

1 Deep-sea anglerfishes (Lophiiformes: Ceratioidei) from the western North Atlantic: testing
2 the efficacy of DNA barcodes

3 Short running title: Taxonomy of deep-sea anglerfishes
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21 **KEYWORDS:** Morphology, *COI*, barcoding, distribution, species identification

22

23 **Abstract**

24 The taxonomy of ceratioid fishes is challenging and frequently based on a small number of
25 female specimens described for each species. Twenty ceratioid specimens caught on Flemish
26 Cap and Grand Bank (western North Atlantic), representing 12 species and six families:
27 *Ceratias holboelli* and *Cryptopsaras couesii* (Ceratiidae); *Himantolophus albinares*
28 (Himantolophidae); *Melanocetus johnsonii* (Melanocetidae); *Lophodolos acanthognathus*,
29 *Oneirodes eschrichtii*, *Dolopichthys karsteni*, and *Leptacanthichthys gracilispinis*
30 (Oneirodidae); *Caulophryne polynema* (Caulophrynidae); *Haplophryne mollis*, *Linophryne*
31 *brevibarbata* and *L. bicornis* (Linophrynidae) were identified by examination of
32 morphological characters. DNA barcode sequences, from the 5' end of the *COI* mitochondrial
33 gene, were developed for 18 specimens and compared with all ceratioid barcode sequences
34 available in public repositories. The analyses extended the ranges of some quantitative traits
35 for certain species, highlighted the possible existence of cryptic species in *C. couesii* with
36 distinct ranges in the Atlantic and Pacific oceans, and indicated a close relationship between
37 *Bertella* and *Dolopichthys* meriting further attention. The authoritative identification of the 18
38 voucher specimens made possible detection of erroneous identifications of some sequences
39 extracted from the repositories and highlighting of taxonomic conflicts that should be the
40 subject of future studies.

41

42 INTRODUCTION

43

44 Lophiiform fishes constitute a morphologically diverse assemblage of marine taxa, most of
45 which share a peculiar and unique mode of feeding characterized most strikingly by the
46 structure of the first dorsal-fin spine, placed on the tip of the snout and modified to serve as a
47 luring apparatus called the illicium (Pietsch & Orr, 2007). The order Lophiiformes, as
48 currently recognized, comprises eighteen families with about 74 genera and 371 species, most
49 occurring below 300 m depth. The Ceratioidei is a suborder of Lophiiformes characterized by
50 the presence of an illicium (except for neoceratiids and some gigantactinids), the lack of
51 pelvic fins and extreme sexual dimorphism, with dwarf males that parasitize the females
52 temporarily or permanently (Pietsch & Orr, 2007).

53 In the first worldwide revision of that suborder, Bertelsen (1951) included 194 known
54 species, but Pietsch (2009) reduced many to synonyms and found a total of 160 species.
55 Subsequently, only a few new species have been described (Stewart & Pietsch, 2010; Pietsch
56 & Kenaley, 2011; Prokofiev, 2014; Ho, Kawai, & Amaoka, 2016; Rajeeshkumar, Meera, &
57 Hashim, 2017). Thus, the suborder Ceratioidei currently comprises 11 families with 35 genera
58 and about 169 species. It is the most diverse vertebrate taxon in bathypelagic ecosystems but
59 specimens are not commonly collected, representatives of some families remaining extremely
60 scarce, while many species share similar morphology. Ceratioid taxonomy and classification
61 are therefore often based on just one or a few metamorphosed females per species and rely
62 principally based on the illicial apparatus, which is often damaged or lost upon capture,
63 making positive identifications difficult (Pietsch, 2009). There are also metamorphic stages,
64 intraspecific variation and aberrant specimens that contribute greatly to the taxonomic
65 uncertainty of this suborder (Bañón, Pietsch, & Piñeiro, 2006).

66 Efforts to improve understanding of the complex evolutionary history of anglerfishes
67 through molecular genetic techniques began with sequencing of a region of the *16S*
68 mitochondrial gene, leading to results that differed in several aspects from conclusions based
69 on morphology (Shedlock, Pietsch, Haygood, Bentzen, & Hasagawa, 2004). When the whole
70 mitogenome was sequenced, analysis revealed previously unappreciated phylogenetic
71 relationships, among the suborders of lophiiforms and among ceratioid families that were not
72 easily reconciled with earlier morphologically based hypotheses (Miya et al., 2010).

73 DNA barcoding, using a fragment of the mitochondrial coding gene from subunit I of
74 the cytochrome c oxidase enzyme (*COI*: Hebert, Cywinska, Ball, & de Waard, 2003), has led
75 to the accumulation of comparable DNA sequences from nearly 20,000 fish species in the

76 Barcode of Life Data System database (Ratnasingham, & Hebert, 2007). Among them, more
77 than 200 are assigned to lophiiform voucher specimens. Recent faunal studies in waters off
78 Atlantic Canada (Kenchington, Baillie, Kenchington, & Bentzen, 2017) and the Pacific coast
79 of Central America (Robertson et al., 2018) have notably increased the number of barcodes of
80 ceratioid species. These barcode sequences have been employed in the identification of
81 *Oneirodes* species from the Pacific Ocean (Steinke, Zemlak, Boutillier, & Hebert, 2009) and
82 *Melanocetus johnsonii* Günther, 1864, from Antarctic waters (Orlov, Orlova, Volkov, &
83 Pelenev, 2015).

84 The purpose of this research was to test the efficacy of the DNA barcoding technique
85 in deep-sea anglerfishes in individuals identified by their morphology. Moreover, this paper
86 documents new material and geographical distributions, and provides descriptions and
87 photographic images of species supported by voucher.

88

89 **MATERIALS AND METHODS**

90

91 **Sample collection and specimen assignation**

92 Sampling was conducted on board R/V *Vizconde de Eza* during annual bottom-trawl surveys
93 on Flemish Cap (FC2015 and FC2017) and Grand Bank (Platuxa 2015: Figure 1). Twenty
94 ceratioid specimens (Table 1) were extracted from the catches and frozen on board. In the
95 laboratory, specimens were thawed, examined, photographed and identified to species
96 following Pietsch (2009). Morphometric measurements are direct distances measured by a
97 digital caliper to the nearest 0.1 mm. Abbreviations as follow: total length (TL), standard
98 length (SL), number of rays in dorsal (D), pectoral (P), anal (A) and caudal (C) fins and
99 branchiostegal rays (BR). Following removal of tissue samples, the voucher specimens were
100 fixed in 10% formalin and transferred to 70% ethanol. They were deposited in the
101 ichthyological collection of the Museo Nacional de Ciencias Naturales (MNCN, Madrid,
102 Spain).

103

104 **DNA extraction, PCR amplification and sequencing**

105 DNA was extracted from 25 mg of muscle tissue taken from each specimen, following the
106 spin column protocol of the Tissue DNA Extraction Kit (Omega-Biotek). The standard 5'
107 barcoding region of the *COI* gene (ca. 650 bp) was amplified by polymerase chain reaction
108 (PCR) using various conditions and primer sets. For six individuals, amplification used the
109 universal primer cocktail for fish DNA barcoding *COI-3* (Ivanova, Zemlak, Hanner, &

110 Hebert, 2007), with initial denaturation at 98° C for 30 s followed by 35 cycles of 98° C for 5
111 s, annealing at 52° C for 5 s and 72° C for 10 s, with a final extension at 72° C for 1 min. PCR
112 was carried out using Phire Green Hot Start II DNA Polymerase (Thermo Scientific);
113 mixtures contained a final volume of 25 µl and included 12.5 µl of 2× Phire Green HS II PCR
114 Master Mix, 2 µl of primer mixture and between 50 and 100 ng of template DNA. For another
115 five individuals, the barcode DNA was amplified using the same approach except that the
116 thermal cycler conditions were modified to annealing at 55° C, 50° C and 46° C with
117 annealing and extension times of 10 s and 15 s respectively. For seven other individuals,
118 amplification used a mixture of different *COI* primers: as forward primer, an equimolar
119 mixture of FF2d (Ivanova et al., 2007) and TelF1 (Dettai et al., 2011) and, as reverse primer,
120 an equimolar mixture of FR1d (Ivanova et al., 2007) and TelR1 (Dettai et al., 2011). PCR
121 reactions were carried out in a final volume of 25 µl including 12.5 µl of RealStart DNA
122 polymerase Premix (Yeastern Biotech), 0.75 µl of each primer and between 50 and 100 ng of
123 template DNA. The cycling conditions were denaturation at 94° C for 15 min followed by 40
124 cycles of 94° C for 30 s, annealing at 45° C for 30 s and 72° C for 1 min, with a final
125 extension at 72° C for 7 min. It was not possible to obtain barcodes from the final two
126 specimens, those of *L. brevibarta* and *H. mollis*.

127 *COI* amplicon bands were visualized on 1.2% agarose gels (Seakem LE Agarose)
128 stained with ethidium bromide and reactions were purified with ExoSAP-IT (Affymetrics)
129 following the manufacturer's instructions. DNA sequencing reactions were carried out in both
130 senses using the M13F (-21) and M13R (-27) primers (Messing, 1983) for amplicons
131 generated with the *COI*-3 universal primer cocktail and, for the remaining seven, using the
132 same forward (FF2d, TelF1) and reverse primers (FR1d, TelR1) as employed for their
133 amplification. The resulting products were resolved in an ABI3130 Genetic Analyzer
134 (Applied Biosystems) and the consensus sequences were obtained after assembling the direct
135 and reverse traces with SEQSCAPE v. 2.5 (Applied Biosystems).

136 The DNA sequence data and photographs of the specimens were deposited in the
137 Barcode of Life Database (BOLD) in a project entitled "Barcoding of deep-sea anglerfishes
138 (Lophiiformes: Ceratioidei)" (code ACRAT). The barcode sequences were also deposited in
139 GenBank under accession numbers MH033857-MH033874.

140

141 **DNA barcoding analysis**

142 All ceratioid barcode sequences available in BOLD and GenBank on 15 March 2018 were
143 extracted and duplicate sequences deleted, leaving 121 (Table 2), which were added to the

144 eighteen generated during the present study (Table 1) for analysis. The sequences were
145 aligned using the MUSCLE algorithm implemented in MEGA6 (Tamura, Stecher, Peterson,
146 Filipski, & Kumar, 2013) and trimmed to 651 bp length. Pairwise genetic distances (p-
147 distance: Nei & Kumar, 2000) between barcode sequences were calculated with
148 SequenceMatrix (Vaidya, Lohman & Meier, 2011).

149 Histograms of the genetic distances within and between species were prepared and
150 examined for the existence of a barcode gap. The specific identification of each barcode was
151 checked by plotting its minimum between-species distance, amongst the 139 available
152 sequences, against its maximum within-species distance, using the ggplot2 R package
153 (Wickham, 2009). The sequences were clustered in a neighbour-joining (NJ) tree (Saitou &
154 Nei, 1987). Non-parametric bootstrap analysis, with 2000 replicates (Felsenstein, 1985), was
155 used to examine its reliability.

156 Each lowest-level cluster of the NJ tree was assigned to a species or genus and the
157 sequences in that cluster re-identified as necessary. The primary criterion for cluster
158 assignment was the morphological identification of a voucher specimen associated with a
159 sequence from the ACRAAT project located in the cluster (10 of 33 clusters). The absence of
160 conflicts amongst identifications of the sequences in the cluster that had been extracted from
161 BOLD and GenBank was also followed as a definitive assignment (8 clusters). For each of 8
162 other putative species, only one sequence was available and its original identification was
163 respected unless that name was assigned to another cluster. The remaining 7 clusters were
164 given generic assignments, with species distinctions indicated but no species names applied.
165 The histograms and scatter plots of genetic distances were repeated, using the cluster
166 assignments in place of original identifications for sequences extracted from BOLD and
167 GenBank.

168

169 **RESULTS**

170

171 **Morphological aspects**

172 Family Ceratiidae Gill, 1861

173 Comprising two genera and four species; five specimens corresponding to two species are
174 recorded among our material.

175

176 *Ceratias holboelli* Krøyer, 1845

177 Figure 2

178 *Ceratias holboelli* Krøyer, 1845: 639. Type locality: southern Greenland, depth 0–340 m.
179 Holotype: ZMUC P61.

180 **Material**

181 MNCN_ICTIO 291.456, 159.2 TL, 112.7 mm SL, ♀, Flemish Cap, 7/7/2015, 48°11.83'N,
182 44°33.77'W, 634 m; MNCN_ICTIO 291.454, 239.6 TL, 172.4 mm SL (illicium amputated),
183 ♀, Flemish Cap, 13/7/2017, 46°44.35'N, 46°38.85'W, 970 m.

184 **Description**

185 Body elongate, maximum height of body 45.6 and 36.9% SL respectively; 2 caruncles on the
186 back; head length 31.2 and 25.9% SL; mouth nearly vertical; illicium 21% SL; esca bulb is
187 oval in shape, pigmented except at the distal tip, esca length 3.0% SL and esca width 1.9%
188 SL; a short single distal esca appendage arising just anterior to esca pore, 1.4% SL; lower
189 jaw teeth 60 and 69; predorsal length 74.0 and 73.5% SL; preanal length 76.1 and 78.4% SL;
190 vomerine teeth absent; D: 4; A: 4; P: 18; C: 8; BR: 6.

191 **Distribution**

192 Broad distribution in all three major oceans of the world, but excluded from the Southern
193 Ocean by its congener *C. tentaculatus* (Pietsch, 2009); in the western Atlantic it ranges from
194 the Greenland Sea extending south to the waters off Rio de Janeiro, Brazil.

195

196 *Cryptopsaras couesii* Gill, 1883

197 Figure 3

198 *Cryptopsaras couesii* Gill, 1883: 284. Type locality: Western North Atlantic, off New York,
199 U.S.A., 39°18'30"N, 68°24'00"W, Albatross station 2101, depth 1686 fathoms. Holotype:
200 USNM 33558.

201 **Material**

202 MNCN_ICTIO 291.457, 68.4 mm TL, 56.1 mm SL, ♀, Grand Banks, 09/6/2015, 42°54.88'N,
203 49°41.40'W, 1055 m; MNCN_ICTIO 291.455, 96.4 mm TL, 78.3 mm SL, ♀, Grand Banks,
204 09/06/2015, 43°06.12'N, 49°29.87'W, 669 m; MNCN_ICTIO 291.458, 113.1 mm TL, 93.2
205 mm SL, ♀, Flemish Cap, 27/06/2015, 48°10.08'N, 45°05.26'W, 420 m.

206 **Description**

207 Body elongate, not globular, maximum height of body 37.9–45.2% SL; 3 caruncles on the
208 back; head length 30.2–36.0% SL; predorsal length 79.9–87.7% SL; preanal length 79.1–
209 87.9% SL; mouth nearly vertical; a bulbous esca articulated near to the basal bone; esca
210 length 2.0–3.6% SL; esca width 1.5–3.0% SL; a single, long and slender distal esca filament

211 6.1–10.3% SL, with some smaller filaments in their base; lower jaw teeth 60–65; vomerine
212 teeth 4–6; D: 4; A: 4; P: 14–17; C: 8; BR: 6.

213 **Distribution**

214 Widely distributed in all three major oceans, between 63°N and 54°S, although this species
215 appears to be absent from the western South Atlantic Ocean (Stewart & Pietsch, 1998).

216

217 Family Himantolophidae Gill, 1861

218 Comprising a single genus and 20 species; one species is recorded among our material.

219

220 *Himantolophus albinares* Maul, 1961

221 Figure 4

222 *Himantolophus albinares* Maul, 1961:111, figs. 11–15. Type locality: Eastern Atlantic, off
223 Câmara de Lobos, Madeira. Holotype: MMF 2598.

224 **Material**

225 MNCN_ICTIO 291.460, 93.5 mm TL, 60.7 mm SL, ♀, Grand Banks, 09/06/2015,
226 43°05.18'N, 49°26.65'W, 831 m.

227 **Description**

228 Body globose, maximum height of body 97% SL; papillae of snout and chin well developed;
229 snout short, 20.9% SL; eye 4.2% SL; head length 45.8% SL; head width 24.5% SL; numerous
230 teeth in upper and lower jaws, longest upper jaw teeth 2.3% SL and longest lower jaw teeth
231 5.6 % SL; caudal peduncle depth 12.4% SL, with a white patch on the dorsal side and another
232 on the ventral side; illicium pigmented, 38.4% SL; esca length 13.5% SL; esca width 8.9%
233 SL; distal esca appendage length 20.6% SL, of black coloration, whitish in the tip, deeply
234 bifurcated at 3.3% SL above its base, with each primary branch simple, not bifurcated (Figure
235 5); posterior esca appendage length 19.4% SL, of white coloration, divided near the base in
236 two simple branches; 2 white and simple posterolateral appendages on the illicium, its length
237 4.3 % SL; D: 5; A: 4; P: 16; C: 9.

238 **Distribution**

239 Mostly on both sides of the Atlantic Ocean, from Iceland to 24°S, near Valdivia Bank; one
240 specimen captured off New Caledonia, in the western South Pacific (Iglesias, 2005).

241

242 Family Melanocetidae Gill, 1878

243 Comprising one genus and six species; one species is recorded among our materials.

244

245 *Melanocetus johnsonii* Günther, 1864

246 Figure 6

247 *Melanocetus johnsonii* Günther, 1864: 302, Pl. 25. Type locality: Sea of Madeira, eastern
248 Atlantic. Holotype: BMNH 1864.7.18.6.

249 **Material**

250 MNCN_ICTIO 291.459, 152.3 mm TL, 125.1 mm SL (illicium amputated), ♀, Flemish Cap,
251 12/07/2015, 46°54.43'N, 43°44.17'W, 775 m.

252

253 **Description**

254 Body globose, maximum height of body 78.1% SL; mouth nearly vertical and the cleft not
255 extending past the eye; the illicium is broken and the esca is missing; snout short, 11.6% SL;
256 eye 3.4% SL; least outside width between frontals 17.1% SL; head length 28.5% SL; upper
257 jaw with about 79 and lower jaw with 54 teeth, longest upper jaw teeth 5.7% SL and longest
258 lower jaw teeth 7.6 % SL; anterior margin of vomer nearly straight, bearing 9 teeth; pectoral
259 lobe width 12.3% SL; caudal peduncle depth 12.0% SL; D: 13; A: 4; P: 19; C: 8.

260 **Distribution**

261 Widely distributed in tropical and subtropical waters of all three major oceans of the world
262 between approximately 66°N and 53°S (Pietsch, 2009); in the western Atlantic it is reported
263 from Argentina to Greenland.

264

265 Family Oneirodidae Gill, 1878

266 Comprising 17 genera with about 74 species; there are nine specimens corresponding to four
267 species among our material.

268 *Lophodolos acanthognathus* Regan, 1925

269 Figure 7

270 *Lophodolos acanthognathus* Regan, 1925: 563. Type locality: North Atlantic, 28°15'N,
271 56°00'W, depth about 1500 m (3000 m wire out). Lectotype: ZMUC P92104. Paralectotypes:
272 BMNH 1925.8.11.15.

273 **Material**

274 MNCN_ICTIO 291.448, 73.8 TL, 56.7 mm SL, ♀, Grand Banks, 8/6/2015, 42°47.40'N,
275 49°51.65'W, 1230 m; MNCN_ICTIO 291.451, 86.9 TL, 66.3 mm SL, ♀, Flemish Cap,
276 29/6/2015, 48°40.22'N, 44°36.93'W, 1417 m; MNCN_ICTIO 291.447, 43.1 TL, 31.2 mm SL,
277 ♀, Flemish Cap, 7/7/2017, 46°59.89'N, 43°43.53'W, 688 m.

278 **Description**

279 Body relatively long, maximum height of body 44.3–50.6% SL; sphenotic spines pointed,
280 7.4–9.0% SL; quadrate spines 2.9–4.4% SL; snout short, 15.7–17.5% SL; symphysal spine
281 well developed; small eyes, 1.7–2.6% SL; illicium length 6.9–14.6% SL; esca bulb ovoid,
282 4.3–6.1% SL width; a pair of unpigmented esca appendages 17–18.7% SL; predorsal length
283 64.7–72.1% SL; preanal length 67.9–72.1% SL; D: 5–6; A: 5; P: 17–18; C: 9.

284 **Distribution**

285 Atlantic, Pacific and Indian oceans (Pietsch, 1974); in the western Atlantic Ocean, it extends
286 from off Greenland and Iceland at about 65°N, to the equator, including the Gulf of Mexico
287 and Caribbean Sea.

288

289 *Oneiroides eschrichtii* Lütken, 1871

290 Figure 8

291 *Oneiroides eschrichtii* Lütken, 1871: 72, Figs. 1–2, Pl. 2. Type locality: Off western coast of
292 Greenland. Holotype: ZMUC 64.

293 **Material**

294 MNCN_ICTIO 291.449, 127.6 mm TL, 98.2 mm SL, ♀, Grand Banks, 15/6/2015,
295 44°43.26'N, 48°54.71'W, 1333 m; MNCN_ICTIO 291.452, 240.6 mm TL, 192.8 mm SL
296 (illicium amputated), ♀, Flemish Cap, 23/6/2015, 47°46.23'N, 46°24.90'W, 1188 m;
297 MNCN_ICTIO 291.450, 124.1 mm TL, 96.4 mm SL, ♀, Flemish Cap, 13/7/2017,
298 46°41.47'N, 46°43.54'W, 1008 m.

299 **Description**

300 Body moderately short, maximum height of body 59.6–66.2% SL; head length 33.0–43.2%
301 SL; head depth 33.9–52.0% SL; premaxilla length 31.8–35.0% SL; lower jaw length 30.7–
302 39.8% SL; illicium length 11.7–17.4% SL; esca bulb width 3.8–4.5% SL; esca bulb length
303 6.4–7.6% SL; esca with a finger-shaped anterior appendage with 4–5 short side-branches
304 pigmented in the tip, a pair of filamentous unpigmented medial esca appendages and an
305 unbranched and unpigmented posterior esca appendage; anterior esca appendage length 4.7
306 and 4.2% SL; posterior esca appendage length 6.1 and 5.7% SL; upper jaw teeth 23–33;
307 lower jaw teeth 28–36; teeth on vomer 4–6; D: 5, A: 4; P: 14–17; C: 9.

308 **Distribution**

309 Nearly cosmopolitan, occurring in the Atlantic, Pacific and Indian Oceans (Pietsch, 2009); in
310 the western Atlantic it is known from Greenland (66°N) south to Bermuda and along the coast
311 into the Gulf of Mexico.

312 **Remarks**

313 The 98.2 mm SL specimen presented the belly dilated as a sign of a large prey recently eaten.
314 The prey, measuring 137.7 mm TL, was identified by DNA barcoding (*COI* gene) as
315 *Scopelogadus beani* (Günther, 1887) (Melamphaeidae).

316

317 *Dolopichthys karsteni* Leipertz & Pietsch, 1987

318 Figure 9

319 *Dolopichthys karsteni* Leipertz & Pietsch, 1987: 406, fig. 1. Type locality: Western North
320 Atlantic, 39°28.0'N, 64°00.6'W, depth 0–1023 m. Holotype: MCZ 60991. Paratypes: MCZ
321 61086 (1), 61090 (1).

322 **Material**

323 MNCN_ICTIO 291.465, 58.0 mm TL, 47.2 mm SL, ♀, Grand Banks, 19/6/2015, 44°01.56'N,
324 48°48.18'W, 1001 m; MNCN_ICTIO 291.453, 165.2 mm TL, 134.4 mm SL, ♀, Flemish Cap,
325 02/07/2017, 47°48.26'N, 43°49.19'W, 959 m.

326 **Description**

327 Body relatively slender, maximum height of body 40.9 and 41.5% SL respectively; snout
328 long, 25.2% and 24.9% SL; mouth large, upper jaw length 34.4% and 26.5% SL; lower jaw
329 length 35.2% and 27.8% SL; head length 46% and 38.9% SL; head depth 37.9% and 30.4%
330 SL; head width 21.4% and 17.6% SL; teeth counts only in the greater specimen, about 100
331 teeth in the upper jaw and 130 in the lower; teeth on vomer 1 and 0; illicium length 31.4% and
332 36.6% SL; esca bulb width 5.1% and 5.2% SL; esca bulb length 7.6% and 7.7% SL; basal
333 anterior portion of esca darkly pigmented with one medial papilla directed anteriorly and two
334 lateral papillae directed posteriorly on the tip; posterior appendage consisting of a swollen
335 basal part darkly pigmented and a long tapering filament, absent in the smallest specimen;
336 posterior esca appendage length 5.5% and 12.7% SL; filament length of the larger specimen
337 6.8% SL; D: 6; A: 5 and 6; P: 17 (only counted in the larger specimen); C: 9.

338 **Distribution**

339 Western North Atlantic, from off Cape Hatteras (USA) to approximately 42°N, 30°W
340 (Pietsch, 2009).

341

342 *Leptacanthichthys gracilispinis* (Regan, 1925)

343 Figure 10

344 *Dolopichthys gracilispinis* Regan, 1925: 563. Type locality: Eastern Pacific, off Panama,
345 6°40'N, 80°47'W, depth about 1750 m. Lectotype: ZMUC P9295, Paralectotypes: BMNH
346 1925.8.11.14 (1).

347 **Material**

348 MNCN_ICTIO 291.466, 56.5 mm TL, 50.6 mm SL, ♀, Flemish Cap, 12/07/2017,
349 46°24.92'N, 46°13.22'W, 859 m.

350

351 **Description**

352 The specimen was damaged, and only a few measurements and counts could be taken. Body
353 elongate, maximum height of body 31.4% SL; head length 31.8% SL; head depth 32.8% SL;
354 premaxilla length 30.4% SL; lower jaw length 33.0% SL; elongate pectoral fin lobe, 8.7% SL;
355 the illicium was abnormally stretched and was not measured; the esca bulb with an
356 unpigmented compressed posterior appendage, 2.0% SL; esca bulb width 3.0% SL; esca bulb
357 length 4.2% SL; sphenotic spines well developed, 7.7% SL; articular spine longer than the
358 quadrate spine; articular spine, 5.1% SL, quadrate spine 3.0% SL; about 89 teeth in upper jaw
359 and 72 in the lower; teeth on vomer 6, 3 in each side; D: 5; A: 5; C: 9.

360 **Distribution**

361 North Atlantic, between 28 °N and 53°N and North Pacific, from off Japan and Hawaiian
362 Islands to the equator (Pietsch, 2009).

363

364 Family Caulophrynidae Goode & Bean, 1896

365 Comprising two genera and five species; one species is recorded among our materials.

366

367 *Caulophryne polynema* Regan, 1930

368 Figure 11

369 *Caulophryne polynema* Regan, 1930: 191 (figs. 1–3). Type locality: Eastern Atlantic, off
370 Funchal Bay, Madeira. Holotype: BMNH 1930.2.7.1.

371 **Material**

372 MNCN_ICTIO 291.461, 150.2 mm TL, 128.3 mm SL, ♀, Flemish Cap, 2/7/2017,
373 48°08.92'N, 44°09.72'W, 986 m.

374

375 **Description**

376 Body globose with long fin rays, but broken in our specimen, maximum height of body 75.1%
377 SL; teeth slender, recurved; translucent filaments present in the illicium, head and body; stem
378 of illicium covered with more than 50 translucent filaments along this length; esca
379 unpigmented and somewhat translucent, consisting in numerous short filaments forming a
380 terminal tassel; esca length 4.5% SL; esca bulb and central lumen absent; illicium fully

381 pigmented, 23.5% SL; snout 17% SL; eye 3.5% SL; symphyial knob well patent in the lower
382 jaw; upper jaw teeth 26; lower jaw teeth 15; vomerine teeth 3; longest upper jaw teeth 6.3%
383 SL; longest lower jaw teeth 7.0 % SL; D: 21; A: 17; P: 19; C: 8; BR: 8.

384 **Distribution**

385 Known from widely scattered localities in the Atlantic (from off Florida to south at
386 approximately 28°S), and eastern Pacific oceans (Pietsch, 2009).

387

388 Family Linophryinidae Regan, 1925

389 Comprising five genera and 27 species; three specimens corresponding to three species of
390 linophryinids are recorded among our materials.

391

392 *Haplophryne mollis* (Brauer, 1902)

393 Figure 12

394 *Aceratias mollis* Brauer, 1902: 297. Type locality: Central Indian Ocean, Valdivia station 175,
395 depth 2200 m. Holotype: ZMB 17713.

396 **Material**

397 MNCN_ ICTIO 291.464, 84.2 mm TL, 64.3 mm SL, ♀, Flemish Cap, 23/6/2015, 47°46.23'N,
398 46°24.90'W, 1188 m.

399 **Description**

400 Body globose, maximum height of body 68.1% SL; preopercle ending in 3 radiating cusps;
401 head length 53.2% SL; eye diameter 3.3% SL; numerous short and slender teeth in upper and
402 lower jaw; barbel absent; illicium short, 3.9% SL; esca nearly spherical; esca length 11% SL;
403 esca width 9.4% SL; posterior esca appendage divided distally into 4 short branches, distal
404 esca appendage length 4.2% SL; longest upper jaw teeth 1.4% SL; longest lower jaw teeth
405 2.6% SL; D: 3; A: 3; P: 14; C: 9.

406 **Remarks**

407 Specimen with unusual coloration, whitish in the anterior part of head but blackish in the rest
408 of body.

409 **Distribution**

410 Widely distributed in the Atlantic, Pacific and Indian oceans (Pietsch, 2009).

411

412 *Linophryne brevibarbata* Beebe, 1932

413 Figure 13

414 *Linophryne brevibarbata* Beebe, 1932: 94, Figs. 26–27. Type locality: 9 miles southeast of
415 Nonsuch Island, Bermuda, 32°12'N, 64°36'W, depth 0–900 fathoms (1647 m). Holotype:
416 USNM 170947. Paratypes: USNM 170948.

417 **Material**

418 MNCN_ICTIO 291.462, 61.1 mm TL, 42.2 mm SL, ♀; Flemish Cap, 2/7/2017, 47°55.54'N,
419 43°59.68'W, 875 m.

420

421 **Description**

422 Body globose; sphenotic spines point obliquely forward; snout 28.4% SL; eye 5.8% SL;
423 longest upper jaw teeth 10.7% SL; longest lower jaw teeth 21.8% SL; illicium length 22%
424 SL; escal bulb ovoid with a single distal appendage with short side-branches; escal bulb
425 length 8.7% SL; escal bulb width 6.8% SL; distal escal appendage 6% SL; a well-developed
426 hyoid barbel divided in three primary branches; secondary branches with a series of simple
427 side branches ending in a small number of photophores embedded in tip, greatest length of
428 barbel 161.7% SL; upper jaw teeth 25; lower jaw teeth 25; vomerine teeth 2; D: 3; A: 3; P:
429 15; C: 9.

430 **Distribution**

431 North Atlantic between approximately 32° and 45° N (Pietsch, 2009).

432

433 *Linophryne bicornis* Parr, 1927

434 Figure 14

435 *Linophryne bicornis* Parr, 1927: 9, Figure 2. Type locality: Near Bermuda, 32°19'N, 64°32'W,
436 2500 m of wire out. Holotype: YPM 2030.

437 **Material**

438 MNCN_ICTIO 291.463, 176.9 mm TL, 144.1 mm SL, ♀, Flemish Cap, 17/7/2015,
439 46°13.63'N, 46°22.72'W, 874 m.

440

441 **Description**

442 Body globose, maximum height of body 70.4% SL; illicium of medium size, 29.1% SL; hyoid
443 barbel undivided, distally bifurcated in two short branches, each carrying 7 stalked
444 photophores and 4 long filaments with internal photophores; total barbel length 95.3% SL;
445 undivided primary stem of barbel 25.4% SL; longest filament 69.9% SL; escal bulb almost
446 circular, esca width length 7.4% SL; two translucent filaments in the upper part of the escal
447 bulb, the longest 12.6% SL and one small white-tipped papillae below each one; longest

448 upper jaw teeth 6.5% SL and longest lower jaw teeth 11.7% SL; upper jaw teeth 31; lower
449 jaw teeth 19; vomerine teeth 4; D: 3; A: 3; P: 12; C: 9.

450 **Distribution**

451 Scattered records in the western North Atlantic and eastern South Indian oceans; three of the
452 five known specimens are reported in the western North Atlantic in Newfoundland, New
453 England, and Bermuda (Pietsch, 2009). Møller et al. (2010) reported one additional
454 unmeasured specimen from Davis Strait, at 1428 m depth.

455

456 **Molecular analysis**

457 The 651 bp in each analyzed sequence included 204 polymorphic and 195 parsimony
458 informative sites. The 139 available ceratioid barcode sequences (Tables 1 & 2) included 78
459 haplotypes, identified to members of all 11 families in the Ceratioidei, to 21 genera and 33
460 valid species (Figure 15 & Figure S1). All alignments are provided as Supporting
461 Information.

462 Following the original identifications for sequences extracted from BOLD and
463 GenBank, within-species genetic distances were 0 to 6.07, while congeneric distances were 0
464 to 6.31 (Table 3). Thus, no barcode gap was evident (Figure 16A). Sixty seven of the
465 sequences (48.2%) had maximum within-species between-species distances concordant with
466 both current taxonomy and the expectation of a barcode gap at a genetic distance of 2 (Area I
467 in Figure 16B). However, 37 sequences (26.6%) had unexpected low between-species
468 distances (Area III), suggestive of recent divergence, hybridization, synonymy or
469 identification errors. Similarly, several specimens clustered with others identified to different
470 species of the same genus (Figure S1). Thirty-four sequences (24.46%), including all those
471 identified to *C. couesii*, *Gigantactis vanhoeffeni* Brauer, 1902, or *Bufoceratias thele* (Uwate,
472 1979), had unexpectedly high within-species distances (Area II), indicating either
473 misidentification or the presence of cryptic species. The *C. couesii* sequences clustered in two
474 different groups, the first containing 18 sequences from Atlantic specimens, including three
475 from the present study (ACRAT project), while the second contained four sequences from
476 Pacific specimens (Figure S1). The only sequence in Area IV of Figure 16B (indicating
477 probable misidentification) was DSLAG439-10, identified to *Caulophryne pelagica* (Brauer,
478 1902). It clustered with an ACRAT specimen identified as *C. polynema* and another from
479 GenBank identified to *Caulophryne jordani*, not with the two other sequences identified as
480 *C. pelagica* Goode & Bean, 1896 (Figure S1).

481 Replacing the original identifications with cluster assignments reduced the coverage of
482 suborder Ceratioidei to 11 families, 21 genera and 33 species, with 121 of the sequences
483 identified to named species. Within-species distances lay between 0 and 2.61 and congeneric
484 distances were 2 to 6.31 (Table 3, Supporting information Table S1). There was a general
485 improvement in the distributions of the distances, with only two sequences failing to conform
486 with the expected barcode gap (Figure 16C, D). The cluster assigned to *L. bicornis* contained
487 three sequences (Figure S1), two of which (AB282854 and AB282855) were separated by an
488 unusually high within-species distance (2.61%), while each had a normal distance from the
489 third sequence (ACRAT017-18). After reassignment of the sequences, six clusters containing
490 15 specimens were unidentified at the species level (Figure S1). They comprised the *C.*
491 *couesii* sequences obtained from the Pacific Ocean, three clusters containing five sequences
492 all originally identified as *G. vanhoeffeni*, a lone, anomalous sequence identified as
493 *Bufoceratias thele*, a cluster containing sequences identified as either *Chaenophryne draco* or
494 *C. melanorhabdus*.

495 The results show some conflictive cases such as the comparisons between the
496 sequences of *B. idiomorpha* and *D. karsteni* where the highest genetic distance is 6.61, a
497 much lower value than the smallest distance observed between species of different genera,
498 which is 8.76. The genetic distances of the *L. bicornis* cluster are also noteworthy. The
499 sequence AB282855 assigned to *A. dolichonema* shows a distance of 1.69 with ACRAT017-
500 18, but 2.64 with AB282854, both assigned to *L. bicornis* (Table S1, Figure S1).

501

502 **DISCUSSION**

503 Identification of ceratioids often confronts the challenges of multiple congeneric and
504 confamilial species, few specimens on which to found descriptions, limited diagnostic
505 characters other than those of the, often lost, illicial apparatus, metamorphic stages,
506 intraspecific variation and aberrant specimens (Bañón, Pietsch, & Piñeiro, 2006; Pietsch
507 2009). DNA barcoding offers a potential solution to those challenges but it is first necessary
508 to have a database of reference sequences, assigned to species through reliable morphological
509 identification of the specimens from which the sequences were derived. Probably the greatest
510 weakness of the barcode approach is the presence of erroneous assignments in the existing
511 databases (Ward et al., 2009).

512 These problems have been illustrated by the present study. Some voucher specimens
513 of the ACRAT project showed new ranges of variation in characteristics used for species
514 identification. The main diagnostic characters of *L. brevibarbata* are based on only four

515 metamorphosed females, which explain why the barbel length measured in our specimen was
516 larger than those previously reported (Bertelsen, 1980, 1982). One specimen of *D. karsteni*
517 (MNCN_ICTIO 291.453) was notably larger than the maximum size previously reported for
518 the species (Leipertz & Pietsch, 1987). That individual also showed morphological
519 differences from existing descriptions, with lower relative length, depth and width of its head,
520 lower relative jaw length, higher tooth counts and a longer posterior esca appendage.

521 The present records also include extensions of known ranges. The specimens of *C.*
522 *polynema* and *D. karsteni* taken off Flemish Cap and *H. albinares* off Grand Bank were the
523 most northeasterly records from the western Atlantic (Moore, Hartel, Craddock, & Galbraith,
524 2003; Pietsch, 2009). Taxonomic diagnoses of those species should be updated to incorporate
525 the new information and further expansions of known ranges of morphological variation,
526 sizes and geographic distributions of ceratioids should be anticipated.

527 The apparent absence of barcode gap proved a useful indicator of misidentifications
528 and taxonomic inconsistencies in the data, while reliably identified voucher specimens made
529 recognition of errors possible. Twenty six of the 121 ceratioid sequences in BOLD and
530 GenBank could be erroneously identified or belong to possible cryptic species. For example,
531 the cluster assigned to *H. albinares* united five sequences previously identified to four
532 species. Two had been correctly identified. Two of the three misidentified came from
533 Australian and Californian waters, when there was only a single published record *H.*
534 *albinares* from the Pacific Ocean (a specimen taken off New Caledonia: Iglesias, 2005). Thus,
535 the two specimens highlight the risk of misidentifications caused by erroneous understanding
536 of species ranges (Bañón, Arronte, Vázquez-Dorado, del Río, & de Carlos, 2013).

537 The analysis presented here also suggests the existence of some cryptic species within
538 the Ceratioidei. As it is presently recognized, *Cryptopsaras couesii* is widely distributed in all
539 three major oceans of the world (Pietsch, 2009), though its esca morphology is variable, in
540 both the number of basal filaments and the length and branching of the distal filament
541 (Bertelsen, 1951), which suggests inter-, rather than intra-, specific variation. The available
542 barcode sequences form two distinct clusters in the NJ tree, each containing exclusively
543 sequences from the Atlantic or Pacific Oceans, respectively, as previously found by
544 Kenchington et al. (2017) using a very similar set of sequences. Apparent cases of cryptic
545 species can arise from specimens of known species being misidentified. That possibility
546 cannot be rejected for *C. couesii* but the nominal species belongs to a monotypic genus and
547 that the genetic distances observed between the two clusters fit within the observed
548 distribution of intrageneric genetic distances seen in the Ceratioidei. Hence, the existence of a

549 cryptic species seems more likely. Since the holotype of *C. couesii* (USNM 33558) came
550 from the Atlantic (off New York, U.S.A., at 39°18'30"N, 68°24'00"W), it is logical to apply
551 its name to the cluster of specimens captured in that Ocean, pending further investigations. A
552 close examination of Atlantic and Pacific specimens of *C. couesii* is needed to determine
553 whether there are morphological distinctions between apparent groups defined genetically and
554 whether one of the Indo-Pacific synonyms of *C. couesii*, such as *Cryptopsaras carunculatus*
555 Günther, 1887, *Cryptopsaras pennifer* Regan & Trewavas, 1932, *Cryptopsaras normani*
556 Regan & Trewavas, 1932 or *Cryptopsaras valdiviae* Regan & Trewavas, 1932, should be
557 resurrected as the name of a distinct species.

558 Another example of possible taxonomic incongruence concerns the genera *Bertella*
559 Pietsch, 1973 and *Dolopichthys* Garman, 1899, which can be differentiated morphologically
560 by the structure of the hyomandibular bone (Pietsch, 1973, 2009). In contrast, the genetic
561 distance between the available *B. idiomorpha* and *D. karsteni* barcode sequences falls within
562 the range expected of intrageneric relationships. The *D. karsteni* cluster contains sequences
563 from faithfully identified specimens but it is possible that the anomaly arose through
564 misidentification of the *B. idiomorpha* sequences. Alternatively, while the range of
565 intergeneric genetic distances in the barcode gene of ceratioids has been well defined by
566 analysis of many sequences across a wide variety of species, it is not known whether
567 nucleotide substitution rates are homogeneous in all taxa of the suborder Ceratioidei. Thus,
568 unusually slow divergence might explain the small distance between the two genera. Further
569 analyses are necessary to clarify their systematics.

570 After analysis, five groupings remain unidentified at the species level. Sequence
571 KP244513 named *B. thele* is not grouped with other sequences of the same species. The most
572 likely option is that this sequence belongs to one of the other two species from the genus
573 *Bufoceratias* (Pietsch, Hsuan-Ching, & Hong-Ming, 2004). Five sequences assigned to two
574 different species, *Chaenophryne draco* and *C. melanorhabdus*, are grouped together, which
575 would imply that at least one of them would be misidentified. The sequences previously
576 identified as *G. vanhoeffeni* are distributed into three closely related independent groups. With
577 the available information it is not possible to assign species to any of these groups, although
578 when looking at the topology of the tree it is likely that they belong to the same genus.

579 The sequence DSLAG439-10, previously identified as *C. pelagica*, is not grouped
580 with the rest of the sequences of this species, which would indicate an error in its assignment.
581 This interpretation is supported by its association in the tree with two other sequences
582 belonging to *C. jordani* and *C. polynema*, the latter being the one that gives name to the

583 grouping because it belongs to a specimen identified in the present study, which also implies
584 that the *C. jordani* sequence, with code AP004417, would also be the result of a
585 misidentification.

586 Despite the general improvement observed in the data set after applying the cluster
587 assignment, the method does not resolve the relationships between *A. dolichonema* and *L.*
588 *bicornis*. The *A. dolichonema* distance to the *L. bicornis* sequences is lower than the cut-off
589 value of 2% used to delimit species in one case and higher in the other. Hybridisation events,
590 erroneous identification or recent divergence between these two species could explain this
591 result. In any case and following the allocation criteria established, this grouping has
592 tentatively been called *L. bicornis*.

593

594 **Conclusions**

595 This research highlights the poor knowledge of intraspecific variation of the morphological
596 characters in scarcely reported ceratioid species, and its importance to keeping the
597 identification guides up to date. All individuals obtained from the nucleotide sequence
598 databases were well identified down to the genus level although some of the allocations to
599 species were erroneous. In some cases, it may be due to the difficulty of establishing certain
600 morphological characteristics. In others, to the fact that the identification guides are
601 incomplete and do not include all the species present in a given area. Starting with a
602 conflicting dataset, which showed no barcoding gap and contained a high number of
603 taxonomic conflicts, the species delimitation strategy employed in this study managed to
604 reduce their number to one.

605

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615

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729

730 **FIGURE 1** Map showing the locations of Grand Bank, Flemish Cap (FC), and Flemish Pass
731 (FP), in the northwest Atlantic, where ceratioid specimens were caught.

732 **FIGURE 2** *Ceratias holboelli*. A, female 112.7 mm SL, MNCN_ICTIO 291.456; B, escal
733 bulb showing escal appendage anterior to escal pore; C, detail of pigmented escal pore with
734 the unpigmented escal appendage behind.

735 **FIGURE 3** *Cryptopsaras couesii*. A, female 56.1 mm SL, MNCN_ICTIO 291.457; B, detail
736 of escal distal filament of female 78.3 mm SL, MNCN_ICTIO 291.455; C, detail of basal
737 escal filaments.

738 **FIGURE 4** *Himantolophus albinares*. A, female 60.7 mm SL, MNCN_ICTIO 291.460; B,
739 anterior part of the head showing the papillae on the snout, mouth and teeth.

740 **FIGURE 5** Distal part of the illicial apparatus of *Himantolophus albinares* showing
741 structures of the esca.

742 **FIGURE 6** *Melanocetus johnsonii*. A, female 125.1 mm SL, MNCN_ICTIO 291.459; B,
743 amputated illicium; C, vomerine teeth.

744 **FIGURE 7** *Lophodolos acanthognathus* A, female 56.7 mm SL, MNCN_ICTIO 291.448; B,
745 esca of *L. acanthognathus* 56.7 mm SL, MNCN_ICTIO 291.448; C, esca of *L.*
746 *acanthognathus* 31.2 mm SL, MNCN_ICTIO 291.447; D, esca of *L. acanthognathus* 66.3 mm
747 SL, MNCN_ICTIO 291.451.

748 **FIGURE 8** *Oneirodes eschrichtii*. A, female 98.2 mm SL, MNCN_ICTIO 291.449; B, detail
749 of esca; C, detail of the escal appendages.

750 **FIGURE 9** *Dolopichthys karsteni*. A, female skinned 134.4 mm SL, MNCN_ICTIO 291.453;
751 B, detail of esca; C, detail of the 3 papillae of the anterior portion of the esca.

752 **FIGURE 10** *Leptacanthichthys gracilispinis*. A, female 50.6 mm SL, MNCN_ICTIO
753 291.466; B, detail of the esca; C, detail of the articular and quadrate spines.

754 **FIGURE 11** *Caulophryne polynema*. A, female 128.3 mm SL, MNCN_ICTIO 291.461; B,
755 detail of the head; C, illicium covered with numerous translucent filaments and the terminal
756 esca; D, detail of esca.

757 **FIGURE 12** *Haplophryne mollis*. A, female 42.2 mm SL, MNCN_ICTIO 291.464, showing
758 an ectoparasite in the caudal zone; B, detail of the head; C, detail of esca showing the distal
759 escal appendage divided distally.

760 **FIGURE 13** *Linophryne brevibarbata*. A, Female 42.2 mm SL, MNCN_ICTIO 291.462; B,
761 detail of esca showing the distal escal appendage; C, detail of the teeth.

762 **FIGURE 14** *Linophryne bicornis*. A, female 144.1 mm SL, MNCN_ICTIO 291.463; B, hyoid
763 barbel; C, terminal short branches of the stem of the illicium showing some stalked

764 photophores and the start of the long filaments; D, detail of esca showing 2 lateral
765 appendages.

766

767 **FIGURE 15** Comparison between the original data (A, B) and the proposed delimitation after
768 neighbor-joining grouping (C, D) based on *COI* genetic distances. Histograms represent the
769 frequencies of intraspecific (blue), intrageneric (red) and intergeneric (green) genetic
770 distances (A, C). Dot plots represent intraspecific compared to interspecific distances for each
771 specimen (B, D). A cut-off value of 2% was used to delimit four different quadrants: (I)
772 concordant with current taxonomy; (II) possible cryptic species or misidentification; (III)
773 recent divergence, hybridisation or synonymy; (IV) possible misidentification. Colour stars
774 (quadrants II and IV) and colour circles (quadrant III) represent different species not
775 concordant with current taxonomy: 1: *B. tele*; 2: *C. pelagica*; 3: *C. couesii*; 4: *G. vanhoeffeni*;
776 5: *C. jordani*; 6: *C. polynema*; 7: *C. holboelli*; 8: *C. tentaculatus*; 9: *C. uranoscopus*; 10: *C.*
777 *draco*; 11: *C. melanorhabdus*; 12: *H. albinares*; 13: *H. appelii*; 14: *H. groenlandicus*; 15: *H.*
778 *sagamius*; 16: *L. bicornis*; 17: *O. acanthias*; 18: *O. bulbosus*; 19: *O. eschrichtii*; 20: *O. notius*;
779 21: *O. thompsoni*.

780

781 **FIGURE 16** Collapsed neighbour-joining tree of *COI* sequences of Ceratioid fishes based on
782 p-distances. Numbers at the main nodes are bootstrap percentages after 2000 replicates. Only
783 values higher than 70% are shown. . Each family is shadowed with a different colour.

784

785

786 **Supporting Information**

787 **Table S1** Pairwise genetic p-distances of all ceratioid specimens included in the study.

788 **Figure S1** Complete neighbour-joining tree including 139 *COI* sequences of Ceratioid fishes
789 based on p-distances. Numbers at the main nodes are bootstrap percentages after 2000
790 replicates. Only values higher than 70% are shown. Subtrees include species
791 assignments. Sequences from own voucher specimens are bolded.

792

793 **TABLE 1** List of ceratioid specimens analysed (ACRAT project dataset), BOLD and GenBank references, locations: Flemish Cap (FC) and
 794 Grand Banks of Newfoundland (GB).

795

Species	Location	BOLD Sample ID¹	BOLD Process ID¹	GenBank Acc. No	Museum collection No
<i>Lophodolos acanthognathus</i>	FC	CRT001	ACRAT001-18	MH033869	MNCN_ICTIO 291.447
<i>Lophodolos acanthognathus</i>	GB	CRT002	ACRAT002-18	MH033868	MNCN_ICTIO 291.448
<i>Oneirodes eschrichtii</i>	GB	CRT003	ACRAT003-18	MH033872	MNCN_ICTIO 291.449
<i>Oneirodes eschrichtii</i>	FC	CRT004	ACRAT004-18	MH033873	MNCN_ICTIO 291.450
<i>Lophodolos acanthognathus</i>	FC	CRT005	ACRAT005-18	MH033870	MNCN_ICTIO 291.451
<i>Oneirodes eschrichtii</i>	FC	CRT006	ACRAT006-18	MH033874	MNCN_ICTIO 291.452
<i>Dolopichthys karsteni</i>	FC	CRT007	ACRAT007-18	MH033864	MNCN_ICTIO 291.453
<i>Ceratias holboelli</i>	FC	CRT008	ACRAT008-18	MH033859	MNCN_ICTIO 291.454
<i>Cryptopsaras couesii</i>	GB	CRT009	ACRAT009-18	MH033860	MNCN_ICTIO 291.455
<i>Ceratias holboelli</i>	FC	CRT010	ACRAT010-18	MH033858	MNCN_ICTIO 291.456
<i>Cryptopsaras couesii</i>	GB	CRT011	ACRAT011-18	MH033862	MNCN_ICTIO 291.457
<i>Cryptopsaras couesii</i>	FC	CRT012	ACRAT012-18	MH033861	MNCN_ICTIO 291.458
<i>Melanocetus johnsonii</i>	FC	CRT013	ACRAT013-18	MH033871	MNCN_ICTIO 291.459
<i>Himantolophus albinus</i>	GB	CRT014	ACRAT014-18	MH033865	MNCN_ICTIO 291.460
<i>Caulophryne polynema</i>	FC	CRT015	ACRAT015-18	MH033857	MNCN_ICTIO 291.461
<i>Linophryne bicornis</i>	FC	CRT017	ACRAT016-18	MH033867	MNCN_ICTIO 291.463
<i>Dolopichthys karsteni</i>	GB	CRT019	ACRAT017-18	MH033863	MNCN_ICTIO 291.465
<i>Leptacanthichthys gracilispinis</i>	FC	CRT020	ACRAT018-18	MH033866	MNCN_ICTIO 291.466

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Table 2 BOLD / GenBank dataset of ceratioid specimens

Family	Species	BOLD Process ID	GenBank Acc. No.
Linophryniidae	<i>Acentrophryne dolichonema</i>		AB282855
Oneirodidae	<i>Bertella idiomorpha</i>	MFC330-08	GU440251
Oneirodidae	<i>Bertella idiomorpha</i>	ANGBF018-12	AB282846
Diceratiidae	<i>Bufoceratias thele</i>		KP244512
Diceratiidae	<i>Bufoceratias thele</i>		KU943196
Diceratiidae	<i>Bufoceratias thele</i>		NC013869
Diceratiidae	<i>Bufoceratias thele</i>		KP244513
Caulophryniidae	<i>Caulophryne jordani</i>		AP004417
Caulophryniidae	<i>Caulophryne pelagica</i>	DSLAGE439-10	
Caulophryniidae	<i>Caulophryne pelagica</i>	MOP605-12	MF956553
Caulophryniidae	<i>Caulophryne pelagica</i>		NC_016020
Centrophryniidae	<i>Centrophryne spinulosa</i>		AB282849
Ceratiidae	<i>Ceratias holboelli</i>	GLF097-14	
Ceratiidae	<i>Ceratias holboelli</i>	GLF106-14	
Ceratiidae	<i>Ceratias holboelli</i>	GLF207-14	
Ceratiidae	<i>Ceratias holboelli</i>	MFC334-08	GU440269
Ceratiidae	<i>Ceratias holboelli</i>	SCAFB1285-09	KY033578
Ceratiidae	<i>Ceratias holboelli</i>	SCFAC572-06	KY033876
Ceratiidae	<i>Ceratias holboelli</i>	SCAFB959-07	KY033877
Ceratiidae	<i>Ceratias holboelli</i>	SCFAD446-09	KY033878
Ceratiidae	<i>Ceratias tentaculatus</i>	FOAG648-08	JN640592
Ceratiidae	<i>Ceratias uranoscopus</i>		NC_013882
Oneirodidae	<i>Chaenophryne draco</i>	FOAD275-05	EF609318
Oneirodidae	<i>Chaenophryne draco</i>	GLF247-14	
Oneirodidae	<i>Chaenophryne draco</i>	GLF315-16	
Oneirodidae	<i>Chaenophryne longiceps</i>	FMV406-09	JQ354036
Oneirodidae	<i>Chaenophryne longiceps</i>	GLF301-16	
Oneirodidae	<i>Chaenophryne longiceps</i>	MFC335-08	GU440270
Oneirodidae	<i>Chaenophryne longiceps</i>	MAECO413-09	
Oneirodidae	<i>Chaenophryne longiceps</i>	SCAFB1291-09	KY033587
Oneirodidae	<i>Chaenophryne melanorhabdus</i>	ANGBF017-12	
Oneirodidae	<i>Chaenophryne melanorhabdus</i>	MFC336-08	GU440271
Ceratiidae	<i>Cryptopsaras couesii</i>	GBGC4132-08	EU403054
Ceratiidae	<i>Cryptopsaras couesii</i>	MAECO417-09	
Ceratiidae	<i>Cryptopsaras couesii</i>	MFC021-08	GU440295
Ceratiidae	<i>Cryptopsaras couesii</i>		KU943197
Ceratiidae	<i>Cryptopsaras couesii</i>	SCAFB1121-09	KY033599
Ceratiidae	<i>Cryptopsaras couesii</i>	SCAFB1106-09	KY033600
Ceratiidae	<i>Cryptopsaras couesii</i>	SCAFB1257-09	KY033601

Ceratiidae	<i>Cryptopsaras couesii</i>	SCFAC889-06	KY033896
Ceratiidae	<i>Cryptopsaras couesii</i>		MF040993
Ceratiidae	<i>Cryptopsaras couesii</i>		MF041024
Ceratiidae	<i>Cryptopsaras couesii</i>		MF041195
Ceratiidae	<i>Cryptopsaras couesii</i>		MF041272
Ceratiidae	<i>Cryptopsaras couesii</i>		MF041289
Ceratiidae	<i>Cryptopsaras couesii</i>		MF041674
Ceratiidae	<i>Cryptopsaras couesii</i>		MF041677
Ceratiidae	<i>Cryptopsaras couesii</i>		MF041715
Ceratiidae	<i>Cryptopsaras couesii</i>		MG856457
Ceratiidae	<i>Cryptopsaras couesii</i>		MG856725
Ceratiidae	<i>Cryptopsaras couesii</i>		NC_013880
Diceratiidae	<i>Diceratias pileatus</i>		NC_013870
Oneirodidae	<i>Dolopichthys karsteni</i>	MAECO423-09	
Oneirodidae	<i>Dolopichthys karsteni</i>	UKFBJ1167-08	KF929827
Gigantactinidae	<i>Gigantactis vanhoeffeni</i>	FMV460-09	JQ354107
Gigantactinidae	<i>Gigantactis vanhoeffeni</i>	MAECO133-06	EU148172
Gigantactinidae	<i>Gigantactis vanhoeffeni</i>	MFC061-08	GU440328
Gigantactinidae	<i>Gigantactis vanhoeffeni</i>		KU943198
Gigantactinidae	<i>Gigantactis vanhoeffeni</i>		NC_013885
Linophrynidae	<i>Haplophryne mollis</i>	SCAFB1322-09	KY033628
Linophrynidae	<i>Haplophryne mollis</i>	SCAFB1107-09	KY033630
Linophrynidae	<i>Haplophryne mollis</i>		AB282856
Himantolophidae	<i>Himantolophus albinus</i>		AB282839
Himantolophidae	<i>Himantolophus appeli</i>	FOAD267-05	EF609375
Himantolophidae	<i>Himantolophus groenlandicus</i>		AB282840
Himantolophidae	<i>Himantolophus sagamius</i>	MFC080-08	GU440342
Linophrynidae	<i>Linophryne bicornis</i>	ANGBF021-12	AB282854
Oneirodidae	<i>Lophodolos acanthognathus</i>	MFC356-08	GU440383
Oneirodidae	<i>Lophodolos acanthognathus</i>	GLF027-13	
Oneirodidae	<i>Lophodolos acanthognathus</i>	MAECO463-09	
Oneirodidae	<i>Lophodolos acanthognathus</i>	SCFAD493-09	KY033661
Oneirodidae	<i>Lophodolos acanthognathus</i>	SCFAD492-09	KY033662
Melanocetidae	<i>Melanocetus johnsonii</i>	FMV908-17	
Melanocetidae	<i>Melanocetus johnsonii</i>	FMV926-17	
Melanocetidae	<i>Melanocetus johnsonii</i>	FPFLB353-12	KJ968144
Melanocetidae	<i>Melanocetus johnsonii</i>	GBGCA7474-15	KM593294
Melanocetidae	<i>Melanocetus johnsonii</i>	MAECO481-09	
Melanocetidae	<i>Melanocetus johnsonii</i>	MAECO482-09	
Melanocetidae	<i>Melanocetus johnsonii</i>		GU440403
Melanocetidae	<i>Melanocetus johnsonii</i>	SCAFB1316-09	KY033676
Melanocetidae	<i>Melanocetus johnsonii</i>		MF041043
Melanocetidae	<i>Melanocetus johnsonii</i>		MF041456
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP030-12	MF956787

Melanocetidae	<i>Melanocetus johnsonii</i>	MOP105-12	MF956786
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP403-12	MF956788
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP404-12	MF956789
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP405-12	MF956790
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP423-12	MF956791
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP424-12	MF956792
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP598-12	MF956793
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP618-12	MF956794
Melanocetidae	<i>Melanocetus johnsonii</i>	MOP739-12	MF956795
Melanocetidae	<i>Melanocetus johnsonii</i>		MG856595
Melanocetidae	<i>Melanocetus johnsonii</i>		MG856897
Melanocetidae	<i>Melanocetus johnsonii</i>		NC_013866
Melanocetidae	<i>Melanocetus murrayi</i>		AP004418
Melanocetidae	<i>Melanocetus murrayi</i>		KU943195
Melanocetidae	<i>Melanocetus murrayi</i>		MF041120
Melanocetidae	<i>Melanocetus murrayi</i>		MG856603
Oneirodidae	<i>Microlophichthys microlophus</i>	MAECO487-09	
Oneirodidae	<i>Microlophichthys microlophus</i>	MAECO488-09	
Neoceratiidae	<i>Neoceratias spinifer</i>		NC_013864
Oneirodidae	<i>Oneirodes acanthias</i>	TZFPA038-06	FJ164937
Oneirodidae	<i>Oneirodes bradburyae</i>	SCAFB1172-09	KY033720
Oneirodidae	<i>Oneirodes bulbosus</i>	FMV421-09	JQ354249
Oneirodidae	<i>Oneirodes eschrichtii</i>	GLF080-14	
Oneirodidae	<i>Oneirodes luetkeni</i>	MOP072-12	MF956896
Oneirodidae	<i>Oneirodes luetkeni</i>	MOP166-12	MF956895
Oneirodidae	<i>Oneirodes luetkeni</i>	MOP269-12	MF956897
Oneirodidae	<i>Oneirodes luetkeni</i>	MOP270-12	MF956892
Oneirodidae	<i>Oneirodes luetkeni</i>	MOP351-12	MF956894
Oneirodidae	<i>Oneirodes luetkeni</i>	MOP420-12	MF956893
Oneirodidae	<i>Oneirodes macrosteus</i>	GLF290-16	
Oneirodidae	<i>Oneirodes macrosteus</i>	GLF139-14	
Oneirodidae	<i>Oneirodes notius</i>	EATF574-10	HQ713098
Oneirodidae	<i>Oneirodes rosenblatti</i>	MOP451-12	MF956898
Oneirodidae	<i>Oneirodes thompsoni</i>		FJ164938
Oneirodidae	<i>Oneirodes thompsoni</i>	MFC367-08	GU440435
Oneirodidae	<i>Puck pinnata</i>	ANGBF016-12	
Gigantactinidae	<i>Rhynchactis macrothrix</i>		NC_013863
Thaumatichthyidae	<i>Thaumatichthys pagidostomus</i>		NC_013875

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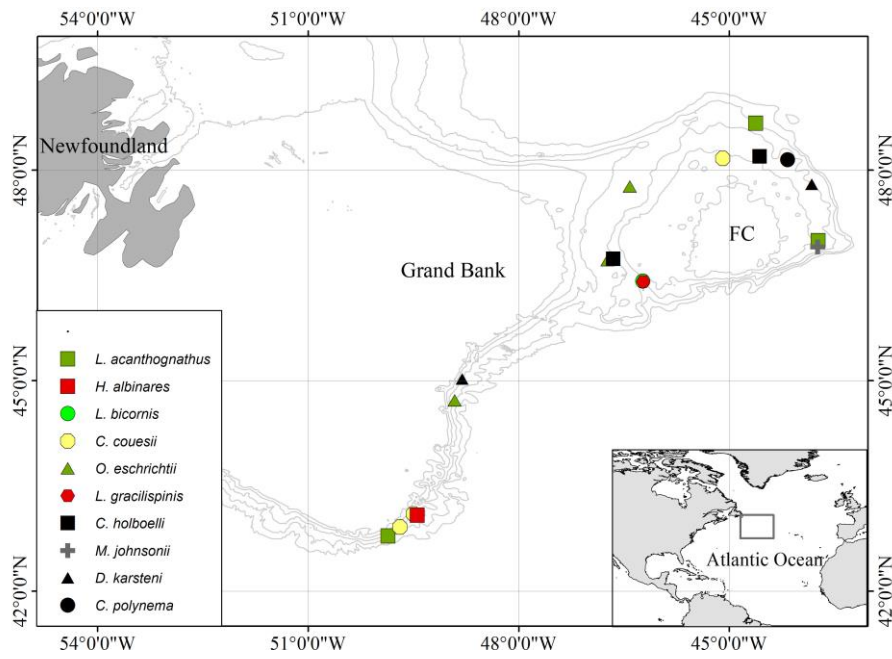
806 **Table 3** Summary of p-distance distributions among Ceratioidei taxa comparing the original
 807 and the proposed assignments of the barcodes.

		No. Comparisons	Min. Distance	Mean Distance	Max. Distance
Within species	Original assignment (n=37)	632	0	0.98	6.07
	Proposed assignment (n=27)	629	0	0.35	2.61
Within genus	Original assignment (n=8)	335	0	3.54	6.31
	Proposed assignment (n=8)	337	2	4.69	6.31
Between genus	Original assignment (n=8)	8893	1.69	17.32	25.96
	Proposed assignment (n=8)	8894	3.38	17.33	25.96

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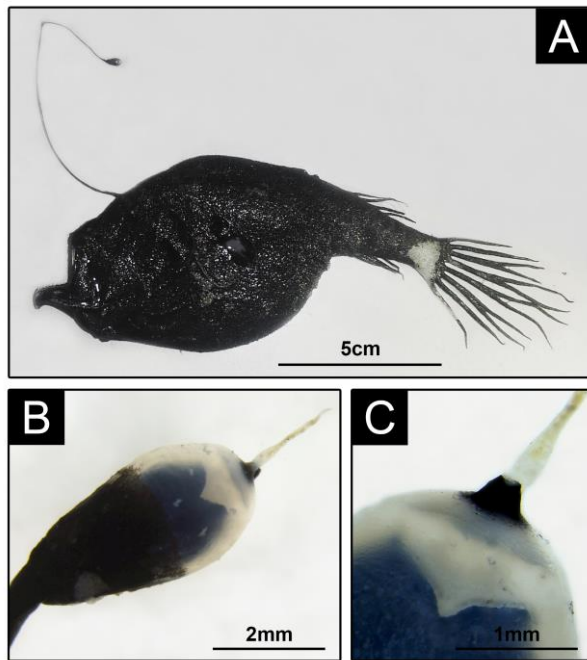
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810 Fig. 1



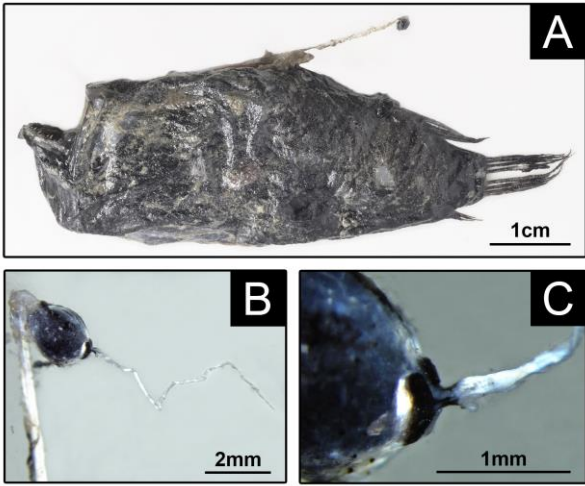
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812 Fig. 2



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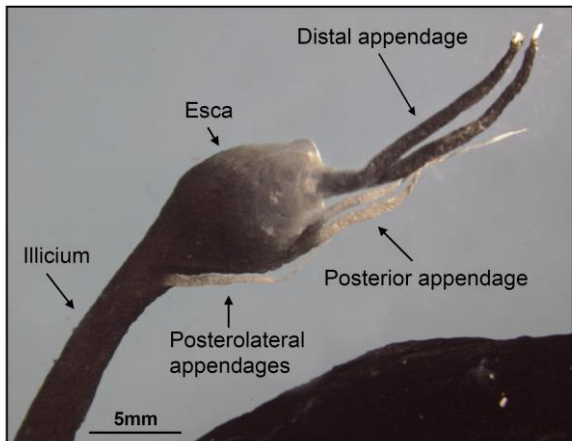
814 Fig. 3



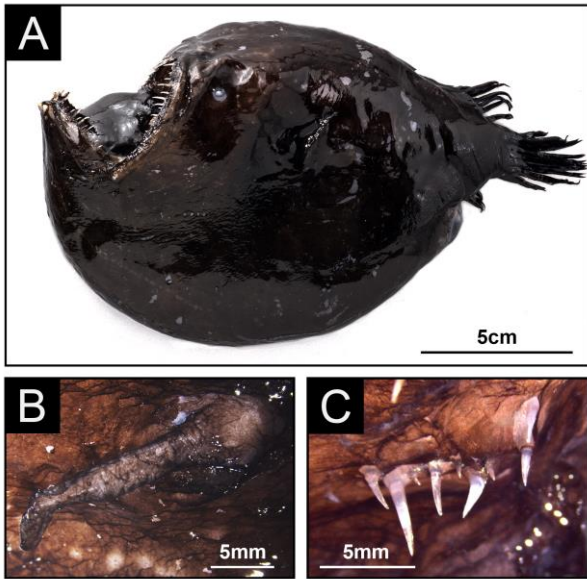
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816 Fig. 4



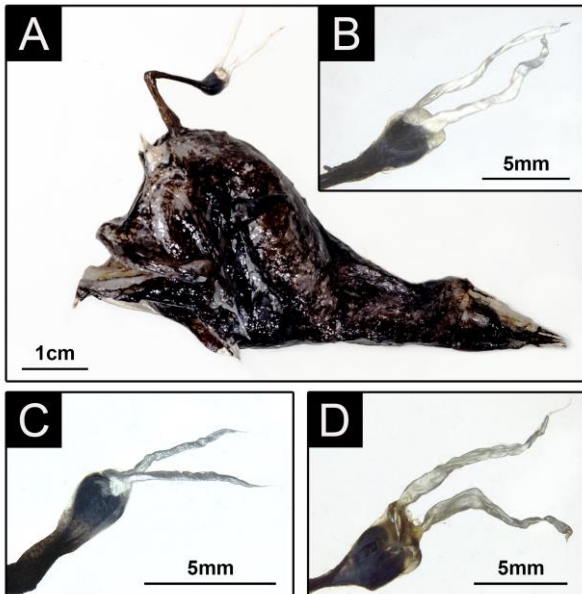
817
818 Fig. 5



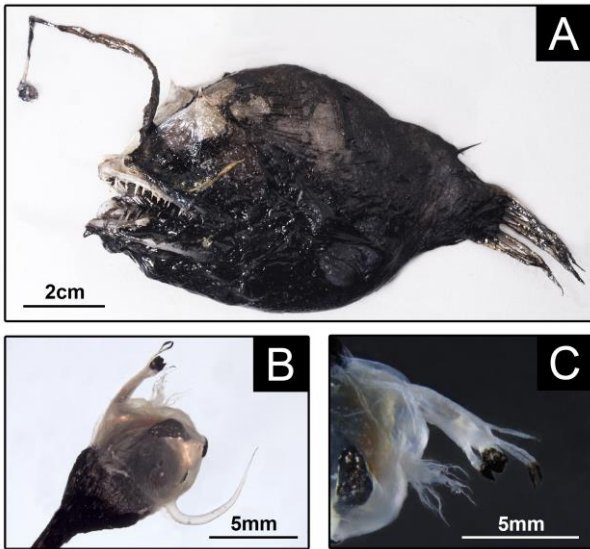
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820 Fig. 6



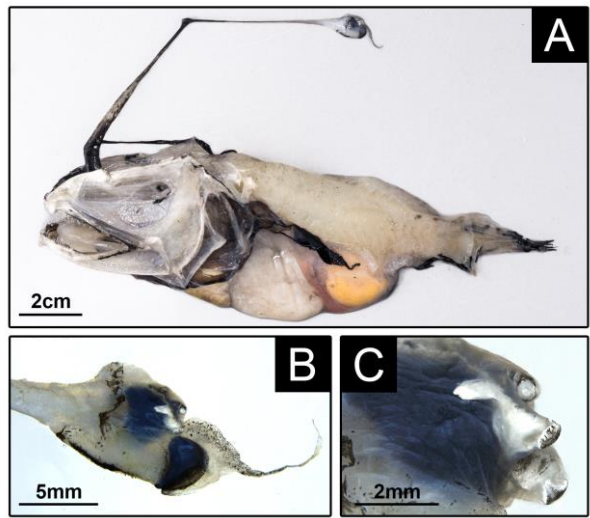
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822 Fig. 7



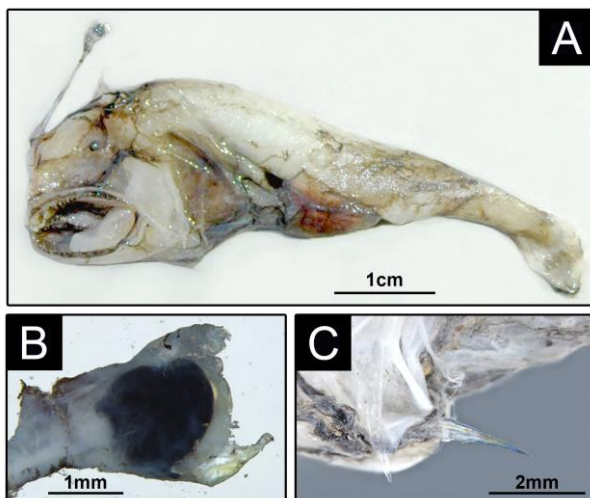
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824 Fig. 8



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826 Fig. 9

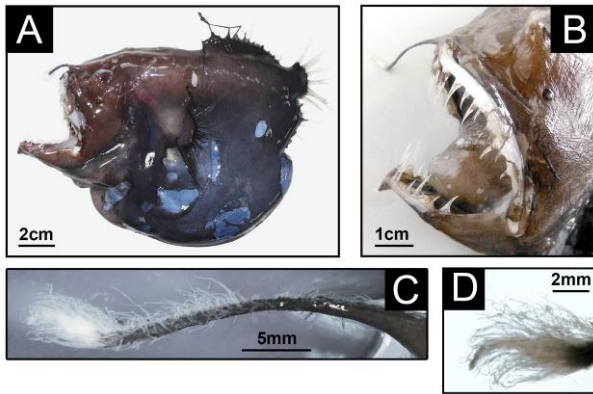


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828 Fig. 10



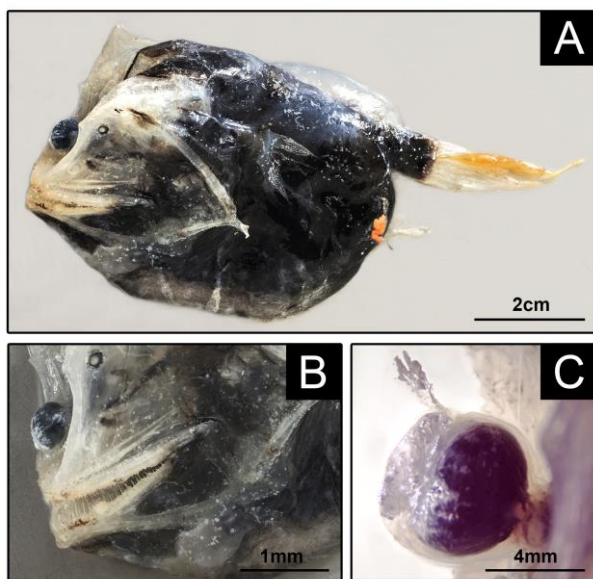
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832 Fig. 11



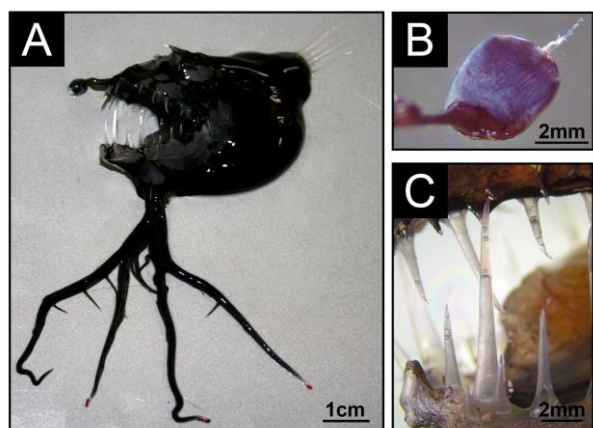
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834 Fig. 12



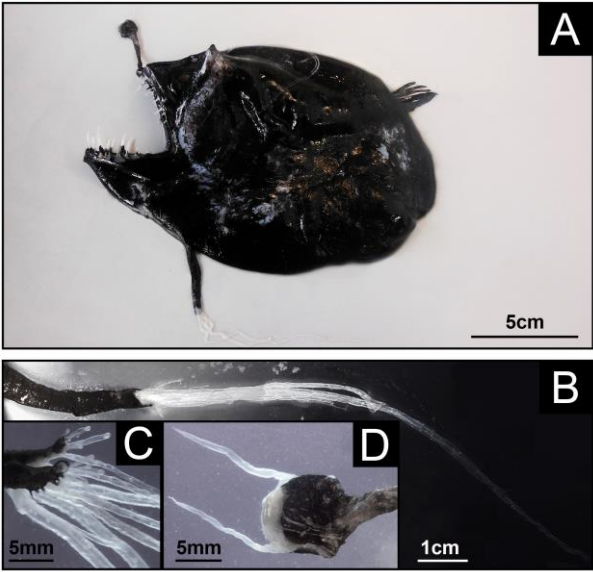
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836 Fig. 13



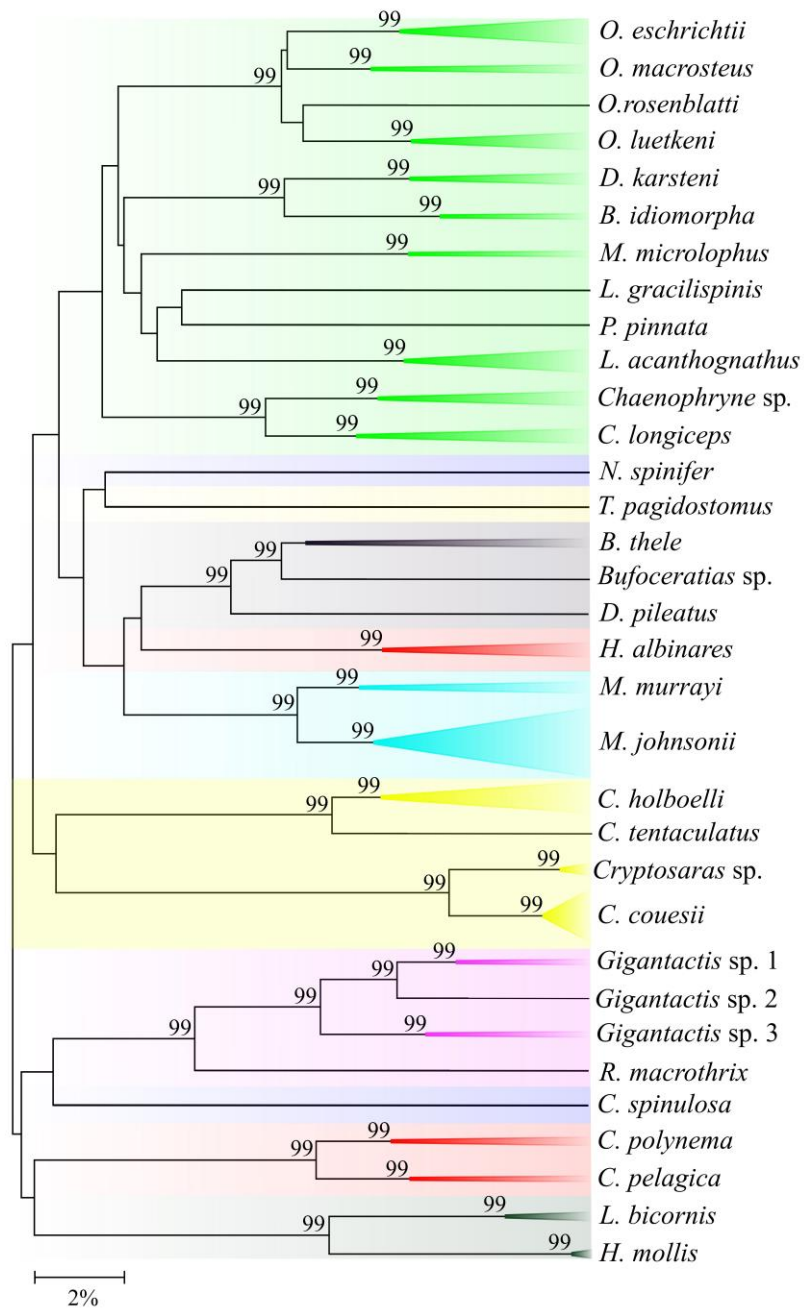
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838 Fig. 14



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840 Fig. 15



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