

1 A new species of the rare deep-sea genus *Sciadonus* Garman, 1899 (Teleostei, Bythitidae)  
2 from off Brazil, with a discussion of the evolution of troglomorphism and miniaturization in  
3 the aphyonid clade

4

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23 **Abstract**

24

25 A new species of the rare, deep-sea genus *Sciadonus* Garman, 1899 (Bythitidae) is described  
26 based on two specimens obtained by the Brazilian R/V *Alpha Crucis* on the continental slope  
27 off São Paulo State, Southeastern Brazil, western South Atlantic. It differs from its congeners  
28 by the combination of the following characters: body pale lacking dark pigmentation except  
29 for on female claspers; a pair of dermal tissue flaps anteriorly on lower jaw; pelvic-fin rays  
30 present; precaudal vertebrae 39 or 40 and total vertebrae 74. The key to the species of  
31 *Sciadonus* is updated. A discussion of the presence and differentiation between troglomorphic  
32 and miniature characteristics among the species in the aphyonid clade is provided and  
33 compared with other bythitids.

34

35 Keywords: aphyonid clade; continental slope; western South Atlantic; R/V *Alpha Crucis*

36

37 **1. Introduction**

38 The genus *Sciadonus* Garman, 1899 was revised by Nielsen (1969, 2018) and holds five  
39 valid species of deep-benthopelagic fishes inhabiting continental slopes and rises, steeps of  
40 oceanic islands and seamounts, and the sea floor in the Pacific and Atlantic oceans (Fricke *et*  
41 *al.*, 2021). The genus is currently allocated in the family Bythitidae, as part of the aphyonid  
42 clade, which includes additional five genera and 22 valid species: *Aphyonus* Günther, 1878  
43 with a species; *Barathronus* Goode & Bean, 1886, with seven species; *Paraphyonus* Nielsen,  
44 2015, with six species; *Nybelinella* Nielsen, 1972, with three species; and *Meteorina* Nielsen,  
45 1969, with four species (Nielsen *et al.*, 1999, 2019; Møller *et al.*, 2016; Nielsen, 2019; Fricke

46 *et al.*, 2021). The aphyonid clade includes some of the deepest living species of vertebrates,  
47 with records down to 5,300 m and, since collecting at these depths rarely take place, are rare  
48 in scientific collections (Nybelin, 1957; Nielsen, 2003).

49 *Sciadonus* was erected by Garman (1889), as part of the family Brotulidae, during the  
50 description of *S. pedicellaris*, which was described based on a single specimen collected off  
51 the Cocos Islands, in the Eastern Pacific. *Sciadonus pedicellaris* is widely distributed in the  
52 western North Atlantic, western South Pacific and eastern North Pacific (Nielsen, 2018;  
53 Nielsen *et al.*, 2019). Within the Brotulidae, Zugmayer (1911a) erected *Leucochlamys* to  
54 include *L. cryptophthalmus*, described based on a specimen obtained from off Spain, Eastern  
55 North Atlantic, at 5,000 meters, diagnosing *Leucochlamys* from *Sciadonus* by the absence of  
56 pelvic fin in the former. Later, Zugmayer (1911b) proposed the family Aphyonidae to include  
57 *Aphyonus gelatinosus* Günther 1878, *Bellottia apoda* Giglioli, 1883, *L. cryptophthalmus*, and  
58 *S. pedicellaris*; Mead *et al.* (1964) briefly discussed the family diagnosis; and Nielsen and  
59 Cohen (1968) redescribed *Bellottia apoda* placing it outside the aphyonid clade.

60 Nybelin (1957) described two aphyonids from the eastern North Atlantic, *Leucochlamys*  
61 *jonassoni* and *Sciadonus kullenbergi*, from the Cape Verde Islands and the Azores,  
62 respectively. The first taxonomic revision of the family Aphyonidae was made by Nielsen  
63 (1969), in which *L. galathea* was described from the Kermadec Trench, southern Pacific, at  
64 4,410 meters, and *S. kullenbergi* was synonymized with *S. pedicellaris*. Nielsen (1969) also  
65 recognized the affinities among the species allocated in *Leucochlamys* and *Sciadonus* but  
66 maintained them as separate genera. However, a few years later, *Leucochlamys* was placed in  
67 synonymy with *Sciadonus*, and the three species previously allocated in the first were  
68 assigned to the latter (Rannou *et al.*, 1975; Cohen and Nielsen, 1978). As more material  
69 became available, Nielsen (2018) reviewed the genus *Sciadonus*, placing *L. galathea* as a  
70 junior synonym of *L. pedicellaris* and adding two new species, *S. longiventralis* Nielsen, 2018

71 from off New Zealand, at 1,000 meters depth, and *Sciadonus robinsi* Nielsen, 2018 from the  
72 western North Atlantic, about 280 nautical miles (ca. 530 Km) off Northeastern Brazil, at  
73 4,000 meters depth.

74 The status of the family Aphyonidae was not questioned until recently, when the  
75 phylogenies including molecular data became available (Betancur-R *et al.*, 2013, 2017;  
76 Møller *et al.*, 2016). The aphyonids were recovered as monophyletic, but nested within the  
77 family Bythitidae, therefore, losing the status of family and becoming the aphyonid clade. The  
78 phylogenetic relationships within the aphyonid clade, however, remain uncertain as a better  
79 taxon-sampling is needed (Møller *et al.*, 2016; Nielsen *et al.*, 2019).

80 In the western South Atlantic, records of aphyonids are scarce and include only three  
81 specimens of *Barathronus bicolor* Goode & Bean, 1886 obtained on the continental slope off  
82 Rio de Janeiro State, and the holotype of *Barathronus linsi* Nielsen, Mincarone & Di Dario,  
83 2015 from the continental slope off Rio Grande do Norte State (Andreatta and Séret, 1995;  
84 Franco *et al.*, 2007; Costa and Mincarone, 2010; Nielsen *et al.*, 2015; Melo *et al.*, 2020).  
85 Recent collections made by the Brazilian R/V *Alpha Crucis*, on the Brazilian continental  
86 slope off São Paulo State, Southern Brazil, obtained two specimens of *Sciadonus*. Those  
87 findings represent the first record of the genus in the South Atlantic, and a new species, which  
88 is described herein, with an updated key to the species of *Sciadonus*, the evaluation of its  
89 conservation status, and a discussion of troglomorphic and reductive characters in the  
90 aphyonid clade.

91

92 **2. Material and Methods**

93 **2.1. Sample collection**

94 The present material was collected by the Brazilian R/V *Alpha Crucis*, using a bottom  
95 trawl net with 27 meters in the lower hope, 10 cm mesh in the body and wings and 2.5 cm  
96 mesh in the codend. The water temperature was measured by the MARPORT sensors on  
97 doors and upper hope and by a CTD sensor. Permits for the collections were issued by the  
98 Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis – IBAMA (8054-  
99 1) and Secretaria da Comissão Interministerial para Recursos do Mar da Marinha do Brasil  
100 (Portaria No. 223).

101

102 **2.2. Morphological analyses**

103 Morphometric and meristic data were taken according to Nielsen *et al.* (1999)  
104 preferably from the left side, unless otherwise stated. Because the eye is tiny and deeply  
105 embedded under the skin, the eye diameter was not measured, and the interorbital distance  
106 was substituted by the head width at the level of the eye. Accounts given along text are  
107 followed by the frequency with an asterisk indicating values for the holotype. Comparative  
108 material as listed in Nielsen (1969) and Nielsen (2018).

109 Neuromast observations and mapping were made under a stereomicroscope with direct  
110 observation of superficial neuromasts and transparency observation of canal neuromasts.  
111 Terminology for the groups of neuromasts follows Coombs *et al.* (1988), but innervation was  
112 not checked for homology inference. For observations of osteological characteristics, counts  
113 of vertebrae and dorsal-fin and anal-fin rays, both specimens were x-rayed at the Laboratório  
114 de Caracterização Tecnológica, Escola Politécnica of the Universidade de São Paulo using a  
115 ZEISS Xradia 510 Versa X-Ray Microscope: VoxelSizeX=4017 microns, voltage 30.165Kv,

116 power 2.0 W, exposure time 60 s. Pictures of the female clasper and gill arches were made  
117 using a ZEISS Discovery V12 Modular Stereo Microscope equipped with an camera and the  
118 auto-montage system to produce a composite image resulted from in-focus focal planes from  
119 multiple images.

120

### 121 **3. Results**

#### 122 **3.1. Taxonomy**

123 Order Ophidiiformes Berg, 1937

124 Family Bythitidae Gill 1861

125 *Sciadonus alphacrucis* n. sp. (Figs. 1–9, Table 1)

126 urn:lsid:zoobank.org:act:A277F257-4B6D-4C10-B723-62C66393535C

127

##### 128 **3.1.1 Material Examined**

129 **Holotype.** MZUSP 125949, 82.7 mm SL, female, western South Atlantic, continental slope  
130 off Ilhabela, off São Paulo State, Brazil, 24°53'55.80"S, 44°24'13.80"W, depth 794 m, 30  
131 Sept. 2019, R/V *Alpha Crucis* station 679.

132 **Paratype.** MZUSP 125950, 60.3 mm SL, male, collected with **holotype**.

133

##### 134 **3.1.2. Diagnosis**

135 *Sciadonus alphacrucis* can be diagnosed by the following combination of characteristics:  
136 body pale, lacking dark pigmentation except for female claspers; a pair of dermal tissue flaps  
137 anteriorly on lower jaw; pelvic-fin rays present; precaudal vertebrae 39 or 40 and total

138 vertebrae 74 or 75. *Sciadonus alphacrucis* can be separated from *S. cryptophthalmus*, *S.*  
139 *jonassoni*, and *S. robinsi* by the pelvic fin present (*vs.* pelvic fin absent), anterior nostril  
140 tubular (*vs.* anterior nostril with low rim), and vomer edentate (*vs.* one or two vomerine fangs  
141 present); from *S. longiventralis* by the pelvic fin shorter (2.6% *vs.* 3.5 % in SL), anal-fin  
142 origin below dorsal-fin rays 44–45 (*vs.* 36); from *S. pedicellaris* by the precaudal vertebrae  
143 fewer (39–40 *vs.* 43–49), total vertebrae fewer (74–75 *vs.* 79–88), and the very thin, thread-  
144 like female claspers (*vs.* thick female claspers). It further differs from *S. cryptophthalmus* and  
145 *S. jonassoni* by lacking black pigmentation on body, except for female claspers (*vs.* distinct  
146 black spots present below dorsal edge, along mid-body and above anal fin).



147  
148 **Figure 1.** *Sciadonus alphacrucis* sp. n. MZUSP 125949, holotype, female, 82.7 mm SL;  
149 western South Atlantic, São Paulo State, off Ilhabela, 794 m depth; in (A) soon after  
150 collection; (B) preserved specimen. Scale bar equals 10 mm.

151



152

153 **Figure 2.** *Sciadonus alphacrucis* sp. n., MZUSP 125950, paratype, male, 60.3 mm; western  
 154 South Atlantic, São Paulo State, off Ilhabela, 794 m depth; in (A) soon after collection (B)  
 155 preserved specimen. Scale bar equals 10 mm.

156

### 157 3.1.3. Description

158 Morphometric data presented in Table 1. Body elongated, oval in cross section anteriorly,  
 159 tapering along caudal region. Skin loose, transparent, and lacking scales.

160 Dorsal-fin origin on anterior fourth of body, at level of 13th (1) or 14th\* (1) vertebra;  
 161 dorsal-fin rays 93 (1) or 95\* (1). Anal-fin origin at posterior third of body, at level of 44th\*  
 162 (1) or 45th (1) dorsal-fin ray, and at level of 41st\* (1) or 42nd (1) vertebra; anal-fin rays 44\*  
 163 (1) or 45 (1). Pectoral fin peduncular, lateral on body, below vertical that passes through tip of  
 164 snout, pectoral-fin rays 11\* (2). Pelvic fin ventral on body, at level of base of pectoral-fin  
 165 peduncle; pelvic-fin ray single\* (2), filamentous and short, right and left pelvic-fin rays  
 166 present (1) or only left pelvic-fin ray present\* (1). Caudal fin rays 6\* (2).

167 Head small and rounded, tip of snout blunt in lateral profile. Eye deep-set, tiny, barely  
 168 visible, at level of mid-upper jaw. Anterior nostril tubular, placed close to upper lip than to  
 169 posterior nostril; posterior nostril opening dorsally on snout, lacking dermal flap. Mouth



170 terminal, cleft oblique, posterior tip of upper jaw extending posterior to level vertical passing  
 171 through level of eye. Dermal flap present anteriorly on tip of lower jaw (Fig. 3).



172

173 **Figure 3.** Head of *Sciadonus alphacrucis* n. sp. in detail (MZUSP 125949, holotype, 82.7 mm  
 174 SL). Black arrow indicates position of eye; white arrow indicates soft-tissue flap of lower jaw.  
 175 Scale bar equals 1 mm.

176

177 **Table 1.** Morphometric data of *Sciadonus alphacrucis* n. sp., holotype (MZUSP 125949) and  
 178 paratype (MZUSP 125950)

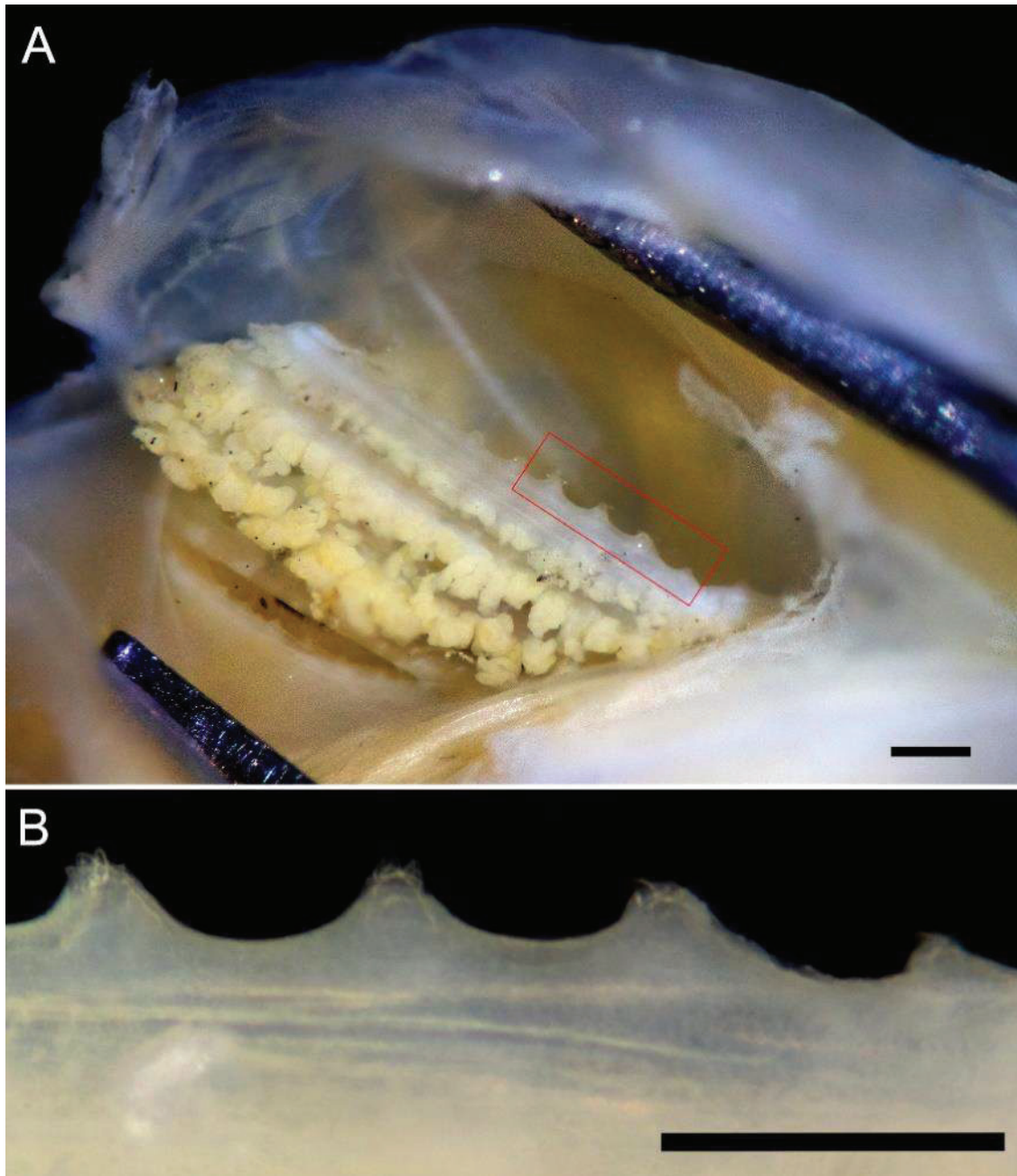
	Holotype (female)	Paratype (male)
Standard Length (mm)	82.7	60.3
Head Length (mm)	9.9	8.6
Proportions of Standard Length		
Head length	10.7	14.2
Depth of body at anal-fin origin	7.9	8.1
Upper-jaw length	5.9	7.9
Pigmented eye diameter	NA	NA
Head width at level of eye	5.6	6.2
Postorbital length	6.1	8.1

Preventral length	11.4	14.6
Preanal length	57.5	62.2
Predorsal length	24.9	27.2
Base of pelvic fin to anal fin	46.6	48.6
Pectoral-fin length	5.9	9.3
Pelvic-fin length	0.7 (left), 0.0 (right)	2.6
Clasper length	1.9 (left) / 2.77 (right)	4.4

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179

180 First gill arch with one raker on basibranchial\* (1), nine rakers on ceratobranchial\* (1)  
181 and one raker on epibranchial\* (1); rakers shorts, with small crown of one to four teeth (Fig.  
182 4). Pseudobranchia absent. Branchiostegal rays 7\* (2).

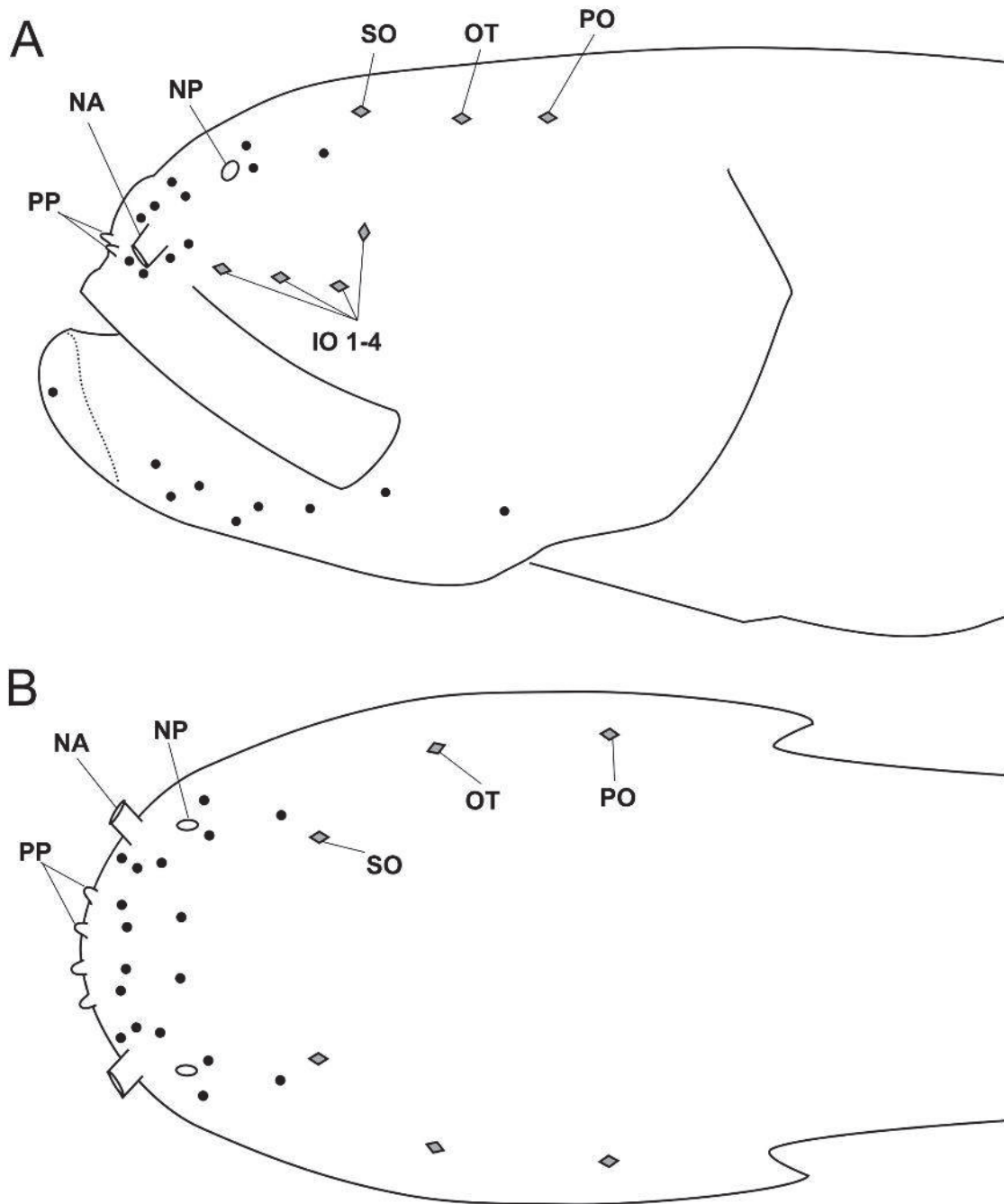


183

184 **Figure 4.** Gill arch and rakers of *Sciadonus alphacrucis* sp. n (MZUSP 125949, holotype,  
185 82.7 mm SL). (A) anterior gill arch in ventral view with (B) red square indicating portion in  
186 detail. Scale bar equals 1 mm.

187

188 *Lateral line (based on holotype)*. Lateral line and cephalic pores absent (Fig. 5). Canal  
189 neuromasts present only on head, deeply embedded under skin, with one postotic neuromast,  
190 one otic neuromast, one supraorbital neuromast, and four infraorbital neuromasts.  
191 Preopercular, mandibular, temporal, supratemporal and trunk neuromasts absent or not  
192 observed. Superficial neuromasts present on head only. Superficial neuromasts in lateral  
193 view: six around anterior nostril, one between anterior and posterior nostril, two posterior to  
194 posterior nostril, and one neuromast anteroventral to supraorbital neuromast; one neuromast  
195 on preopercle; seven neuromasts on mandibular line, and one on dentary dermal flap.  
196 Superficial neuromasts in dorsal view: two next to tip of snout, between anterior nares, and  
197 one between posterior nares. Tip of snout with two papillae.

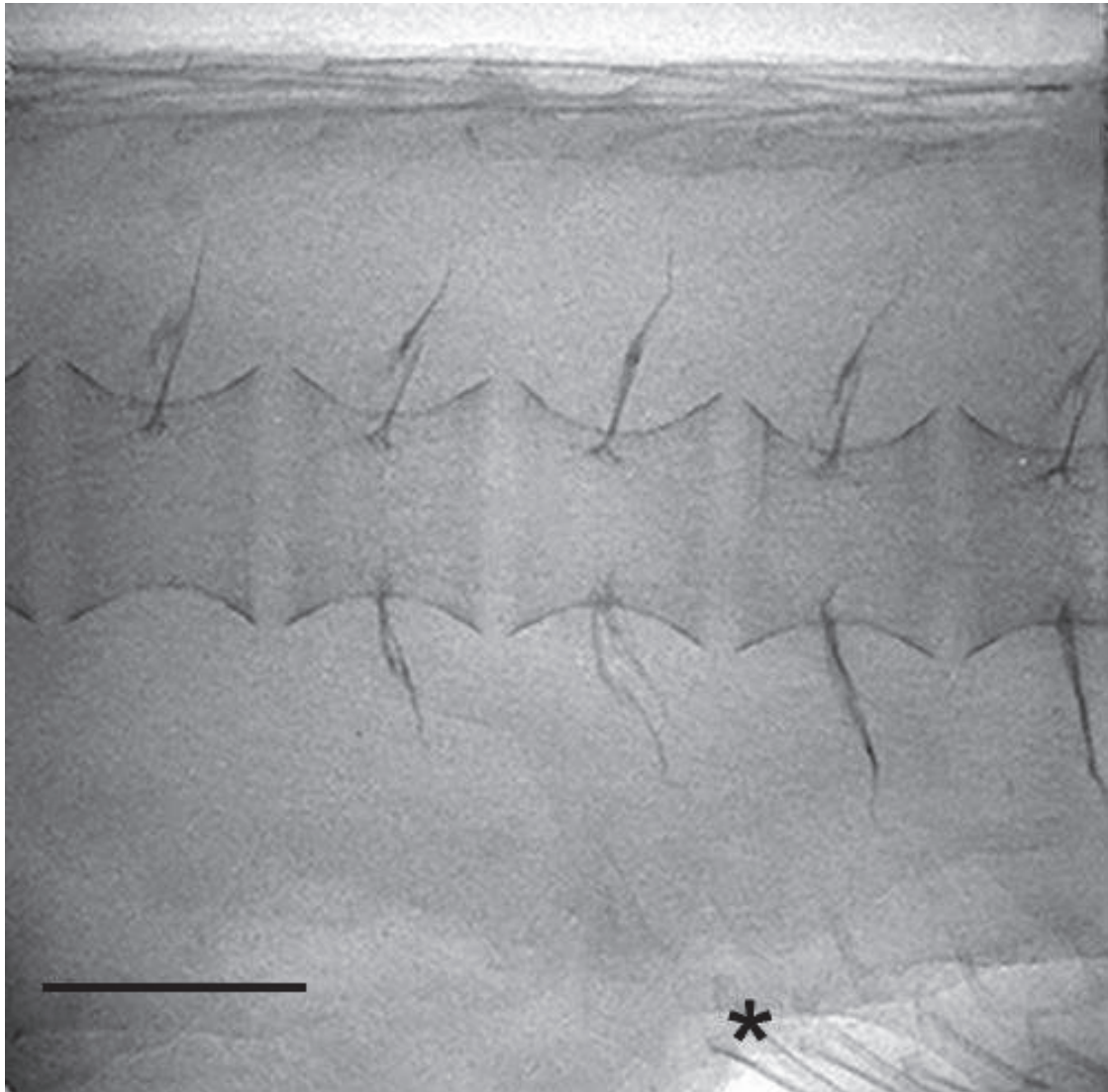


198

199 **Figure 5.** Latero-sensory organs on head of *Sciadonus alphacrucis* sp. n (MZUSP 125949,  
 200 holotype, 82.7 mm SL) in (A) lateral and (B) dorsal views. The canal neuromasts are  
 201 indicated by gray triangles and the superficial neuromasts, by black dots. Abbreviations: IO,  
 202 infraorbital canal; OT, otic canal; SO, supraorbital canal; and PO, postotic canal; NA, anterior  
 203 nostril; NP, posterior nostril; and PP papillae.

204

205 *Axial skeleton (from radiographs)*. Skeleton poorly calcified and difficult to observe in x-  
206 rayed specimens. Precaudal vertebrae 39 (1) or 40\* (1), total vertebrae 74 (1) or 75\* (1).  
207 Pleural ribs and epipleural ribs not observed. Vertebral centra truncate, rectangular in lateral  
208 view, with height 1.5 times length, lacking zigapophysis, basapophysis, and parapophysis  
209 (Fig. 6). Neural arch and spines thin, present in all precaudal and caudal vertebrae, about  
210 equal in anterior half of body, gradually decreasing in size in caudal region; haemal arch and  
211 spine thin, present in all caudal vertebrae, gradually decreasing in size posteriorly.



212

213 **Figure 6.** Vertebrae micro-radiography at level of anal-fin origin in *Sciadonus alphacrucis* sp.  
214 n., with the transition from pre-caudal to caudal vertebrae (MZUSP 125949, holotype, 82.7  
215 mm SL). Asterisk indicates the first anal-fin ray; scale bar equals 1 mm.

216

217 *Dentition.* Premaxillary teeth 34 (1), 31\* (1), conical, straight, arranged in one to two  
218 irregular rows, fangs absent. Dentary teeth 25 (1), 35\* (1), conical, posteriorly curved,  
219 arranged in one to two irregular rows, fangs absent. Vomerine teeth 4 (1), 5\* (1), conical,  
220 tiny, and arranged in small patch.

221

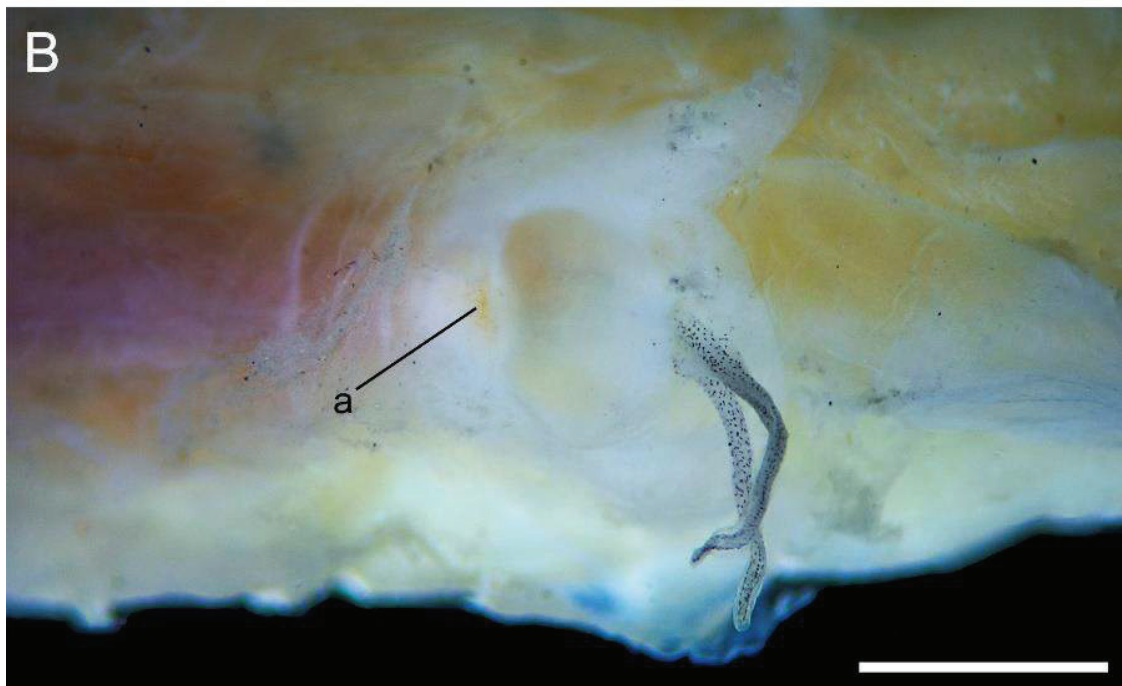
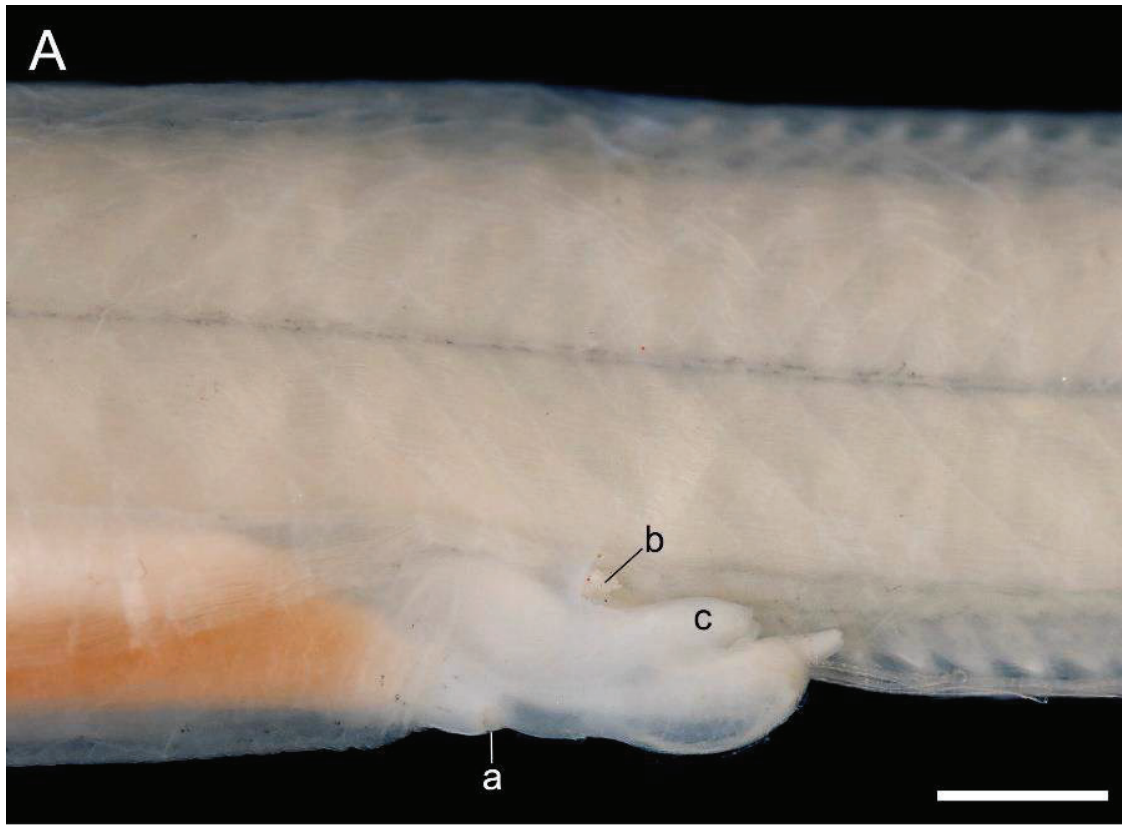
222 *Coloration.* Freshly collected specimens uniformly pale. Skin, bones, visceral and parietal  
223 peritonea transparent, body musculature white. Melanophores present exclusively in the eye,  
224 almost indistinguishable in adults, and on female claspers, but easily discernible in embryos.  
225 Internal structures of head (brain, facial nerves, bones of upper and lower jaws, eye, and gill  
226 filaments), pericardial cavity (heart), abdominal cavity (liver, digestive tube, testes or uterus  
227 with embryos), and body musculature (epaxial and hypaxial muscles, muscles of the pectoral,  
228 dorsal and anal fins) visible (Figs. 1A, 2A). Color of specimens after fixation in formalin and  
229 preservation in ethanol pale beige (Figs. 1B, 2B).

230

231 *Sexual dimorphism.* Species with internal fertilization and lecithotrophic viviparity. Male with  
232 single penis, bulb-shaped; urogenital opening dorsal to penis, surrounded by left and right,  
233 possibly, vestigial claspers; urogenital hood dorsal to penis, ending in a sulcus formed by two  
234 wing-like prolongations on each side of penis; distal tip of penis pointy and triangular; anal  
235 papilla opening ventrally and anteriorly to penis (Fig. 7A).

236 Female pregnant, with well-developed uterus containing many embryos. Urogenital  
237 opening large, positioned immediately posterior to anus (Fig. 7B). A pair (left and right) of  
238 thin and slender claspers present immediately posterior to urogenital opening; left clasper 1.6  
239 mm (1.9% in SL), right clasper 2.3 mm (2.8 % in SL).





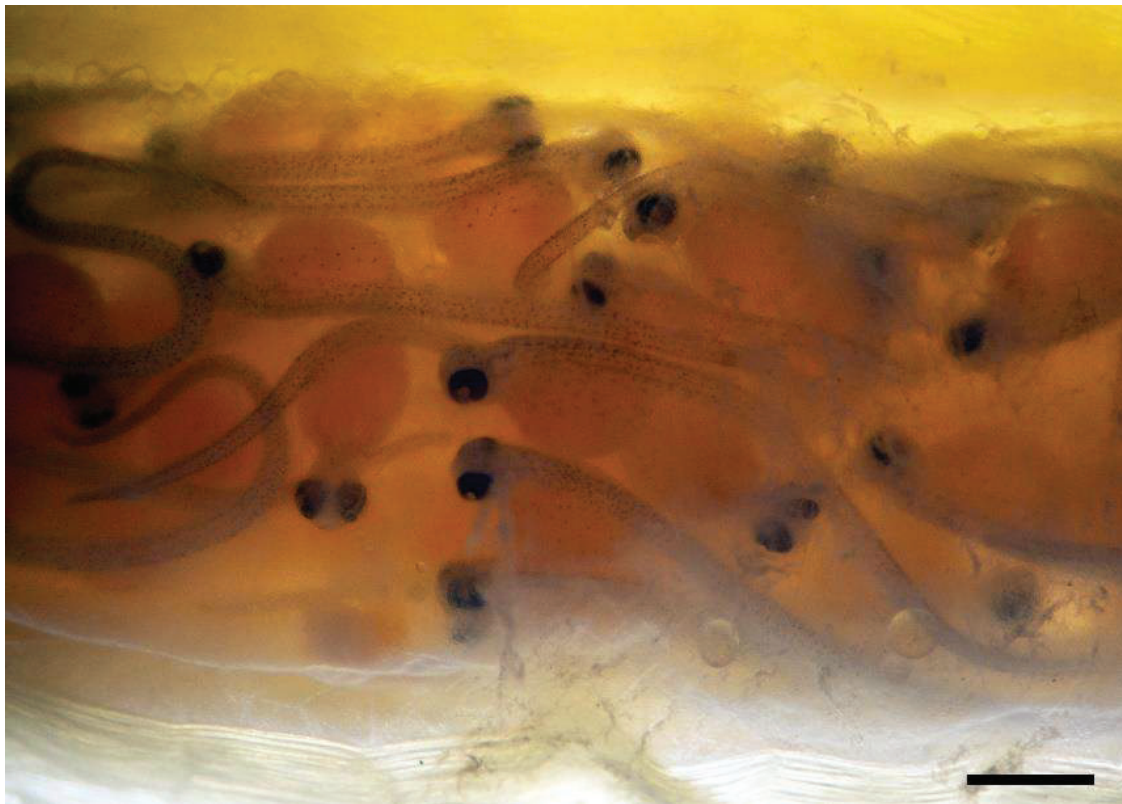
240

241 **Figure 7.** Reproductive apparatus of *Sciadonus alphacrucis* n. sp. (A) detail of male in lateral  
242 view (MZUSP 125950, paratype, 60.3 mm SL); in (B) detail of female in ventral view

243 (MZUSP 125949, holotype, 82.7 mm SL). Abbreviations: a: anus, b: vestigial male clasper, c:  
244 wing-like prolongations. Scale bar equals 1 mm.

245

246 *Description of embryos.* Lecitotrophic embryos visible through transparent skin, about 4.0  
247 mm TL (Fig. 8). Body thin and elongated, with well-developed yolk sack; no structure  
248 connecting embryo to uterus. Head of embryo small and rounded; eyes black, enlarged and  
249 occupying most part of head. Pigmentation on body present, with small melanophores  
250 arranged in three rows along entire body; few scarce melanophores on dorsal part of yolk  
251 sack.



252

253 **Figure 8.** Embryos of *Sciadonus alphacrucis* sp. n. in detail, visible through transparent skin  
254 (MZUSP 125949, holotype, 82.7 mm SL). Scale bar equals 1 mm.

255

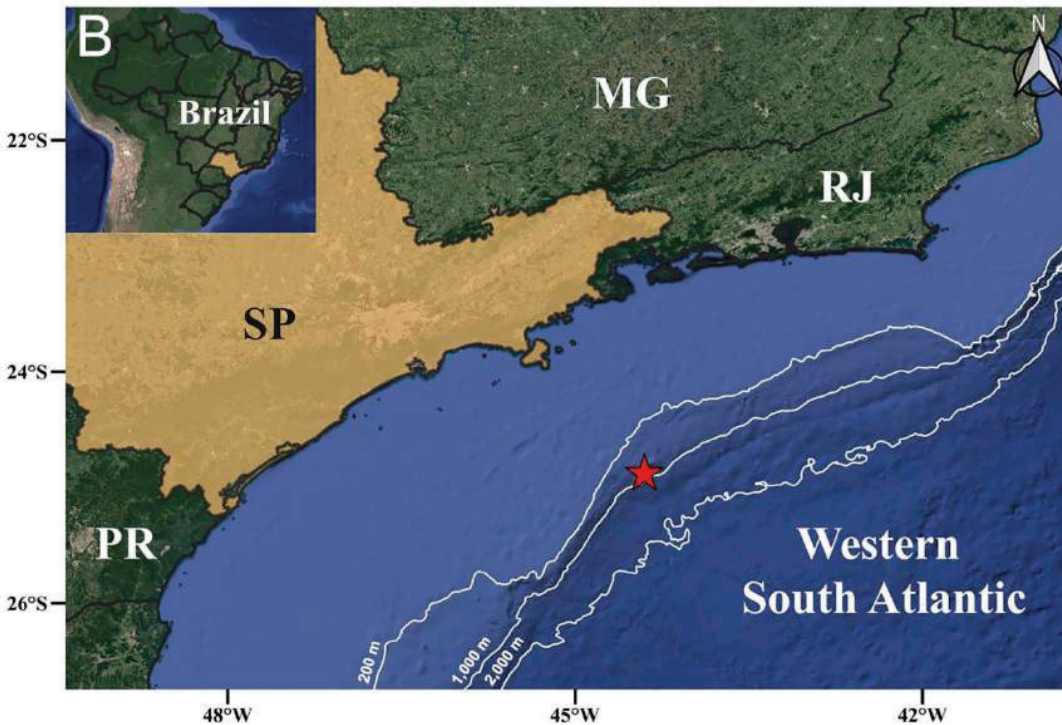
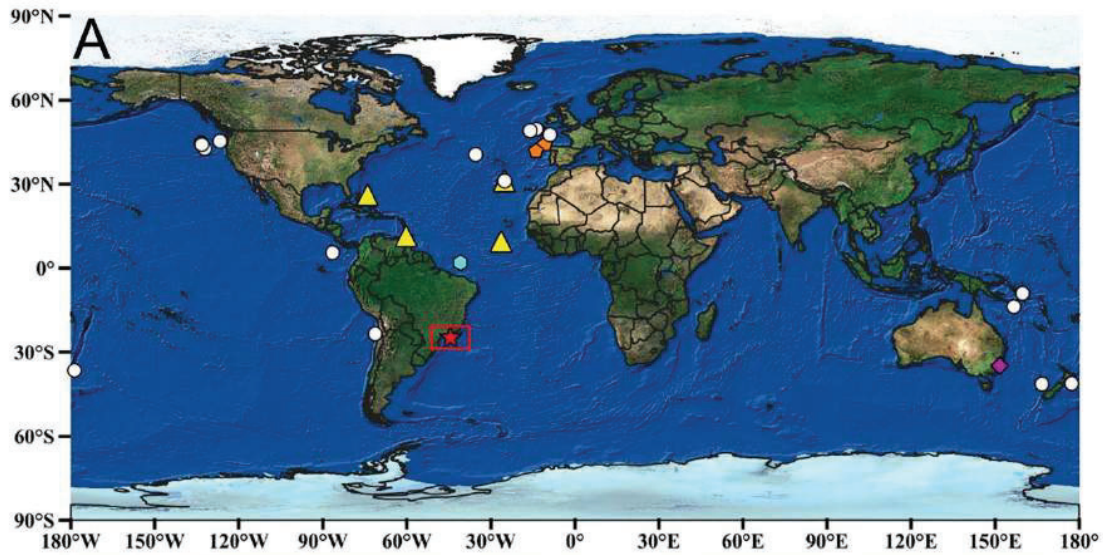
256 **3.2. Etymology**

257 The specific name honors the Brazilian R/V *Alpha Crucis*. A noun in apposition.

258

259 **3.3. Distribution and habitat**

260 The two known specimens of *S. alphacrucis* were collected by the same haul, on the  
261 continental slope off Southeastern Brazil, western South Atlantic, at 794 meters depth,  
262 suggesting that the species is benthopelagic (Fig. 9). It is the only species in the genus  
263 inhabiting depths shallower than 1,000 meters. The presence of mud/clay on the fishing doors  
264 and nets indicates the predominance of muddy bottom in the region. The water mass is  
265 composed by the Antarctic Intermediate Water (Silveira *et al.*, 2020), with temperature of  
266 22.3° C at surface and 5.6° C at bottom. The two specimens, an adult male and a pregnant  
267 female, were collected on the same station and recovered close to each other in the net wing.



268

269 **Figure 9.** The distribution of *Sciadonus*: in (A), global map of distribution with all records  
 270 known up to date; in (B) a detailed map indicating the type locality of *S. alphacrucis* sp. n.  
 271 Symbols: red star, *S. alphacrucis*; orange pentagon, *S. cryptophthalmus*; yellow triangle, *S.*  
 272 *jonassoni*; purple diamond, *S. longiventralis*; white circle, *S. pedicellaris*; and blue hexagon,  
 273 *S. robinsi*.

274

### 275 **3.4. Conservation status**

276         The genus *Sciadonus* includes some of the rarest fish species worldwide, with only 36  
277 specimens known in scientific collections, including the two specimens listed herein (Nielsen,  
278 2018) – a misprint in Nielsen (2018) states 304 instead of 34. The members of the family  
279 Bythitidae, including *S. alphacrucis*, are viviparous and probably lack pelagic larvae,  
280 indicating low fecundity and low larval dispersal capability. However, proper information  
281 about growth, age of first maturation, and reproductive strategies are unavailable for all  
282 species in the family. Anthropogenic impacts include the exploration of oil and gas in the  
283 Santos Basin and fisheries activities targeting deep-sea crabs (*e.g.*, *Chaceon* spp.), shrimps  
284 (*e.g.*, family Aristeiidae), cephalopods (*e.g.*, Argentine short-fin squid *Illex argentinus*), and  
285 fishes (*e.g.*, Argentinean hake *Merluccius hubbsi*, Brazilian coddling *Urophycis brasiliensis*,  
286 and Brazilian monkfish *Lophius gastrophysus*) (Perez and Pezzuto, 2006; Pezzuto *et al.*,  
287 2006; Perez *et al.*, 2020). Additionally, a considerable amount of anthropogenic litter was  
288 collected in the same haul as *S. alphacrucis*, composed mostly of plastic, fisheries debris  
289 (hooks and line), and metal cans (MRSM and AAG pers. obs., 2019). Nevertheless, we are  
290 unable to evaluate the effects of those impacts on the species. Considering the insufficient  
291 information about the newly described species biology and distribution allied to possible  
292 impacts caused by the presence of human activities in the area where it occurs, following the  
293 IUCN Red List Categories and Criteria (IUCN, 2019), *S. alphacrucis* is categorized as Data  
294 Deficient.

295

### 296 **4. Key to the species of *Sciadonus***

297	1a. Distinct, black spots below dorsal edge or spots below dorsal edge and along mid-body	
298	and above anal fin .....	2
299	1b. No distinct black spots, but faint black pigmentation may occur dorsally and ventrally .....	
300	.....	3
301		
302	2a. Black spots dorsally from above gill cover to caudal fin; 13–16 pectoral-fin rays; head	
303	18.0–18.5 % SL; tissue flaps anteriorly on lower jaw absent .....	
304	..... <i>S. cryptophthalmus</i> (Zugmayer, 1911)	
305	2b. Black spots below dorsal edge, above anal fin and in midline; 9–10 pectoral-fin rays; head	
306	14.5–17.0 % SL; a pair of tissue flaps anteriorly on lower jaw present or absent .....	
307	..... <i>S. jonassoni</i> (Nybelin, 1957)	
308		
309	3a. Dorsal-fin rays 90–107; anal-fin origin below dorsal-fin rays 44–56, and vertebrae 44–49 .	
310	.....	4
311	3b. Dorsal-fin rays 81–87; anal-fin origin below dorsal-fin rays 30–36 and vertebrae 38–41 ....	
312	.....	5
313		
314	4a. Precaudal vertebra 39–40; total vertebra 74–75; anal-fin origin under vertebrae 41–42 .....	
315	..... <i>S. alphacrucis</i> sp. n.	
316	4a. Precaudal vertebra 43–49; total vertebra 79–88; anal-fin origin under vertebrae 44–49 .....	
317	..... <i>S. pedicellaris</i> Garman, 1899	
318		

- 319 5a. Predorsal length 28.5% SL; length of pelvic present (3.5% SL); a pair of distinct soft  
 320 tissue flaps anteriorly on lower jaw ..... *S. longiventralis* Nielsen, 2018
- 321 5b. Predorsal length 42.5% SL; pelvic fins absent; no flaps on tips of lower jaw .....  
 322 ..... *S. robinsi* Nielsen, 2018

323

## 324 **5. Discussion**

### 325 **5.1. Taxonomic comparisons**

326 Besides *Sciadonus*, the aphyonid clade include additional five genera – *Aphyonus*,  
 327 *Barathronus*, *Meteorina*, *Nybelinella*, and *Parasciadonus* – and can be distinguished among  
 328 other bythitids by the absence of scales, the skin loose and transparent, the precaudal  
 329 vertebrae numbering 26 to 50, and the swim bladder absent (Nielsen *et al.*, 1999; Nielsen,  
 330 2015; Møller *et al.*, 2016). The gelatinous body, pigmentation reduced or absent, and eyes  
 331 poorly developed or not visible externally are other useful diagnostic characters, although  
 332 they can also be found in the anchialine cave species of the ophidiiform genera *Diancistrus*,  
 333 *Lucifuga*, *Ogilbia*, and *Typhliasina* (Møller *et al.*, 2004, 2006; García-Machado *et al.*, 2011;  
 334 Hernández *et al.*, 2020).

335 Up to date, only one phylogenetic hypothesis is available for the genera and species  
 336 included in the aphyonid clade (*e.g.*, Møller *et al.*, 2016), and the placement of the newly  
 337 described species in the genus *Sciadonus* is based on the presence of the pectoral peduncle  
 338 being about three times as long as high (*vs.* length and height equals in the other genera).  
 339 *Sciadonus alphacrucis* differs from those species placed in *Aphyonus* by having 11 pectoral-  
 340 fin rays (*vs.* 17–19) and distal tip of upper jaw slightly posterior to vertical through the eye  
 341 (*vs.* upper jaw extending well behind the vertical through the eye); from those in *Barathronus*  
 342 by having 10, short gill rakers on first arch (*vs.* gill rakers on first arch long, 23–25), six

343 caudal-fin rays (*vs.* 9 or 10), and vertebral centra rectangular in lateral view (*vs.* hourglass  
344 shaped); and from those in *Parasciadonus* and *Meteoria* by the presence of a pelvic fin (*vs.*  
345 absent) and presence of gill rakers on the first branchial arch (*vs.* absent) (Nielsen, 1969,  
346 2015, 2016, 2018, 2019; Nielsen *et al.*, 1999).

347       Among its congeners, *S. alphacrucis* shares with *S. jonassoni*, *S. longiventralis* and *S.*  
348 *pedicellaris* the presence of a well-developed dermal flap on the anterior tip of the lower jaw,  
349 which is absent in *S. cryptophthalmus* and *S. robinsi*. The absence of pigmentation on body  
350 and the reduced eyes brings *S. alphacrucis* closer to *S. longiventralis*, *S. pedicellaris*, and *S.*  
351 *robinsi*, and the presence of the pelvic fin, to *S. longiventralis* and *S. pedicellaris* – although it  
352 is thinner and shorter in the latter (3.5% in SL in *S. alphacrucis* and *S. longiventrais vs.* 0.6 %  
353 SL in *S. pedicellaris*). The elongated and slender body in *S. alphacrucis* resembles *S.*  
354 *pedicellaris*, but the former has fewer precaudal and total vertebrae (39–40 *vs.* 43–49 and 74–  
355 75 *vs.* 79–88, respectively) (Nielsen, 1969, 2018). Additionally, the female of *S. alphacrucis*  
356 has very distinctive, long and slender black pigmented claspers, which is unique among its  
357 congeners.

358

## 359 **5.2. Evolution of troglomorphic traits and miniaturization in the aphyonid clade.**

360       Convergent evolution of highly specialized phenotypic and genetic characteristics  
361 between deep-sea and cave fishes had already been noticed (Munk, 1965; Thinès, 1969;  
362 Poulson, 2001; Policarpo *et al.*, 2021). Even though the deep sea and subterranean water  
363 bodies resemble entirely different environments, both are partially or completely depleted  
364 from sunlight and, therefore, are heterotrophic ecosystems dependent upon energy transfer  
365 from the surface (Barr, 1968). Nevertheless, animals that live in these dark habitats might  
366 have two sets of morphological adaptations that evolved convergently: the reductive traits



367 include characteristics that lose their functionality in darkness, such as the eyes and body  
368 pigmentation; and constructive traits consist of the characters that enhance non-visual  
369 orientation, the ability to identify food or predators and interspecific communication, such as  
370 the sensory organs of lateral line and dermal papillae (Parzefall, 1996; Romero and Green,  
371 2005; Klaus *et al.*, 2013; Soares and Niemiller, 2013).

372         The aphyonid clade is composed of highly modified, deep-sea bythitids that have a  
373 unique morphology including the eye progressively degenerated and covered under the skin,  
374 the body generally transparent or white, with melanophores scarce or absent in most species,  
375 and the skin loose from musculature (Nielsen, 1969, 2018; Policarpo *et al.*, 2021). As in most  
376 cavefishes, the depigmentation of body is normally correlated with the degree of eye  
377 reduction (Pazerfall, 1996), but the presence of melanophores and enlarged eyes in the  
378 embryos of *Nybelinia erikssoni* (Nybelin, 1957), *Barathronus affinis* Brauer 1906, and *L.*  
379 *alphacrucis* indicate that those characteristics reduce ontogenetically and, therefore, are not  
380 paedomorphic (Nybelin, 1957; Nielsen, 1969; this contribution). The reduction of lateral-line  
381 canals in head and trunk is compensated by the appearance of superficial neuromasts on the  
382 head, and the presence of papillae on the tip of the snout, which probably improve their ability  
383 to explore their environment (Soares and Niemiller, 2013).

384         Among the ophidiiforms and in addition to the aphyonid clade, troglomorphic traits  
385 convergently evolved in the bythitid genus *Lucifuga* and the dinematchthyid genera  
386 *Diancistrus*, *Ogilbia*, and *Typhliasina*, all of which are composed of obligatory-cavernicolous  
387 species (Romero and Paulson, 2001). In those species, the reductive characters appear in  
388 different levels, as follows: eyes reduced and body pigmented in *Diancistrus typhlops*  
389 Nielsen, Schwarzhans & Hadiaty, 2009, *L. lucayana* Møller, Schwarzhans, Iliffe & Nielsen,  
390 2006, *L. gibarensis* Hernández, Møller, Casane & García-Machado, 2020 and *L. spelaeotes*  
391 Cohen & Robins, 1970, or eyes not externally visible and body lacking pigmentation in *L.*

392 *dentata* Poey, 1858; *L. simile* Nalbant, 1981 and *L. subterranea* Poey, 1858, *Ogilbia*  
393 *galapagosensis* (Poll & LeLeup, 1965) and *Typhliasina. pearsei* (Hubbs, 1938) (Eigenmann,  
394 1909; Møller *et al.*, 2004, 2006; García-Machado *et al.*, 2011; Hernández *et al.*, 2020). In  
395 other hand, the bythitid genus *Grammonus* include three cave species – *G. nagaredai* Randall  
396 & Hughes, *G. thielei* Nielsen; Daniel & Cohen, 1976, and *G. yunokawai* Nielsen, 2007 – that  
397 have well-developed eyes and pigmented body (Nielsen and Cohen, 2004; Nielsen, 2007;  
398 Randall and Hughes, 2009).

399 Miniaturization is another evolutionary processes that causes size reduction allied to the  
400 appearance of paedomorphic features, including diminution the latero-sensory canals, number  
401 of fin rays and body scales, and the simplification of osteological structures (Weitzman and  
402 Vari, 1988; Hanken and Wake, 1993; Britz *et al.*, 2009). Aphyonids are relatively small  
403 reaching the maximum 225 mm in total length, and reductive traits include the lack of scales  
404 on body and head, pyloric caeca and swim bladder, the reduction of head lateral-line canals  
405 and absence of the trunk canal, skeleton mostly cartilaginous, operculum lacking spines,  
406 pelvic fins reduced or absent, and neural and haemal spines poorly developed (Nielsen, 1969,  
407 2015, 2019; Nielsen *et al.*, 2019). A detailed osteological description in a species of the  
408 aphyonid clade is still missing, but the studied conducted by Hilton *et al.*, (2021) in  
409 *Parabrotula plagiophthalmus* Zugmayer, 1911 revealed severe reductions in several bones of  
410 the neurocranium, suspensorium, opercle, mandibular, hyoid and gill arches, pectoral gridle,  
411 as well as the absence of the infraorbital bones, pelvic gridle, and the extreme reduction of the  
412 fifth ceratobranchial.

413

414 **Declaration of competing interest**

415 The authors declare that they have no known competing financial interests or personal  
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417

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