previously considered conspecific in our former revision (Uiblein et al. 2008).
42 Furthermore, detailed morphological studies of *Spectrunculus* specimens from the South
43 Atlantic, Southern Indian Ocean and Pacific (including three recently obtained specimens
44 from Japan) indicated the need to reconsider the formerly synonymized *S. radcliffei* Jordan &
45 Thompson, 1914 as a valid species.

46 Thus, in the present study, we describe *S. stenostio* new species and resurrect *S.*
47 *radcliffei*, considering also intraspecific regional and/ sex or size-related morphological and

48 color variation in the now four valid species. In addition to diagnostic, descriptive and
49 distribution information for each species, an identification key is provided.

50

51 **MATERIAL AND METHODS**

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

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

66 One large *Spectrunculus* specimen (127 cm SL; CAS-ICH 25724), of which only the
67 right otolith and the posteriormost part of the tail had been retained, had been studied in detail
68 by Hubbs and Follett (1978) when still intact and hence the published meristic and
69 morphometric data were used, while the otolith could be investigated by us. Of another large
70 specimen (128 cm SL; CAS-ICH 90121) a hand-written sheet with unpublished
71 morphometric and meristic data from D.J. Long, taken shortly after collection of the
72 specimen, was used.

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

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

83 Morphometric data were rounded to two decimal digits in numbers < 4 , to one decimal
84 digit in numbers < 10 and to whole numbers in higher values except for one decimal digit in
85 averages provided in tables.

86 Institutional abbreviations follow Sabaj (2020). Other abbreviations are: HT = holotype;
87 PT = paratype; SL = standard length; TL = total length; HL = head length; Min = Minimum;
88 Max = Maximum; n = number (count); N = North; S = South; E = East; W = West.

89

90 RESULTS

91 *Spectrunculus* Jordan and Thompson, 1914

92 Giant Cuskeel

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

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

97

98 **Diagnosis**

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

112

113 **Remarks**

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

122

123 *Spectrunculus stenostio* new species

124 Figures 1–4; Tables 1–3

125 *Spectrunculus grandis* (Günther, 1877); Duhamel et al. 2005; in part: Nielsen & Hureau

126 1980; Uiblein et al. 2008.

127

128 **Material studied (n=32)**

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

132 Paratypes, all North Atlantic (n=22): ZMUB 18477 (ZMUB-MAR-ECO 12291), male,
133 650 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.
134 42-368, bottom trawl, 2063–2107 m depth, 8 July 2004; ZMUB 18478 (ZMUB-MAR-ECO
135 13347), female, 825 mm SL (pale), 42°46.2'N, 29°16.2'W, R/V G.O. SARS, sta. 46-372,
136 bottom trawl, 3005–3050 m depth, 11 July 2004; ZMUB 18479 (ZMUB-MAR-ECO 2617),
137 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,
138 sta. 50-373, bottom trawl, 2593–2607 m depth, 12 July 2004; ZMUB 18480 (ZMUB-MAR-
139 ECO 13977), male, 670 mm SL and female, 840 mm SL (both pale), 42°55.32'N, 28°8.35'W
140 to 42°53.05'N, 28°8.33'W, R/V G.O. SARS, sta. 52-374, bottom trawl, 2973–2979 m depth,
141 13 July 2004; ZMUB 18481 (ZMUB-MAR-ECO 13821), male, 680 mm SL (pale), 53°7.8'N,
142 34°45.6'W, R/V G.O. SARS, sta. 68-384, bottom trawl, 2306–2374 m depth, 25 July 2004.
143 ZMUB 18482 (ZMUB-MAR-ECO 16013), male, 725 mm SL, ZMUB 18483 (ZMUB-MAR-
144 ECO 16027), male, 975 mm SL, ZMUB 18484 (ZMUB-MAR-ECO 16041), female, 858 mm
145 SL and ZMUB 18485 (ZMUB-MAR-ECO 16055), female, 765 mm SL (all pale),
146 42°34.91'N, 28°2.64'W to 42°33.91'N, 28°5.84'W, M/S LORAN, sta. 1, bottom longline,
147 2925–2827 m depth, 5 July 2004; ZMUB 18486 (ZMUB-MAR-ECO 17105), female, 950

148 mm SL, ZMUB 18487 (ZMUB-MAR-ECO 20065), female, 742 mm SL, ZMUB 18488
149 (ZMUB-MAR-ECO 20079), male, 625 mm SL, ZMUB 18489 (ZMUB-MAR-ECO 20093),
150 female, 825 mm SL), ZMUB 18490 (ZMUB-MAR-ECO 20107), male, 685 mm SL, ZMUB
151 18492 (ZMUB-MAR-ECO 20135), female, 925 mm SL, ZMUB 18494 (ZMUB-MAR-ECO
152 20163), female, 885 mm SL (all pale) and ZMUB 18491 (ZMUB-MAR-ECO 20121),
153 female, 895 mm SL (pale with several large brown rings on body), same station data as HT;
154 ZMUC P77793, 960 mm SL, ZMUC P77794 800 mm SL, ZMUC P77795, male, 960 mm SL
155 and ZMUC P77796, 730 mm SL (all pale), 43°39.3'N, 22°37.8'W, R/V WALTHER
156 HERWIG, sta. 82-352, beam trawl, 1900–2080 m depth, 8 June 1982.

157 Non-types, S Indian Ocean E (*n*=4): MNHN 2003-0598, 754 mm SL (dark) and MNHN
158 2003-0599, 962 mm SL (light brown), Kerguelen, 50°50.3' S, 69°44.1' E, F/V Ile Bourbon,
159 longline, 1768 m depth, 11 Oct 2002; SAIAB 118942, 2, 706 mm SL (dark) and 1001 mm SL
160 (light brown), near Lena Tablemount, 53°30'S, 48°31.5'E, F/V Shinsei Maru nr. 3, longline,
161 2112 m depth, 19 May 2010.

162 SW Pacific (*n*=5): CSIRO H-5304.01, female, 1060 mm SL (light brown when fresh,
163 pale after preservation), 38°34'S, 149°28'E to 38°36'S, 149°33'E, 1954–1979 m depth, 19
164 April 2000; CSIRO H-6036.02, female, 510 mm SL (light brown when fresh, pale after
165 preservation), 32°3'S, 159°52'E to 32°2'S, 159°51'E, NORFANZ cruise, R/V TANGAROA,
166 station 0308/071, 1920–1934 m depth, 24 May 2003. NMNZ P.031193, female, 610 mm SL
167 (pale), 42°55.59'S, 172°39.21'E, R/V TANGAROA, sta. TAN 9406/226, 1694–1707 m
168 depth, 22 June 1994; NMNZ P.033111, female, 1030 mm SL (pale), ~37°30'S, ~176°30'E;
169 USNM 215295, 248 mm SL (pale), 42°11'S, 175°11'E, 2602–2619 m depth, 20 Sep 1966.

170

171 **Diagnosis**

172 Number of dorsal-fin rays 137–148, anal-fin rays 102–112, total vertebrae 80–88, pre-
173 anal length 47–55 % in SL, pelvic- to anal-fin origin 34–44 % in SL, orbit length 9.9–12 in %
174 head length, otolith ostium width 15–21 in % sulcus length and 19–29 in % ostium length;
175 maximum size to 110 cm SL.

176

177 **Description**

178 The most important meristic and morphometric characters as well as the otolith
179 characters are shown in Tables 1–3. Body elongate, laterally compressed, tapering towards
180 tail. Pectoral-fin depth 5.7–7.9 times in SL, tail length 1.76–1.90 times in SL and preanal
181 length 1.01–1.15 times in tail length. Head length 4.7–5.6 in SL and 2.23–2.75 in preanal
182 length; head depth through eye 7.8–9.5 times in SL. Orbit circular, shorter than snout, 2.09–
183 2.80 in snout length. Anterior gill arch with 8–10 long and 10–13 rudimentary rakers.
184 Pseudobranchial filaments 0–2.

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

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

193 **Coloration.**— Freshly or recently caught specimens with pale creamy body and head,
194 unpaired fins dark brown along distal margins or more entirely, as observed in the 19 type
195 specimens collected by the MAR-ECO cruise, N Atlantic, in 2004. One of those specimens
196 showed in addition several large brown rings on body. Of four specimens collected in the S

197 Indian Ocean the two smaller ones (706-754 mm SL) were dark brown and the two larger
198 ones (962-1001 mm SL) light brown. In three of those specimens the unpaired fins were dark
199 brown.

200

201 **Etymology**

202 The new species name is composed of the Latin word for narrow or slender “*tenuis*” and
203 the otolith structure “*ostium*”. The ablative of the combined term is “*stenostio*”, meaning
204 “with a narrow ostium”.

205

206 **Distribution**

207 N Atlantic and S Indian Ocean to SW Pacific, 1694 to 3050 m depth. No records from
208 the S Atlantic.

209

210 **Remarks**

211 Among the studied specimens that could be sexed were 9 males and 15 females. No
212 sexual dimorphism could be found in any meristic and morphometric characters including
213 otolith characters.

214 A clear negative allometry in otolith length, but not in ostium and sulcus shape, was
215 detected (Fig. 4). Apart from a slight decrease in relative orbit length with size (Fig. 4), no
216 other allometric changes in body shape were encountered in *Spectrunculus stenostio*.

217 A slight shift towards a lower number of total vertebrae was found in the Indo-Pacific
218 population, while dorsal- and anal-fin ray number do not follow this trend (Table 2).

219 Small-sized specimens (< 200 mm SL) not known, the smallest specimen studied is 248
220 mm SL.

221

222 *Spectrunculus crassus* (Vaillant, 1888)

223 Figures 1–4; Tables 2–5

224

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

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

227 *Spectrunculus grandis* non (Günther, 1877) in part: Nielsen & Hureau 1980

228 *Spectrunculus crassus* Uiblein et al. 2008; Hanke et al. 2015

229

230 **Material studied (n=58)**

231 *Holotype.* MNHN 1986-0552, 284 mm SL (light brown; described as dark brown in
232 original description by Vaillant 1888), NE Atlantic, 44°20'N, 17°11'W, R/V TALISMAN sta.
233 136, 4255 m depth; 26 August 1883.

234 Non-types, N Atlantic (n=49): MNHN 1979-0221, 329 mm SL (pale), 56°38'N, 11°6'W,
235 R/V J. CHARCOT, sta. 2721, 2466 m depth, 17 July 1976; MNHN 1979-0222, 142 mm SL
236 (light brown), 56°38'N, 11°6'W, R/V J. CHARCOT, sta. 2721, 2466 m depth, 17 July 1976;
237 MNHN 1979-0223, 280 mm SL (light brown), 56°33'N, 11°11'W, J. CHARCOT, sta. 2721,
238 2483–2513 m depth, 17 July 1976; MNHN 1979-0224, 400 mm SL (dark), 56°33' 0"N,
239 11°10'58.8"O, Jean Charcot, sta. Cp04, 2483–2513 m, 17 July 1976; MNHN 1999-0708, 327
240 mm SL (light brown), 56°15'N, 10°16'W, R/V N.O.THALASSA, 2020 m depth, 27 April
241 1999; ZMUB 18351 (ZMUB-MAR-ECO 8081), female, 250 mm SL (dark) and ZMUB
242 18352 (ZMUB-MAR-ECO 8067), male, 253 mm SL (light brown), 42°54.91'N, 30°20.37'W
243 to 42°53.11'N, 30°20.92'W, R/V G.O. SARS, sta. 40-367, bottom trawl, 2660–2670 m depth,
244 7 July 2004. ZMUB 18353 (ZMUB-MAR-ECO 13053), male, 216 mm SL (light brown),
245 ZMUB 18354 (ZMUB-MAR-ECO 2679), 2 females, 240–282 mm SL and male, 260 mm SL
246 (all dark) and ZMUB 18355 (ZMUB-MAR-ECO 12419), female, 187 mm SL (light brown),

247 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
248 trawl, 2973–2979 m depth, 13 July 2004; ZMUB 18356 (ZMUB-MAR-ECO 11582), male,
249 220 mm SL (light brown), 53°16.8'N, 35°31.8'W, R/V G.O. SARS, sta. 72-386, bottom trawl,
250 2522–2567 m depth, 27 July 2004; ZMUB 18463 (ZMUB-MAR-ECO 12291), 3 males, 482–
251 522 mm SL and 522 mm SL (all dark), 42°48.6'N, 29°38.36'W to 42°46.64'N, 29°38.59'W,
252 R/V G.O. SARS, sta. 42-368, bottom trawl, 2063–2107 m depth, 8 July 2004; ZMUB 18464
253 (ZMUB-MAR-ECO 10891), 3 females, 435–575 mm SL (all dark), 51°55.08'N, 30°25.02'W
254 to 51°56.14'N, 30°24.44'W, R/V G.O. SARS, sta. 62-380, bottom trawl, 1872–1959 m depth,
255 20 July 2004; ZMUB 18465 (ZMUB-MAR-ECO 13807), female, 445 mm SL (light-brown
256 speckled) and ZMUB 18466 (ZMUB-MAR-ECO 13821), male, 420 mm SL, 7 females, 375–
257 480 mm SL and 405 mm SL (all dark), 53°7.8'N, 34°45.6'W, R/V G.O. SARS, sta. 68-384,
258 bottom trawl, 2306–2374 m depth, 25 July 2004; ZMUB 18467 (ZMUB-MAR-ECO 20275),
259 female, 490 mm SL, ZMUB 18468 (ZMUB-MAR-ECO 20261), female, 465 mm SL and
260 ZMUB 18469 (ZMUB-MAR-ECO 20247), female, 480 mm SL (all dark), 42°25.49'N,
261 29°48.14'W to 42°25.49'N, 29°46.13'W, M/S LORAN, sta. 13, bottom longline, 2429–2018 m
262 depth, 8 July 2004; ZMUB 18470 (ZMUB-MAR-ECO 17133), female, 510 mm SL (dark),
263 42°23.26'N, 29°59.71'W to 42°24.88'N, 30°0'W, M/S LORAN, sta. 15, bottom longline,
264 2650–2675 m depth, 9 July 2004; ZMUB 18471 (ZMUB-MAR-ECO 16433), 470 mm SL,
265 ZMUB 18472 (ZMUB-MAR-ECO 16419), 510 mm SL and ZMUB 18473 (ZMUB-MAR-
266 ECO 16405), female, 475 mm SL (dark), 42°37.77'N, 28°22.18'W to 42°37.58'N,
267 28°19.16'W, M/S LORAN, sta. 5, bottom longline, 2125–2436 m depth, 6 July 2004; ZMUB
268 18474 (ZMUB-MAR-ECO 17119), female, 480 mm SL (dark), 42°25.49'N, 29°48.14'W to
269 42°25.49'N, 29°46.13'W, M/S LORAN, sta. 13, bottom longline, 2429–2018 m depth, 8 July
270 2004; ZMUB 18475 (ZMUB-MAR-ECO 17189), female, 330 mm SL (dark), 42°36.14'N,
271 29°20.05'W to 42°37.82'N, 29°19.51'W, M/S LORAN, sta. 16, bottom longline, 3366–3280

272 m depth, 9 July 2004; ZMUB 18476 (ZMUB-MAR-ECO 17393), female, 522 mm SL (dark),
273 42°25.33'N, 29°38.2'W to 42°25.37'N, 29°40.42'W, M/S LORAN, sta. 12, bottom longline,
274 1580–1964 m depth, 8 July 2004; ZMUB 19505 (ZMUB MAR-ECO 9757), 5 females, 455–
275 540 mm SL and 2 specimens, 476–530 mm SL (all dark), 51°27.02'N, 29°19.73'W to
276 51°28.02'N, 29°19.54'W, R/V G.O.SARS, st.56-378, bottom bottom trawl, 1872–1950 m
277 depth, 17 July 2004; ZMUC P77797, 500 mm SL (dark), 43°39.3'N, 22°37.8'W, R/V
278 WALTHER HERWIG, sta. 82-352, beam trawl, 1900–2080 m depth, 8 June 1982; ZMUC
279 P77805, female, 490 mm SL (dark), 43°33.6'N, 22°33.4'W, WALTHER HERWIG, sta. 82-
280 350, beam trawl, 1800–1970 m depth, 8 June 1982.

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

284 NE Pacific, off Oregon ($n=5$): CAS-ICH 36991, female (?), 458 mm SL (dark),
285 44°37'24"N, 125°39'54"W to 44°37'18"N 125°41'6"W, 2816 m depth, beam trawl, 13 Apr
286 1976; CAS-ICH 40222, male, 334 mm SL (dark), Cascadia Abyssal Plain, 45°9'18"N,
287 125°38'18"W to 45°10'30"N, 125°38'0"W, 2669 m depth, 45°10'30"N, beam trawl; CAS-ICH
288 62977, male, 362 mm SL (dark), Cascadia Abyssal Plain, 47°50'30"N, 127°2'36"W, 2519 m
289 depth, beam trawl; OSUO 11743, 345 mm SL (light brown), 44°40'N, 126°0'W, 2800 m
290 depth, 21 August 1965; OSUO 11775, 239 mm SL (light brown), 45°31.7'N, 127°28.4'W,
291 2800 m depth, 4 February 1973.

292 SE Pacific: NHMB 191, HT of *Spectrunculus coheni*, 106 mm SL (dark), 8°23'S,
293 80°25'W, R/V ANTON BRUUN, beam trawl, 2945–2966 m depth, 31 October 1965.

294

295 **Diagnosis**

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

302

303 **Description**

304 The most important meristic and morphometric characters as well as the otolith
305 characters are shown in Tables 2–5. Body elongate, laterally compressed, tapering towards
306 tail. Pectoral-fin depth 6.9–8.3 times in SL, tail length 1.78–1.86 times in SL and preanal
307 length 1.16–1.33 times in tail length. Head length 4.6–5.6 in SL and 2.00–2.72 in preanal
308 length; head depth through eye 8.2–11 times in SL. Orbit circular, shorter than snout, 1.56–
309 2.26 times in snout length. Anterior gill arch with 8–10 long and 8–12 rudimentary rakers.
310 Pseudobranchial filaments 0–2.

311 Origin of dorsal fin above vertebra 7–9, well in front of distal tip of pectoral fin. Pelvic
312 fins with two rays reaching about halfway from base to anal-fin origin. Pectoral fins on lower
313 half of body, rather short, 9.6–11 times in SL, and rather wide at fin base, the width 23–27
314 times in SL.

315 Otolith (Fig. 2) oval to elongate (length to height ratio 1.34–2.10), with pointed
316 posterior tip. Anterior tip rounded. Sulcus moderately long, 43–72 % of otolith length, with
317 separate colliculi and located at the center of inner face. Ostium vertically enlarged, its width
318 22–30 % of sulcus length and 31–40 % of ostium length in fish of 187 mm SL and larger;
319 ostium width 59 % of ostium length in the 110 mm juvenile.

320 **Coloration.**— Fresh or recently caught fish mostly entirely dark brown. Among the 42
321 specimens collected during the MAR-ECO expedition in the N Atlantic in 2004, 37 showed
322 uniformly dark-brown colored body, head and fins; one larger specimen (445 mm SL) had a
323 speckled color pattern with dark dots or blotches on pale background on head, body and fins;
324 four of the five smallest specimens (187–253 mm SL) had light brown body and head color
325 with ventral parts of head and belly pale bluish grey. Long-time preserved specimens
326 including HT are entirely light brown.

327

328 **Distribution**

329 Atlantic and E Pacific; 1580 to 4255 m depth.

330

331 **Remarks**

332 Among the specimens that could be sexed were ten males and 27 females. No sexual
333 dimorphism could be found in any of the meristic and morphometric characters including
334 otoliths (see also, Uiblein et al. 2008).

335 Slight positive allometry in jaw length and negative allometry in orbit length was found
336 (Fig. 4). Orbit in head length in the E Pacific population is slightly shorter than in the
337 Atlantic. Otolith length showed negative allometry, while ostium and sulcus shape did not
338 when the entire size range is considered (Fig. 4). However, the smallest specimen showed a
339 slightly wider and shorter ostium which – when combined – indicate an early life-history shift
340 in otolith form (i.e., from small-sized juveniles to larger-sized subadults and adults).

341 No regional variation in meristic characters could be detected.

342

343 *Spectrunculus grandis* (Günther, 1877)

344 (Figures 1–4; Tables 2,3,6)

345 *Sirembo grandis* Günther, 1877 (type locality: Northwest Pacific, E of Central Japan,
346 34°37'N, 140°32'E)
347 *Spectrunculus grandis*: Hubbs & Follett 1978; in part: Nielsen & Hureau 1980; Uiblein et al.
348 2008
349

350 **Material studied (n=7)**

351 *Holotype*, BMNH 1887, 675 mm SL (pale; described as brown in original description by
352 Günther 1877), Northwest Pacific, E of Central Japan, 34°37'N, 140°32'E, R/V Challenger,
353 sta. 237, 3431 m depth, 17 June 1875.

354 Non-types, SW Pacific (n=3): CSIRO H-6036.01, male, 450 mm SL (pale), 32°3'S,
355 159°52'E to 32°2'S, 159°51'E; NORFANZ cruise, R/V TANGAROA, station # 0308/071,
356 1920–1934 m depth, 24 May 2003; LACM 43564-1, 200 mm SL (light brown), 42°11'S,
357 175°11'E, 2602–2619 m depth, 20 Sept 1966; NMNZ P.041204, female, 840 mm SL (dark),
358 58°36'S, 161°23'E, 1496–1638 m depth, 19 August 2004.

359 NE Pacific (n=3): CAS-ICH 25724, male, 1270 mm SL (light brown), California, 40
360 miles west southwest of the Farallon Islands, ~37°30'N, ~132°4'W, surface, above ca. 3000 m
361 depth; CAS-ICH 90121, 1283 mm SL (dark), California, off Trinidad Head, 41°50'N,
362 125°10'W, surface, above ca. 2500 m depth, 16 Sept 1996; OSUO 11789, 370 mm SL (light
363 brown), Northeast Pacific, 44°41.8'N, 127°22.7'W, 3021 m depth, 12 June 1974.

364

365 **Diagnosis**

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

370

371 **Description**

372 The most important meristic and morphometric characters as well as the otolith
373 characters are shown in Tables 2, 3 and 6. Body elongate, laterally compressed, tapering
374 towards tail. Pectoral-fin depth in HT 7.2 times in SL, tail length 1.80–1.88 times in SL and
375 preanal length 1.04–1.14 times in tail length in HT and two non-types. Head length 4.9–5.9 in
376 SL and 2.22–2.89 in preanal length; head depth through eye 8.57 times in SL. Orbit circular,
377 shorter than snout, 1.98–3.27 times in snout length. Anterior gill arch with 7–10 long and 11–
378 19 rudimentary rakers. Pseudobranchial filaments 1–2.

379 Origin of dorsal fin above vertebrae 9–10, well in front of distal tip of pectoral fin.
380 Pelvic fins with two rays in each reaching about 1/4 to 1/3 from its base to anal-fin origin.

381 Pectoral fins on lower half of body, rather short, 10–12 times in SL, and moderately wide at
382 fin base, the width 17–19 times in SL.

383 Otolith (Fig. 2) oval to slightly elongated (length to height ratio 1.20–1.67), posteriorly
384 flattened or with only a weakly pointed tip. Variably formed anteriorly, no pointed tip. Sulcus
385 long, 49–61 % of otolith length with separate colliculi and located at the center or slightly
386 dorsally of inner face. Ostium width 24–29 % of sulcus length and 35–39 % of ostium length.

387 **Coloration.**— Two specimens collected in the SW Pacific in 2000 and 2003 (510-1060 mm
388 SL) both showed light brown body and head color when fresh (the smaller specimen slightly
389 paler and pale greyish from below eye to belly) and were found to be pale after preservation,
390 the unpaired fins still being slightly darker. A large NE Pacific specimen (1270 mm SL) had
391 pinkish orange color when fresh (Hubbs and Follett 1978). The largest specimen studied from
392 the same area collected drifting at the surface in 1996 was still entirely dark brown when
393 studied in 2019. Long-term preserved HT (collected in 1877), is pale, creamy whitish (Fig.
394 1).

395

396 **Distribution**

397 W to NE Pacific; 1496 to 3431 m depth.

398

399 **Remarks**

400 Otolith length appears to follow the negative allometric trend as in the other three
401 *Spectrunculus* species and the two largest *S. grandis* have particularly short pelvic fins (Fig.
402 4). However, too few specimens were available for study to allow us to investigate
403 intraspecific variation (sex- size- or population-related) more closely.

404 Small-sized specimens (< 200 mm SL) not known, the smallest specimen studied is 200
405 mm SL.

406

407 *Spectrunculus radcliffei* Jordan and Thompson, 1914
408 (Figures 1–4; Table 2,3,5,7)

409 *Spectrunculus radcliffei* Jordan and Thompson, 1914 (type locality: NW Pacific, Japan,
410 35°10'N, 139°37'E)

411 *Spectrunculus grandis* non (Günther, 1877), in part: Nielsen & Hureau 1980; Uiblein et al.
412 2008

413

414 **Material studied (n=24)**

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

417 Non-types, S Atlantic (n=6): CAS-ICH 40233, female, 378 mm SL (light brown), off
418 Cape of Good Hope, 35°07'S, 18°25.6'E, ca. 1000 m depth; SAIAB 47240, 541 mm SL
419 (dark), off Cape Columbine, Western Cape, 32°22'S, 16°09'E, 1150 m depth, trawl, 14 Jan

420 1995; SAM F023413, 188 mm SL (pale), 33°52'S 16°51'E, RV Africana II, 2440 m depth, 9
421 Dec 1959; SAM F027093, 190 mm SL (pale), 33°49'S, 16°30'E, RV Africana II, 2743 m
422 depth, 27 Aug 1959; ZMUC P77702, 196 mm SL (light brown), 33°36'S, 16°15'E, R/V
423 AFRICANA II, sta. 191, 3080 m depth, beam trawl, 24 Aug 1959; ZMUC P77704, 192 mm
424 SL (light brown), 34°46'S, 16°42'E, R/V AFRICANA II, sta. 316, 3360 m depth, beam trawl,
425 8 December 1959.

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

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

432 SW Pacific (n=2): NMNZ P.041951, male, 332 mm SL (pale), 34°31.5'S, 166°21'E,
433 2930 m depth, Sept 1982; NMV A25135.002, female, 423 mm SL (pale), 32°3.98'S,
434 159°52.8'E to 32°2.26'S, 159°51.11'E, NORFANZ cruise, R/V TANGAROA, sta. TAN
435 0308/071, 1920–1934 m depth, 24 May 2003.

436 NE Pacific (n=11): OSUO 11722, 88 mm SL (dark), off Oregon Coast, 44°48.8'N,
437 125°36.5'W, ca. 2800 m depth, 8 March 1972; OSUO 11738, 94 mm SL (light brown),
438 45°56.4'N, 127°39.1'W, 2763 m depth, 13 March 1973; CAS-ICH 246805, male, 478 mm SL
439 (light brown), 45°18'42"N, 126°34'24"W, R/V Yaquina, beam trawl, 2750 m depth, 2 Dec
440 1974; CAS-ICH 32364, male, 495 mm SL (light brown), off Oregon, 44°57'18"N,
441 126°37'18"W to 44°58'0"N 126°42'42"W, 2850 m depth, beam trawl; CAS-ICH 33083, male,
442 665 mm SL (light brown) and female, 536 mm SL (dark), off Oregon, near Cascadia
443 Channel, 45°22'24"N, 127°27'48"W to 45°23'54"N 127°28'36"W, 2788 m depth, beam trawl;
444 CAS-ICH 39821, male, 640 mm SL (light brown), off Oregon, 45°21'30"N, 127°33'0"W to

445 45°21'42"N, 127°38'30"W, 2800 m depth, beam trawl; CAS-ICH 40234, male, 446 mm SL
446 (pale), off Oregon, Cascadia Abyssal Plain., 45°27'48"N, 126°17'24"W to 45°27'0"N,
447 126°21'0"W, 2606 m depth, beam trawl; CAS-ICH 40235, 307 mm SL (light brown), off
448 Oregon, Cascadia Abyssal Plain, 45°27'48"N, 126°17'24"W to 45°27'0"N, 126°21'0"W, 2606
449 m depth, beam trawl; CAS-ICH 62566, 340 mm SL (light brown), off Oregon, Cascadia
450 Abyssal Plain, 44°5'18"N, 125°23'35"W to 44°7'6"N, 125°21'48"W, 2940 m depth, beam
451 trawl; LACM 45789, 1205 mm SL (light brown), ca 37°N 123°W, ca. 3000 m depth.

452

453 **Diagnosis**

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

458

459 **Description**

460 The most important meristic and morphometric characters as well as the otolith
461 characters are shown in Tables 2,3,5 and 7. Body moderately elongate, laterally compressed,
462 tapering towards tail. Pectoral-fin depth 6.1–10 times in SL, tail length 1.67–1.81 times in SL
463 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
464 preanal length; head depth through eye 6.8–12 times in SL. Orbit circular, shorter than snout,
465 1.27–3.18 times in snout length, slightly larger in small specimens. Anterior gill arch with 8–
466 9 long and 9–13 rudimentary rakers. Pseudobranchial filaments 0–3.

467 Origin of dorsal fin above vertebra 7–11, well in front of distal tip of pectoral fin.

468 Pelvic fins with two rays each reaching about 1/3 from its base to anal-fin origin. Pectoral

469 fins on lower half of body, rather short, 8.8–12 times in SL, and moderately wide at fin base
470 in most specimens, the width 18–24 times in SL.

471 Otolith (Fig. 2) oval in larger fish (length to height ratio 1.40–1.58) and elongate in
472 smaller fish (length to height ratio 1.72–1.76), with slightly pointed posterior tip, anteriorly
473 rather blunt. Sulcus long in larger specimens, 61–74 % of otolith length and shorter in
474 juveniles (51–57 % of otolith length), with separate colliculi and located at the center of inner
475 face. Ostium width 24–30 % of sulcus length and 32–40 % of ostium length in fish of 192
476 mm SL and larger; ostium width 44–49 % of ostium length in two 188 and 190 mm SL
477 juveniles.

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

483

484 **Distribution**

485 Pacific and SE Atlantic; ca. 1000 to 3360 m depth. No records from the Indian Ocean.

486

487 **Remarks**

488 Among the studied specimens the four females and eight males showed no sex-related
489 differences in morphological or color characters.

490 Head, orbit and ostium length show negative allometry when the entire size range (i.e.
491 small-sized juveniles to largest-sized adults) is considered (Fig. 4). No such pattern was
492 found for pre-anal and pelvic-fin length and ostium width. Two of the three smallest
493 specimens (size range 188–196 mm) showed a relatively wide ostium compared to all other

494 conspecifics (including the 192 mm SL specimen shown in Fig. 3F; Fig. 4), possibly
495 indicating a rather abrupt early life-history modification in otolith form. Like in
496 *Spectrunculus grandis*, the largest specimen of *S. radcliffei* showed a clearly shorter pelvic
497 fin (Fig. 4).

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

501

502 **Distinction of each of the four *Spectrunculus* species (Table 8)**

503 *Spectrunculus stenostio* differs from the other three species by the clearly narrower
504 ostium and by the mostly higher number of total vertebrae; *S. crassus* differs from the other
505 three species in the combination of low dorsal-fin, anal-fin and vertebrae counts, mostly
506 larger eyes and lower maximum size; *S. radcliffei* differs from the other three species in the
507 combination of a mostly shorter preanal length, shorter pelvic-to anal-fin origin distance and
508 by higher anal-fin rays counts; *S. grandis* differs from the other three species in the
509 combination of all nine characters.

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

513

514 **Identification key**

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

- 518 1 – Dorsal-fin rays 135–148, anal-fin rays 101–112, total vertebrae 77–88, eye diameter in
519 subadult or adult specimens 6.4–13 times in head length, maximum size to 100 cm SL or
520 larger, body and head color in freshly caught or recently fixated and/or preserved specimens
521 pale grey or pale whitish, light brown or dark brown, all major oceans 2
- 522 – Dorsal-fin rays 121–139, anal-fin rays 91–102, total vertebrae 72–79, eye diameter in
523 subadult or adult specimens 5.8–8.2 times in head length, maximum size 60 cm SL, body and
524 head color in freshly caught or recently fixated and/or preserved specimens light brown in
525 juveniles or subadults and dark grey or dark brown (rarely speckled) in larger specimens,
526 Atlantic and E Pacific *Spectrunculus crassus*
- 527 2 – Pre-anal length 1.83–2.15 times in SL and 1.01–1.15 in tail length (=subequal or only
528 slightly shorter), distance between pelvic- and anal-fin origins 2.28–3.17 times in SL, total
529 vertebrae 80–88, all major oceans 3
- 530 – Pre-anal length 2.22–2.48 times in SL and 1.24–1.43 in tail length, distance between pelvic-
531 and anal-fin origins 3.02–3.58 times in SL, total vertebrae 78–83, Pacific and S Atlantic
532 *S. radcliffei*
- 533 3 – Dorsal-fin rays 135–137, anal-fin rays 101–105, total vertebrae 77–80, maximum size
534 130 cm SL (otolith ostium width 2.56–2.86 in its length and 4.2–4.4 times in sulcus length),
535 Pacific *S. grandis*
- 536 – Dorsal-fin rays 137–148, anal-fin rays 102–112 (106–108 in the SW Pacific population [co-
537 occurrence with *S. grandis*]), total vertebrae 80–88, maximum size 110 cm SL (otolith ostium
538 width 3.45–5.3 in its length and 4.8–6.7 times in sulcus length), N Atlantic, S Indian Ocean
539 and SW Pacific *S. stenostio*.
- 540
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605
606
- 607 **Figure captions**
- 608 Figure 1. A-C: *Spectrunculus stenostio* (A) HT, ZMUB 18493, 825 mm SL, N. Atlantic (F.
609 Uiblein); (B) SAIAB 11892, 706 mm SL, S Indian Ocean (F. Uiblein); (C) NMNZ P.033111,
610 1030 mm SL, SW Pacific (P.R. Møller). D-F: *S. crassus*. (D) ZMUB 18355, 187 mm SL, N.
611 Atlantic (MAR-ECO cruise); (E) HT, MNHN 1886-0552, 284 mm SL, N Atlantic (J.
612 Pfliger); (F) ZMUB 18463, 500 mm SL, N. Atlantic (MAR-ECO cruise); G-I: *S. grandis*. (G)

613 HT, BMNH 1887, 675 mm SL (F. Uiblein); (H) NMNZ P.041204, 840 mm SL, SW Pacific
614 (P.R. Møller); (I) CAS 25724, 1270 mm SL, NE Pacific (Moulin Studios, San Francisco); J-
615 M: *S. radcliffei*. (J) HT (postlarva), FMNH 57123, 56 mm SL, NW Pacific (FMNH
616 Zoological Collections); (K) SAM 47240, 541 mm SL, S Atlantic (F. Uiblein); (L)
617 ZMUCP2397445, 945 mm SL, NW Pacific (M. Krag); (M) ZMUC P2397724, 1020 mm SL,
618 NW Pacific (M. Krag). Length of black or white scale bars is 5 cm.

619

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

623

624 Figure 3. Images of otoliths of *Spectrunculus*. (A) *S. stenostio*, ZMUB 18480, 670 mm SL, N
625 Atlantic (F. Uiblein); (B) *S. crassus*, ZMUB 18464, 575 mm SL, N Atlantic (F. Uiblein); (C-
626 E) *S. grandis*. (C) HT, BMNH 1887, 675 mm SL, NW Pacific (CT scan, B. Clark); (D) CAS
627 25724, 1270 mm SL, NE Pacific (F. Uiblein); (E) LACM 43564, 200 mm SL, SW Pacific
628 (M.A. Krag); (F-H) *S. radcliffei*. (F) ZMUC P77704, 192 mm, S Atlantic (M.A. Krag); (G)
629 ZMUCP2397445, 945 mm SL, NW Pacific (from left head side, shown side-reversed; M.
630 Krag); (H) ZMUC P2397724, 1020 mm SL, NW Pacific (M. Krag). All otoliths from right
631 head side, if not otherwise indicated. Dotted lines with arrows indicate the approximate
632 measurement positions for ostium width (left side of figure) and sulcus length (right side of
633 figure). Length of black or white scale bars is 5 mm.

634

635 Figure 4. Relationships between morphological characters in the four *Spectrunculus* species.

636

637

The Systematics of the ophidiid genus *Spectrunculus* (Teleostei, Ophidiiformes)**revisited with description of a new species and resurrection of *S. radcliffei*****Acknowledgements**

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Tables

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

SL (mm)	HT			PTs, N Atlantic			S Indian Ocean			SW Pacific			
	N Atlantic	Min	Mean	Max	n	Min	Mean	Max	n	Min	Mean	Max	n
Meristic characters													
Dorsal-fin rays	143	139	142.5	148	20	137	140.0	143	4	137	139.8	144	5
Caudal-fin rays	8	8	8.2	9	19	8	8.3	9	4	8	8.0	8	4
Anal-fin rays	109	102	107.1	112	17	105	107.0	110	4	106	107.0	108	5
Precaudal vertebrae	24	23	24.4	26	20	22	23.5	25	4	23	23.6	24	5
Total vertebrae	84	81	83.9	88	20	81	82.0	83	4	80	80.8	82	5
First dorsal-fin ray above vertebra nr.	10	9	9.8	11	20	9	9.8	10	4	9	9.4	10	5
Dorsal-fin ray above anal-ray nr.	41	35	38.8	41	14	34	34.3	35	3	34	38.6	42	5
First anal-fin rays below vertebra nr.	30	26	28.2	30	14	26	27.0	28	3	25	28.2	31	5
Pectoral-fin rays	28	27	27.7	28	3	24	26.3	28	4	25	26.8	29	4
Developed gill rakers	10	9	9.5	10	4	9	9.0	9	2	8	9.0	10	4
Total gill rakers	20	19	20.3	21	4	20	20.5	21	2	19	20.8	22	4
Morphometric characters in % SL													
Head length	20	18	20.0	21	21	18	19.0	20	4	19	19.7	20	4
Body depth at anus	17	16	17.5	20	21	18	19.8	22	2	15	19.6	25	4
Snout length	4.6	4.6	5.3	5.9	21	5.1	5.2	5.4	2	5.3	5.6	5.9	4
Upper jaw length	9.6	8.9	9.9	11	21	9.9	9.9	10	2	9.5	10.1	11	4
Head width at postmaxilla	8.4	8.1	9.3	10.1	19	8.3	8.8	9.4	2	9.1	10.6	13	4
Depth of postmaxilla	2.61	2.24	2.67	3.19	21	2.13	2.29	2.44	2	2.04	2.23	2.43	2
Orbit length	2.19	1.95	2.20	2.50	21	2.30	2.37	2.45	2	2.06	2.16	2.23	4
Interorbital length	5.9	5.2	6.1	6.9	21	6.0	6.2	6.3	2	6.4	6.9	7.2	4
Postorbital length	14	12	13.8	15	21	13	13.7	14	2	13	13.6	15	4
Preamal distance	50	47	49.3	55	21	47	50.1	53	4	47	48.1	50	4
Predorsal distance	27	26	29.0	33	21	25	25.5	26	2	25	28.0	31	4
Distance between pelvic- and anal-fin origin	41	34	38.0	44	21	39	38.8	39	2	34	36.1	37	4
Pelvic-fin length	15	11	13.7	18	16	11	12.5	14	2	12	12.7	15	4
in % head length													
Upper jaw length	48	47	49.7	53	21	49	49.9	50	2	48	51.1	54	4
Orbit length	11	9.9	11.0	12	21	11	11.9	12	2	10	10.9	11	4
Otolith characters in % SL													
Otolith length	2.21	1.50	2.17	2.55	16	1.88	2.01	2.15	3		2.84	1	
Otolith height	1.19	1.06	1.22	1.35	16	1.14	1.17	1.18	3		1.70	1	
Sulcus length	1.41	1.19	1.49	1.73	16	1.38	1.40	1.44	3		1.55	1	
Ostium length	1.00	0.84	1.09	1.22	16	0.89	0.93	0.95	3		1.15	1	
Ostium width	0.26	0.20	0.26	0.31	16	0.24	0.25	0.26	3		0.31	1	
in % otolith length													
Otolith height	54	44	56.6	71	16	55	58.1	61	3		60	1	
Sulcus length	64	60	69.0	81	16	67	69.9	74	3		54	1	
Ostium length	45	45	50.2	58	16	44	46.1	47	3		40	1	
Ostium width	12	9	12.1	16	16	12	12.5	14	3		11	1	
Ostium width in % of:													
Otolith height	22	15	21.5	25	16	20	21.6	22	3		18	1	
Sulcus length	71	67	73.0	79	16	64	66.0	67	3		74	1	
Ostium length	26	19	24.1	29	16	26	27.2	29	3		27	1	

Table 2. Three meristic characters for the four species of *Spectrunculus* (entire size range considered), with counts for the holotype of each species underlined. The counts for the HT of *S. coheni* (Mayer & Nalbant, 1972) are emphasized in bold italics. Dashed lines applied to better distinguish among species.

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

SL (mm)	<i>S. stenostio</i>				<i>S. crassus</i>				<i>S. grandis</i>				<i>S. radcliffei</i>			
	Min 248	Mean 796.9	Max 1060	n 32	Min 216	Mean 416.1	Max 575	n 54	Min 200	Mean 726.9	Max 1283	n 7	Min 307	Mean 623.6	Max 1205	n 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-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
Introrbital 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
Ostium width in % of:																
Otolith height	44	56.8	71	21	48	59.7	75	31	60	73.7	83	3	63	66.8	72	5
Sulcus length	54	68.2	81	21	47	61.4	72	30	49	56.6	61	3	61	66.6	74	5
Ostium length	40	48.9	58	21	34	45.2	54	31	34	41.8	46	3	47	49.6	54	5
Ostium width	9.3	12.1	16	21	12	15.8	20	31	12	15.5	18	3	15	18.0	19	5

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

SL (mm)	S. crassus HT			N Atlantic			SE Atlantic			NE Pacific		
	N Atlantic 284	Min 216	Mean 429.1	Max 575	n 47		Min 282	Mean 239	Max 347.6	n 458	Mean 458	n 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-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	2.26	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							

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

SL (mm)	<i>S. crassus</i>				<i>S. radcliffei</i>			
	Min 106	Mean 136.3	Max 187	n 4	Min 56	Mean 143.4	Max 196	n 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-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

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

SL (mm)	HT	NW Pacific			SW Pacific			NE Pacific		
		Min 200	Mean 496.7	Max 840	n 3	Min 370	Mean 974.3	Max 1283	n 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-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	
Preanal 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	

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

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.

	<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







