
A new species and first record of *Dracoderes* (Kinorhyncha: Allomalorhagida: Dracoderidae) from American waters, with an identification key of the genus

Cepeda Diego ^{1,*}, Pardos Fernando ¹, Sánchez Nuria ^{1,2}

¹ Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, José Antonio Novais St. 12, 28040, Madrid, Spain

² Laboratoire Environnement Profond, Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Centre Bretagne - ZI de la Pointe du Diable, CS 10070 - 29280, Plouzané, France

* Corresponding author : Diego Cepeda, email address : diegocepeda@ucm.es

Abstract :

A new species of *Dracoderes*, *D. spyro* sp. nov., is described from Hispaniola Island (Caribbean Sea), and represents the first record of this genus in American waters. The new species is distinguished from its congeners by the presence of lateroventral spines on segments 3–4 and 6–9, lateral accessory spines on segment 5, lateroventral tubes on segments 2, 5 and 10, and laterodorsal tubes on segment 8. Additionally, a dichotomous key to the species level for the genus *Dracoderes* is included.

Keywords : Taxonomy, Morphology, Caribbean Sea, Dominican Republic, Haiti, Kinorhynchs

28 1. Introduction

29 The phylum Kinorhyncha comprises a group of meiofaunal, holobenthic, free-living
30 organisms that inhabit the upper centimetres of sandy and muddy marine soft bottoms
31 (Neuhaus, 2013; Sørensen and Pardos, 2008). Until recently, the phylum was composed
32 of two orders, Cyclorhagida and Homalorhagida, (Higgins, 1964; Zelinka, 1896)
33 comprising 23 genera (Dal Zotto et al. 2013; Sánchez et al. 2014; Sørensen, 2013).
34 However, more recent analyses, based on either ribosomal genes, or ribosomal genes
35 combined with morphology, indicated the paraphyly of Cyclorhagida, as the former
36 cyclorhagid genus *Dracoderes* Higgins and Shirayama, 1990 turned out to be more
37 closely related with homalorhagid taxa (Dal Zotto et al. 2013; Sørensen et al. 2015;
38 Yamasaki et al. 2013). As a result, the systematics of the phylum were modified,
39 accommodating the family Dracoderidae within the new class Allomalorhagida,
40 together with the former homalorhagid taxa and the recently established genus
41 *Franciscideres* Dal Zotto et al., 2013 (Sørensen et al. 2015).

42 Kinorhynchs spend their whole life cycle in the sediment, have a limited
43 locomotion and are gonochoristic. Thus, kinorhynch species have been considered to
44 usually show regional distribution patterns limited to a few hundreds of kilometres
45 (Artois et al. 2011; Kozloff, 1972; Yamasaki et al. 2014). Nevertheless, unequal species
46 richness and biogeographical distribution patterns may be found among kinorhynch
47 species by focusing on upper taxonomic categories such as genera or families (Neuhaus,
48 2013; Sørensen et al. 2012). Thus, there are some highly diverse taxa, e.g., the genus
49 *Echinoderes* Claparède, 1863 and the family Pycnophyidae, that are distributed
50 worldwide and together represents more than two thirds of the total number of known
51 kinorhynch species. On the contrary, other taxa display much more restricted
52 biogeographical distributions and are composed of a single or a few species, e.g., the
53 monotypic *Polacanthoderes* Sørensen, 2008 only known from the South Shetland
54 Archipelago in the Antarctic Ocean (Sørensen, 2008) or *Neocentrophyes* Higgins, 1969
55 composed of two species restricted to the Indian Ocean (Higgins, 1969). This was also
56 the case of the genus *Dracoderes* that appeared to have a distribution limited to the Seto
57 Inland Sea and the Sea of Japan until the description of a new species from the Atlantic
58 coast of Spain (Sørensen et al. 2012).

59 *Dracoderes* currently accommodates six species, five from the northwestern
60 Pacific Ocean, namely *D. abei* Higgins and Shirayama, 1990 (Seto Inland Sea, Sea of

61 Japan and northwest Pacific); *D. nidhug* Thomsen et al., 2013 (Korea, Sea of Japan); *D.*
62 *orientalis* Adrianov, 1999 in Adrianov and Malakhov, 1999 (Korea, Sea of Japan); *D.*
63 *snufkini* Yamasaki, 2015 (Okinawa, East China Sea); and *D. toyoshioae* Yamasaki,
64 2015 (Okinawa, East China Sea); and one from Galicia at the Atlantic coast of Spain: *D.*
65 *gallaicus* Sørensen et al., 2012. The genus is morphologically characterized by a
66 combination of mouth cone with nine outer oral styles alternating in size, neck with nine
67 placids dorsal and midlaterally interrupted by cuticular foldings, cuticle of first segment
68 as a closed ring, cuticle of remaining segments divided into one tergal and two sternal
69 plates, dorsal spines on at least segments 3-9 with the anteriormost spine middorsally
70 located, following ones in paradorsal position alternatingly displaced left or right
71 regarding to the middorsal line and posteriormost spine middorsal or paradorsally
72 located, and lateroventral spines on at least segments 6-9 (Higgins and Shirayama,
73 1990; Sørensen et al. 2012; Yamasaki, 2015). The most significant morphological
74 differences among species of *Dracoderes* are the position of tubes and dorsal spines, the
75 shape and size of trunk segments, the shape of pectinate fringe and the shape of tergal
76 extensions (Sørensen et al. 2012; Thomsen et al. 2013; Yamasaki, 2015). There is also
77 sexual dimorphism in *Dracoderes*, as males possess three pairs of penile spines on
78 segment 11 (Sørensen et al. 2012).

79 Samples of meiofauna from the Caribbean Sea and adjacent waters collected by
80 Dr R. P. Higgins in 1976 and 1980 and deposited in the Smithsonian National Museum
81 of Natural History of Washington (NMNH) gave the authors the opportunity to study
82 several specimens of *Dracoderes* from Hispaniola Island, the second largest land mass
83 of the Greater Antilles after Cuba, where kinorhynchs have been scarcely studied. There
84 are few papers dealing with the biodiversity of this phylum in the Caribbean Sea
85 (Higgins, 1983; Kirsteuer, 1964; Neuhaus et al. 2014; Pardos et al. 2016; Sørensen,
86 2006). The present study contributes to the understanding of the taxonomy and
87 biogeographical distribution of the allomalorhagid *Dracoderes* as well as to the
88 knowledge of kinorhynch biodiversity of the Caribbean Sea and adjacent waters.

89

90 **2. Material and methods**

91 The studied specimens of *Dracoderes* were collected at four different localities in
92 Hispaniola Island, Caribbean Sea (western Atlantic Ocean). Detailed information on the

93 localities and sampling data are summarized in Fig. 1A-C and Table 1. Samplings were
94 performed using a meiobenthic dredge (Higgins, 1988). After sampling, meiofauna was
95 extracted from sediment using the bubble and blot method defined by Higgins (1964).
96 Meiofaunal specimens were fixed in 4% formalin and then preserved in Carosafe[®] or
97 70% ethanol.

98 The fixed kinorhynchs were picked up under a Motic[®] SMZ-168 stereo zoom
99 microscope with the help of an Irwin loop. Initially, specimens were washed with
100 distilled water in order to remove formalin. For light microscopy (LM), specimens were
101 dehydrated through a graded series of 25%, 50%, 75% and 100% glycerin and finally
102 mounted on a glass slide or a Cobb's aluminium slide holder in Fluoromount G[®] and
103 sealed with Depex[®]. The mounted specimens were studied and photographed using an
104 Olympus[®] BX51-P microscope with differential interference contrast (DIC) optics
105 equipped with an Olympus[®] DP-70 camera. Measurements were obtained with
106 Olympus cellSens[®] software. The identification at genus level of the specimens was
107 done according to the dichotomous key provided by Sørensen and Pardos (2008). For
108 scanning electron microscopy (SEM), specimens were dehydrated through a graded
109 series of 80%, 90%, 95% and 100% ethanol. Then, specimens were cleaned by an
110 ultrasonic cleaner for 10-15 s, transferred to acetone and critical point dried. Finally, the
111 kinorhynchs were mounted on aluminium stubs, coated with gold and examined with a
112 JSM[®] 6335-F JEOL SEM in the ICTS Centro Nacional de Microscopía Electrónica
113 (Universidad Complutense de Madrid, Spain). Images and line drawing were mounted
114 using Adobe[®] Photoshop 6.0 and Illustrator CC-2014 software.

115

116 **3. Results**

117 *Taxonomic account*

118 Class Allomalorhagida Sørensen et al., 2015

119 Family Dracoderidae Higgins and Shirayama, 1990

120 Genus *Dracoderes* Higgins and Shirayama, 1990

121 ***Dracoderes spyro* sp. nov.**

122 urn:lsid:zoobank.org:act:1C598D96-958E-4A3D-82A7-3E07270089F9

123 (Figs. 2–4 and Tables 2–3)

124 *3.1 Type material*

125 Holotype, adult female, collected on 10 November 1980 at Cabo Haitiano, Haiti,
126 Hispaniola Island, western Atlantic Ocean: 19° 46'12''N, 072° 11'00''W (L4) (Fig. 1C)
127 at 3–5 m depth in mud; mounted in Fluoromount G[®], deposited at NMNH under
128 accession number: USNM1480327. Paratypes, six adult females and five males; three of
129 them with same collecting data as holotype, mounted in Fluoromount G[®], deposited at
130 NMNH under accession numbers: USNM1480328, USNM1480329, USNM1480333;
131 two of them collected on 02 November 1980 at Puerto Plata, Dominican Republic,
132 Hispaniola Island, western Atlantic Ocean: 19° 48'12''N, 070° 42'00''W (L1) (Fig. 1C)
133 at 5 m depth in sandy mud, mounted in Fluoromount G[®], deposited at NMNH under
134 accession numbers: USNM1480330, USNM1480334; two of them collected on 04
135 November 1980 at Isabela Bay, Dominican Republic, Hispaniola Island, western
136 Atlantic Ocean: 19°53'18''N, 071°05'36''W (L3) (Fig. 1C) at 4 m depth in silty mud,
137 mounted in Fluoromount G[®], deposited at NMNH under accession numbers:
138 USNM1480331, USNM1480335; two of them collected on 03 November 1980 at
139 Puerto Blanco, Dominican Republic, Hispaniola Island, western Atlantic Ocean:
140 19°54'24''N, 070°56'24''W (L2) (Fig. 1C) at 3 m depth in silty mud, mounted in
141 Fluoromount G[®], deposited at NMNH under accession numbers: USNM1480332,
142 USNM1480336; two of them collected on 15 March 1976 at Puerto Príncipe, Haiti,
143 Hispaniola Island, western Atlantic Ocean: 18°32'21''N, 072°20'05''W (L5) (Fig. 1C)
144 at 5 m depth in mud, mounted in Fluoromount G[®], deposited at NMNH under accession
145 numbers: USNM1480337, USNM1480338.

146 *3.2 Non-type material*

147 159 additional specimens from all the previous localities, mounted for LM, deposited at
148 NMNH under accession numbers USNM1480339-USNM1480496; and 3 additional
149 specimens mounted for SEM and stored at the Invertebrates Collection of the
150 Meiofaunal Laboratory of the Universidad Complutense de Madrid (UCM), Spain.

151 *3.3 Diagnosis*

152 *Dracoderes* with middorsal spines on segments 2 and 9, paradorsal spines on segments
153 3–8, lateroventral spines on segments 3–4 and 6–9, lateral accessory spines on segment
154 5, lateroventral tubes on segments 2, 5 and 10 and laterodorsal tubes on segment 8.

155 *3.4 Etymology*

156 The species is named after the dragon “Spyro”, the main character of the platform video
157 games series *Spyro the Dragon*TM, originally released by the defunct Universal
158 Interactive Studios.

159 *3.5 Description*

160 See Table 2 for measurements and dimensions, and Table 3 for summary of spine, tube,
161 nephridiopore and sensory spot locations.

162 Head consists of retractable mouth cone and introvert (Figs. 2A-B, D and 4A-C).
163 Internal part of mouth cone with three rings of inner oral styles. Exact number,
164 arrangement and morphology of inner oral styles not determined. External part of mouth
165 cone with 9 outer oral styles (Fig. 2B). Outer oral styles alternate in size between longer
166 and shorter ones. Five long styles appear anterior to the odd numbered introvert
167 sections, whereas four shorter ones appear anterior to the even numbered ones, except in
168 the middorsal section 6 where a style is missing. Both longer and shorter styles with two
169 jointed subunits, terminating into a hook-like structure, and a basis with lateral,
170 pectinate fringes and a widened median area with bushy fringe tips (Fig. 2B). Introvert
171 with seven rings of scalids. Scalids with a long distal part and a shorter basal sheath.
172 Basal sheath laterally extending into long, filiform fringes (Figs. 2D and 4C). Nine
173 trichoscalids (Figs. 2D and 4C) distributed as single ones in sections 2, 4, 6, 8 and 10,
174 and as paired ones in sections 5 and 7. Exact number, arrangement and detailed
175 morphology of scalids not determined as they tended to be collapsed when mounted, so
176 further examination was not possible.

177 Neck with nine placids and a distinct joint between the neck and segment 1
178 (Figs. 2C and 3A-B); midventral and midlateral placids wider (17 μm wide at base) than
179 others (10-14 μm wide at base). Ventral placids close each other; subdorsal, laterodorsal
180 and midlateral placids separated by cuticular folds (Figs. 2C and 3A-B).

181 Trunk with eleven segments (Figs. 2A, 3A-B and 4A-B); segment 1 consists of
182 closed cuticular ring; segments 2-11 consist of one tergal and two sternal plates (Figs.

183 2A, 3A-B and 4A-B). Tergosternal junctions intracuticular (only visible with LM) (Fig.
184 2F). Midsternal junctions externally visible as conspicuous lines in both LM and SEM
185 (Figs. 2F, 3B and 4B, F-G). Cuticle of segments 1–8 with longitudinal ridges in dorsal,
186 lateral and ventral areas (Figs. 2A, E, 3A-B and 4A-B, D, F-G, I). Tergal anterior plates
187 middorsally bulging; posterior ones flattened, with tapering outline in lateral view (Fig.
188 4B). Sternal plates widest at segment 5, but almost constant in width throughout the
189 trunk, tapering at the last trunk segments (Figs. 2A, F, 3A-B and 4B). Sternal plates
190 relatively (MSW-5:TL average ratio = 30.5%), giving the animal a plump general
191 appearance (Figs. 2A, 3A-B and 4A-B). Cuticular hairs absent (except on sternal plates
192 of segment 11). Posterior margin of segments 1–2 serrated, with a convex midventral V-
193 shaped extension and rounded indentations without serrated edges in the lateroventral
194 position (Figs. 2E-F, 3A-B and 4F); posterior margin of remaining segments strongly
195 serrated without V-shaped extension, with rounded indentations without serrated edges
196 in the lateroventral position (Figs. 2E, F, 3A-B and 4A-B, F-G). Well-developed
197 pectinate fringes absent.

198 Segment 1 without spines or tubes. Pair of sensory spots in ventrolateral and
199 ventromedial positions, two pairs of sensory spots in subdorsal and laterodorsal
200 positions (Fig. 3A-B); sensory spots on this and remaining segments small, rounded,
201 with a ring of cuticular papillae surrounding a central pore (Fig. 4I).

202 Segment 2 with middorsal spine (Figs. 2E, 3A and 4A, D); dorsal spines on this
203 and remaining segments thin and acicular, composed of a basal sheath with two deep
204 incisions accompanied by a central pore, and an acicular end portion with smooth
205 margins (Fig. 4E). Trunk cuticles around the insertion points of the spines on this and
206 following segments with conspicuous subcuticular structures (Figs. 2E, F and 3A, B);
207 most basal part of the spine inside the segments' cuticle shows spherical, condyle-like
208 articulation, similar to a ball-and-socket articulation. Paired tubes present in
209 lateroventral position (Figs. 2F, 3B and 4F); tubes on this and remaining segments
210 short, flattened, stouter basally, distally with a median, longitudinal cleft surrounded by
211 two flat, membranous wings (Fig. 4H). Two pairs of sensory spots in subdorsal position
212 (Figs. 2E and 3A); paired sensory spots in ventrolateral, ventromedial and paraventral
213 positions (Figs. 2F and 3B).

214 Segment 3 with paradorsal spine located to the left or to the right (Figs. 2E, 3A
215 and 4A, D). Left or right displacement of paradorsal spines along the whole trunk varies

216 among specimens (Figs. 2E, 3A and 4A) within the same population, and there are no
217 apparent left/right preference correlated with sex or sampling location. Additional
218 spines in lateroventral position (Figs. 2F, 3B and 4F); trunk cuticle around the insertion
219 point of lateroventral acicular spines on this and following segments enforced, forming
220 conspicuous subcuticular lines longitudinally directed (Figs. 2F and 3B). Unpaired
221 sensory spots in middorsal and paradorsal positions, the latter located in a paradorsal
222 position opposite to the side of the dorsal spine on the same segment (Figs. 2E and 3A);
223 paired sensory spots in subdorsal, laterodorsal and ventrolateral positions (Figs. 2E-F
224 and 3A-B).

225 Segment 4 with paradorsal spine located on the opposite side of that on the
226 preceding segment (Figs. 2E, 3A and 4A, D). Additional spines in lateroventral position
227 (Figs. 2F, 3B and 4F). Unpaired sensory spots in middorsal and paradorsal positions, the
228 latter located in a paradorsal position opposite to the side of the dorsal spine on the
229 same segment (Figs. 2E and 3A); paired sensory spots in subdorsal, laterodorsal,
230 ventrolateral and ventromedial positions (Figs. 2E-F, 3A).

231 Segment 5 with paradorsal spine located on the opposite side of that on the
232 preceding segment (Figs. 2E and 3A). Additional spines in lateral accessory position
233 (Figs. 2F, 3B and 4G-H). Paired tubes present in lateroventral position (Figs. 2F, 3B and
234 4G-H). Arrangement of sensory spots identical with segment 3 (Figs. 2E-F and 3A-B).

235 Segment 6 with paradorsal spine located on the opposite side of that on the
236 preceding segment (Figs. 2E and 3A). In a single specimen, the paradorsal spines of this
237 and the subsequent segment occurred on the same side (*i.e.*, did not alternately shift
238 sides), which is a deviation of the general morphological pattern of the species (Fig.
239 4A). Additional spines in lateroventral position (Figs. 2F, 3B and 4G, J). Arrangement
240 of sensory spots identical with segment 3 (Figs. 2E-F and 3A-B).

241 Segment 7 similar to segment 4, except for the paradorsal spine and paradorsal
242 sensory spot located on the opposite side of those on the segment 4 (Fig. 3A).

243 Segment 8 with paradorsal spine located on the opposite side of that on the
244 preceding segment (Fig. 3A). Additional spines in lateroventral position (Figs. 2F, 3B
245 and 4G, J). Paired tubes in laterodorsal position (Figs. 3A and 4J). Unpaired sensory
246 spots in middorsal and paradorsal positions, the latter located in a paradorsal position

247 opposite to the side of the dorsal spine on the same segment (Fig. 3A); paired sensory
248 spots in subdorsal and ventrolateral positions (Figs. 2F and 3A-B).

249 Segment 9 with unpaired middorsal and paired lateroventral spines (Figs. 2F,
250 3A-B and 4A, G). Longitudinal cuticular ridges lacking dorsal, lateral and ventrally
251 (Figs. 3A-B and 4A-B). Pair of sensory spots in paradorsal, subdorsal, laterodorsal,
252 ventrolateral and ventromedial positions (Figs. 2F and 3A-B). Nephridiopores in lateral
253 accessory positions (Fig. 3B); pore not sieve-like, formed by a minute, posteriorly
254 directed opening with a few papillae.

255 Segment 10 lacking spines, with paired lateroventral tubes (Figs. 2G, 3B, D and
256 4K-L). Pair of sensory spots in paradorsal and subdorsal positions (Fig. 3A, C).

257 Segment 11 with lateral terminal spines (Figs. 2A, G, 3A-B and 4A-B, K-L).
258 Gonopores of females not observed. Males with three pairs of penile spines; dorsal one
259 longest, with very thick basis, smooth; medial one slightly shorter, attaching on the
260 basis of the longest penile spine; ventral one shortest, crenulated, attaching on the outer
261 lateral margin of the lateral terminal spine (Figs. 2H, 3C-D and 4L). Pair of sensory
262 spots on the tips of the tergal extensions, giving these extensions a nipple-like
263 appearance (Figs. 2G, 3A-D and 4K-L). Tergal extensions bulged, triangular, extending
264 well beyond sternal plates (Figs. 2G, 3A-D and 4A-B, K-L); dorsal side of tergal
265 extensions smooth (Fig. 3A, C), with ventral surface densely covered with short,
266 papillary hairs (Figs. 3B, D and 4K-L). Posterior margins of sternal plates slightly
267 rounded, without any projecting parts (Figs. 2G, 3B, D and 4K-L).

268 *3.6 Remarks on morphological features*

269 One of the examined specimens showed a modified alternate pattern of paradorsal
270 spines, possessing three consecutive spines in the same side of the paradorsal position
271 (Fig. 4A).

272 Two of the examined specimens carried ciliophoran epibionts attached to the
273 laterodorsal surface of the segment 9 (Fig. 5A-B).

274 *3.7 Associated kinorhynch fauna*

275 *Dracoderes spyro* sp. nov. appeared together with *Cristaphyes* sp (Cepeda et al., in
276 press), *Cristaphyes* cf. *longicornis* (Higgins, 1983), *Echinoderes astridae* Sørensen,
277 2014, *Echinoderes* sp (Cepeda et al., in press), *Echinoderes spinifurca* Sørensen et al.,

278 2005 and *Fujuriphyes* sp (Cepeda et al., in press) in Puerto Blanco (L2); with
279 *Cristaphyes* sp in Isabela Bay (L3); with *Fujuriphyes* sp in Puerto Plata (L1); and with
280 *Echinoderes* sp in Cabo Haitiano (L4).

281

282 4. Discussion

283 4.1 Taxonomy

284 *Dracoderes spyro* sp. nov., clearly belongs to the genus *Dracoderes* by the combination
285 of the following morphological features: mouth cone with 9 outer oral styles alternating
286 in size between longer and shorter ones, neck consisting of nine placids with the dorsal
287 and midlateral ones separated by cuticular folds, segment 1 of trunk composed of a ring
288 cuticular plate and remaining segments composed of one tergal and two sternal cuticular
289 plates, dorsal spines on segments 2–9 of which the first and the last ones appear in
290 middorsal position and the remaining ones in paradorsal position alternatingly laterally
291 displaced and males possessing three pairs of penile spines (Sørensen et al. 2012;
292 Yamasaki, 2015). *Dracoderes spyro* sp. nov. can be easily distinguished from its
293 congeners by the arrangement of the spines, tubes and the sensory spots locations,
294 namely, having two pairs of subdorsal sensory spots on segment 1 and a single
295 middorsal (perispinal) and paradorsal sensory spots on segments carrying paradorsal
296 spines, whereas the remaining *Dracoderes* species possess one pair of subdorsal (if
297 present in this position) sensory spots and a pair of perispinal sensory spots on segments
298 carrying paradorsal spines (Sørensen et al. 2012; Thomsen et al. 2013; Yamasaki,
299 2015).

300 Regarding the nature and arrangement of spines/tubes, the recently described *D.*
301 *toyoshioae* from Okinawa, Japan (northwest Pacific Ocean) shows most resemblance
302 with *D. spyro* sp. nov. Nevertheless, the description of *D. toyoshioae* was based on a
303 single adult female exoskeleton lacking most spines and tubes, only inferred by the
304 presence of the respective subcuticular structures. Thus, the author assumed the nature
305 of these spines/tubes, stating the need of additional specimens in order to better
306 determine the morphological characters of this species (Yamasaki, 2015). *Dracoderes*
307 *toyoshioae* is characterized by having lateroventral spines/tubes on segments 2–10,
308 lateral accessory spines/tubes on segments 2–8, ventrolateral acicular spines on segment
309 1 and dorsal cuticular structures (possibly spines) on segments 1–9 (Yamasaki, 2015),

310 while *D. spyro* sp. nov. also has lateroventral spines/tubes on segments 2–10 (tubes on
 311 segments 2, 5 and 10, and acicular spines on segments 3–4 and 6–9) but possesses
 312 lateral accessory spines only on segment 5, lacks ventrolateral acicular spines on
 313 segment 1 and has dorsal spines on segments 2–9. Furthermore, *D. spyro* sp. nov.
 314 possesses laterodorsal tubes on segment 8 which are absent in *D. toyoshioae*. The
 315 remaining congeners of the genus are characterized by having lateroventral spines/tubes
 316 on segments 5–9 or 5–10 (Adrianov and Malakhov, 1999; Sørensen et al. 2012;
 317 Thomsen et al. 2013; Yamasaki, 2015), while *D. spyro* sp. nov. also has lateroventral
 318 spines on segments 3 and 4. Another morphological feature that makes *D. spyro* sp.
 319 nov. easily recognizable, as previously mentioned, is the presence of laterodorsal tubes
 320 on segment 8, which are absent in the remaining known congeners.

321 Based on the morphology of the posterior margin of segment 1, *D. spyro* sp.
 322 nov. is similar to *D. abei*, *D. gallaicus* and *D. nidhug*, having this margin strongly
 323 serrated and extending midventrally to form a triangular expansion. However, *D. abei*
 324 and *D. gallaicus* are characterized by having the posterior margin of segment 1 with
 325 rounded indentations (not serrated) from lateroventral to ventrolateral positions,
 326 whereas *D. spyro* sp. nov. and *D. nidhug* only have these rounded indentations in the
 327 lateroventral position. Furthermore, *D. spyro* sp. nov. also possesses the posterior
 328 margin of segment 2 extending midventrally to form a triangular extension, which is
 329 absent in *D. abei*, *D. gallaicus* and *D. nidhug* (Sørensen et al. 2012; Thomsen et al.
 330 2013). On the other hand, *D. orientalis* and *D. toyoshioae* are characterized by having
 331 the posterior margin of segment 1 finely serrated, not extending midventrally (Adrianov
 332 and Malakhov, 1999; Yamasaki, 2015), whereas *D. snufkini* has long, extremely marked
 333 serrations on the ventral side (Yamasaki, 2015).

334 4.2 Key to species of *Dracoderes*

335 1 Middorsal subcuticular structure (possibly basal structure of spine) present on
 336 segment 1; ventrolateral spines on segment 1 present ... *D. toyoshioae*

337 - Middorsal subcuticular structure absent on segment 1; ventrolateral spines on segment
 338 1 absent ... 2

339 2 Middorsal spine on segment 2 absent; subdorsal tubes present on segment 2 ... *D.*
 340 *nidhug*

- 341 - Middorsal spine on segment 2 present; subdorsal tubes absent on segment 2 ...3
 342 3 Lateroventral spines/tubes present on segments 2-10; laterodorsal tubes on segment 8
 343 present ... *D. spyro* sp. nov
 344 - Lateroventral spines/tubes present on some segments from 2 to 10 but never on
 345 segments 3-4; laterodorsal tubes on segment 8 absent... 4
 346 4 Lateroventral tubes on segment 2 absent ... *D. orientalis*
 347 - Lateroventral tubes on segment 2 present ... 5
 348 5 Lateral accessory spines present on segment 5 ... *D. gallaicus*
 349 - Spines absent in lateral series on segment 5 ... 6
 350 6 Lateroventral tubes on segment 10 absent; primary pectinate fringe of segment 1
 351 strongly developed, with long, wide serrations on the ventral side not forming a V-
 352 shaped extension... *D. snufkini*
 353 - Lateroventral tubes on segment 10 present; primary pectinate fringe of segment 1
 354 scarcely developed, with short, rounded serrations on the ventral side forming a V-
 355 shaped

356 4.3 Distribution of the genus

357 Until the discovery of *D. gallaicus*, which was described from Galicia, northeastern
 358 Spain, eastern Atlantic Ocean (Sørensen et al. 2012), the genus *Dracoderes* was thought
 359 to be a kinorhynch taxon geographically limited to East Asia, as the only known species
 360 were *D. abei*, from Mukaishima yacht harbor, Japan (Higgins and Shirayama, 1990) and
 361 *D. orientalis* from Ulsan Bay, South Korea (Adrianov and Malakhov, 1999) (Fig. 1B,
 362 D). Later, additional three species of the genus were also described from the same area
 363 (Thomsen et al. 2013; Yamasaki, 2015), leaving *D. gallaicus* as the only *Dracoderes*
 364 species outside this area (Fig. 1B, D). With the description of *D. spyro* sp. nov. from
 365 Hispaniola Island, we extend the geographical distribution of the genus to American
 366 waters (Fig. 1A-C). Furthermore, this record marks the southernmost limit of the genus'
 367 distribution, which is still unknown from the Southern Hemisphere (Fig. 1A-D).

368

369 5. References

- 370 Adrianov, A.V., Malakhov, V.V., 1999. Cephalorhyncha of the world ocean, first ed.
371 KMK Scientific Press, Moscow.
- 372 Artois, T., Fontaneto, D., McInnes, S., Todaro, M.A., Sørensen, M.V., Zullini, A., 2011.
373 Ubiquity of microscopic animals? Evidence from the morphological approach in species
374 identification, in: Fontaneto, D. (Ed.), Biogeography of Microscopic Organisms: Is
375 Everything Small Everywhere? Cambridge University Press, Cambridge. pp. 244–283.
- 376 Cepeda, D., Sánchez, N., Pardos, F., in press. First extensive account of the phylum
377 Kinorhyncha from Haiti and the Dominican Republic (Caribbean Sea), with the
378 description of four new species. Mar. Biodivers., in press.
- 379 Claparède, A.R.E., 1863. Zur Kenntnis der Gattung *Echinoderes* Duj. Beobachtungen
380 über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von
381 Normandie angestellt. Verlag von Wilhelm Engelmann, Leipzig.
- 382 Dal Zotto, M., Di Domenico, M., Garraffoni, A., Sørensen, M.V., 2013. *Franciscideres*
383 gen. nov. – a new, highly aberrant kinorhynch genus from Brazil, with an analysis of its
384 phylogenetic position. Syst. Biodivers. 11, 303–321.
385 <https://doi.org/10.1080/14772000.2013.819045>.
- 386 Higgins, R.P., 1964. Three new kinorhynchs from the North Carolina Coast. B. Mar.
387 Sci. 14, 479–493. <https://doi.org/10.2307/3225864>.
- 388 Higgins, R.P., 1969. Indian Ocean Kinorhyncha, 2: Neocentrophyidae, a new
389 homalorhagid family. P. Biol. Soc. Wash. 82, 113–128.
- 390 Higgins, R.P., 1983. The Atlantic Barrier reef ecosystem at Carrie Bow Cay, Belize, II:
391 Kinorhyncha. Smithson. Contrib. Mar. Sci. 18, 1–131.
392 <https://doi.org/10.5479/si.01960768.18.1>.
- 393 Higgins, R.P., 1988. Kinorhyncha, in: Higgins, R.P.; Thiel, H. (Eds.), Introduction to
394 the study of meiofauna. Smithsonian Institution Press, Washington D.C., pp. 328–331.
- 395 Higgins, R.P., Shirayama, Y., 1990. Dracoderidae, a new family of the cyclorhagid
396 Kinorhyncha from the Inland Sea of Japan. Zool. Sci. 7, 939–946.
- 397 Kirsteuer, E., 1964. Zur Kenntnis der Kinorhynchen Venezuelas. Zool. Anz. 173, 388–
398 393.

- 399 Kozloff, E.N., 1972. Some aspects of development in *Echinoderes* (Kinorhyncha).
400 Trans. Am. Microscop. Soc. 91, 119–130. <https://doi.org/10.2307/3225404>.
- 401 Neuhaus, B., 2013. Kinorhyncha (=Echinodera), in: Schmidt-Rhaesa, A. (Ed.),
402 Handbook of Zoology, Gastrotricha, Cycloneuralia and Gnathifera, Volume 1
403 Nematomorpha, Priapulida, Kinorhyncha, Loricifera. De Gruyter, Hamburg, pp. 181–
404 350.
- 405 Neuhaus, B., Pardos, F., Sørensen, M.V., Higgins, R.P., 2014. New species of
406 *Centroderes* (Kinorhyncha: Cyclorhagida) from the Northwest Atlantic Ocean, life
407 cycle and ground pattern of the genus. Zootaxa 3901, 1–69.
408 <https://doi.org/10.11646/zootaxa.3901.1.1>.
- 409 Pardos, F., Sánchez, N., Herranz, M., 2016. Two sides of a coin: the phylum
410 Kinorhyncha in Panama. I) Caribbean Panama. Zool. Anz. 265, 3–25.
411 <https://doi.org/10.1016/j.jcz.2016.06.005>.
- 412 Sánchez, N., Pardos, F., Sørensen, M.V., 2014. A new kinorhynch genus, *Mixtophyes*
413 (Kinorhyncha: Homalorhagida), from the Guinea Basin deep-sea, with new data on the
414 family Neocentrophyidae. Helgol. Mar. Res. 68, 221–239.
415 <https://doi.org/10.1007/s10152-014-0383-6>.
- 416 Sørensen, M.V., 2006. New kinorhynchs from Panama, with a discussion of some
417 phylogenetically significant cuticular structures. Meiofauna Marina 15, 51–77.
- 418 Sørensen, M.V., 2008. A new kinorhynch genus from the Antarctic deep sea and a new
419 species of *Cephalorhyncha* from Hawaii (Kinorhyncha: Cyclorhagida: Echinoderidae).
420 Org. Divers. Evol. 8, 230.e1–230.e18. <https://doi.org/10.1016/j.ode.2007.11.003>.
- 421 Sørensen, M.V., 2013. Phylum Kinorhyncha. Zootaxa 3703, 63–66.
422 <https://doi.org/10.11646/zootaxa.3703.1.13>.
- 423 Sørensen, M.V., 2014. First account of echinoderid kinorhynchs from Brazil, with the
424 description of three new species. Mar. Biodivers. 44, 251–274.
425 <https://doi.org/10.1007/s12526-013-0181-4>.
- 426 Sørensen, M.V., Dal Zotto, M., Rho, H.S., Herranz, M., Sánchez, N., Pardos, F.,
427 Yamasaki, H., 2015. Phylogeny of Kinorhyncha based on morphology and two

428 molecular loci. PLoS ONE 10, e0133440.
429 <https://doi.org/10.1371/journal.pone.0133440>.

430 Sørensen, M.V., Heiner, I., Ziemer, O., 2005. A new species of *Echinoderes* from
431 Florida (Kinorhyncha: Cyclorhagida). Proc. Biol. Soc. Wash. 118, 499–508.
432 [https://doi.org/10.2988/0006-324X\(2005\)118\[499:ANSOEF\]2.0.CO;2](https://doi.org/10.2988/0006-324X(2005)118[499:ANSOEF]2.0.CO;2).

433 Sørensen, M.V., Herranz, M., Rho, H.S., Min, W.G., Yamasaki, H., Sánchez, N.,
434 Pardos, F., 2012. On the genus *Dracoderes* Higgins & Shirayama, 1990 (Kinorhyncha:
435 Cyclorhagida) with a redescription of its type species, *D. abei*, and a description of a
436 new species from Spain. Mar. Biol. Res. 8, 210–231.
437 <https://doi.org/10.1080/17451000.2011.615328>.

438 Sørensen, M.V., Pardos, F., 2008. Kinorhynch systematics and biology – an
439 introduction to the study of kinorhynchs, inclusive identification keys to the genera.
440 Meiofauna Marina 16, 21–73.

441 Thomsen, V.G., Rho, H.S., Kim, D., Sørensen, M.V., 2013. A new species of
442 *Dracoderes* (Kinorhyncha: Dracoderidae) from Korea provides further support for a
443 dracoderid-homalorhagid relationship. Zootaxa 3682, 133–142.
444 <https://doi.org/10.11646/zootaxa.3682.1.6>.

445 Yamasaki, H., 2015. Two new species of *Dracoderes* (Kinorhyncha: Dracoderidae)
446 from the Ryukyu Islands, Japan, with a molecular phylogeny of the genus. Zootaxa
447 3980, 359–378. <https://doi.org/10.11646/zootaxa.3980.3.2>.

448 Yamasaki, H., Hiruta, S.D., Kajihara, H., 2013. Molecular phylogeny of kinorhynchs.
449 Mol. Phylogenet. Evol. 67, 303–310. <https://doi.org/10.1016/j.ympev.2013.02.016>.

450 Yamasaki, H., Hiruta, S.D., Kajihara, H., Dick, M.H., 2014. Two kinorhynch species
451 (Cyclorhagida, Echinoderidae, *Echinoderes*) show different distribution patterns across
452 Tsugaru Strait, Northern Japan. Zool. Sci. 31, 421–429.
453 <https://doi.org/10.2108/zs140011>.

454 Zelinka, K., 1896. Demonstration von Tafeln der Echinoderes – Monographie. Verh.
455 Dtsch. Zool. Ges. 6, 197–199.

456

457 ACKNOWLEDGEMENTS

458 We would like to thank Dr Jon Norenburg and Katie Ahlfeld for loaning the material
459 that made the present study possible.

460 FUNDING SOURCES

461 Cepeda was supported by a predoctoral fellowship of the Complutense University of
462 Madrid (CT27/16-CT28/16).

463 The authors declare no conflicts of interest.

464

465 TABLES

466 Table 1. Data on sampling localities and habitat of the collected specimens.

Station code	Location	Geographical coordinates	Sampling date	Sediment	Depth (m)
L1	Puerto Plata, Dominican Republic	19° 48' 12" N 70° 42' 00" W	02/11/1980	Sandy mud	5
L2	Puerto Blanco, Dominican Republic	19° 54' 24" N 70° 56' 24" W	03/11/1980	Silty mud	3
L3	Isabela Bay, Dominican Republic	19° 53' 18" N 71° 05' 36" W	04/11/1980	Silty mud	4
L4	Cabo Haitiano, Haiti	19° 46' 12" N 72° 11' 00" W	10/11/1980	Mud	3–5
L5	Puerto Príncipe, Haiti	18° 32' 21" N 72° 20' 05" W	15/03/1976	Mud	5

467

468 Table 2. Measurements of adult *Dracoderes spyro* sp. nov. from Hispaniola Island,
469 including number of measured specimens (*n*), mean and standard deviation (SD).
470 Because there were no remarkable differences in sizes or dimensions between the two
471 sexes or sampling locations, measurements are not shown by sexes or populations.
472 Abbreviations: ac, acicular spine; LA, lateral accessory, LD, laterodorsal; LTS, lateral
473 terminal spine; LV, lateroventral spine/tube; MD, middorsal spine; MSW-5, maximum
474 sternal width (on segment 5); PD, paradorsal spine; S, segment lengths; SW-10,
475 standard width (on segment 10); TL, total length of trunk; tu, tube.

Character	Range	Mean (SD; <i>n</i>)
TL (μm)	158.8–275.3	196.8 (25.8; 34)
MSW-5 (μm)	47.8–63.9	59.3 (3.0; 34)
MSW-5/TL (%)	22.6–33.6	30.5 (3.0; 34)
SW-10 (μm)	32.4–49.6	43.4 (5.0; 34)

SW-10/TL (%)	14.0–26.6	22.4 (3.6; 34)
S1 (µm)	28.7–37.6	33.9 (2.1; 34)
S2 (µm)	18.8–30.2	27.0 (2.9; 34)
S3 (µm)	18.8–33.4	25.5 (3.9; 34)
S4 (µm)	21.1–35.8	31.8 (4.0; 34)
S5 (µm)	24.5–37.9	33.0 (3.6; 34)
S6 (µm)	24.1–39.8	33.2 (3.9; 34)
S7 (µm)	22.2–38.8	31.1 (4.0; 34)
S8 (µm)	23.7–35.6	28.9 (3.0; 34)
S9 (µm)	20.0–37.2	27.7 (3.3; 34)
S10 (µm)	17.1–30.6	25.7 (3.0; 34)
S11 (µm)	18.8–30.5	25.0 (2.8; 34)
MD 2 (ac) (µm)	15.9–36.4	29.3 (4.0; 34)
PD 3 (ac) (µm)	21.7–37.9	32.0 (4.1; 34)
PD 4 (ac) (µm)	19.7–41.9	34.5 (5.2; 34)
PD 5 (ac) (µm)	26.4–45.2	36.0 (4.7; 34)
PD 6 (ac) (µm)	14.9–38.7	33.9 (4.8; 33)
PD 7 (ac) (µm)	23.7–41.6	31.4 (4.2; 33)
PD 8 (ac) (µm)	17.6–34.4	28.3 (3.9; 32)
MD 9 (ac) (µm)	20.9–34.1	29.0 (3.1; 30)
LV 2 (tu) (µm)	5.5–13.2	10.1 (1.6; 34)
LV 3 (ac) (µm)	14.7–26.6	19.8 (2.5; 34)
LV 4 (ac) (µm)	14.0–26.0	21.6 (2.7; 34)
LV 5 (tu) (µm)	6.3–15.7	9.6 (2.0; 34)
LA 5 (ac) (µm)	18.9–29.0	23.4 (2.5; 34)
LV 6 (ac) (µm)	17.4–28.6	23.1 (2.6; 34)
LV 7 (ac) (µm)	16.4–29.9	23.8 (3.1; 34)
LD 8 (tu) (µm)	5.1–9.9	7.5 (1.1; 20)
LV 8 (ac) (µm)	18.5–31.5	23.7 (3.5; 34)
LV 9 (ac) (µm)	16.2–30.5	24.3 (3.5; 34)
LV 10 (tu) (µm)	6.0–11.3	8.4 (1.6; 20)
LTS (µm)	108.2–152.5	130.8 (9.7; 34)

476

477 Table 3. Summary of nature and arrangement of sensory spots, spines and tubes in
478 *Dracoderes spyro* sp. nov. Abbreviations: LA, lateral accessory; LD, laterodorsal; LV,
479 lateroventral; MD, middorsal; PD, paradorsal; PV, paraventral; SD, subdorsal; VL,
480 ventrolateral; VM, ventromedial; ac, acicular spine; lts, lateral terminal spine; m, male
481 condition of sexually dimorphic character; ne, nephridiopore; ps, penile spine; ss,
482 sensory spot; tu, tube; * indicates unpaired structures.

Segment	MD	PD	SD	LD	LA	LV	VL	VM	PV
1			ss	ss ss			ss	ss	
			ss						
2	ac		ss			tu	ss	ss	ss
			ss						
3	ss	ac* ss*	ss	ss		ac	ss		
4	ss	ss* ac*	ss	ss		ac	ss	ss	
5	ss	ac* ss*	ss	ss	ac	tu	ss		
6	ss	ss* ac*	ss	ss		ac	ss		
7	ss	ac* ss*	ss	ss		ac	ss	ss	
8	ss	ss* ac*	ss	tu		ac	ss		
9	ac	ss	ss	ss	ne	ac	ss	ss	
10		ss	ss			tu			
11			ss			lts, psx3 (m)			

483

484 FIGURE LEGENDS

485 **Fig. 1.** Map showing the sampling locations of *Dracoderes spyro* sp. nov. in Hispaniola
 486 Island, Caribbean Sea, western Atlantic Ocean (A, C) and the distribution of the
 487 remaining species of the genus (B, D)

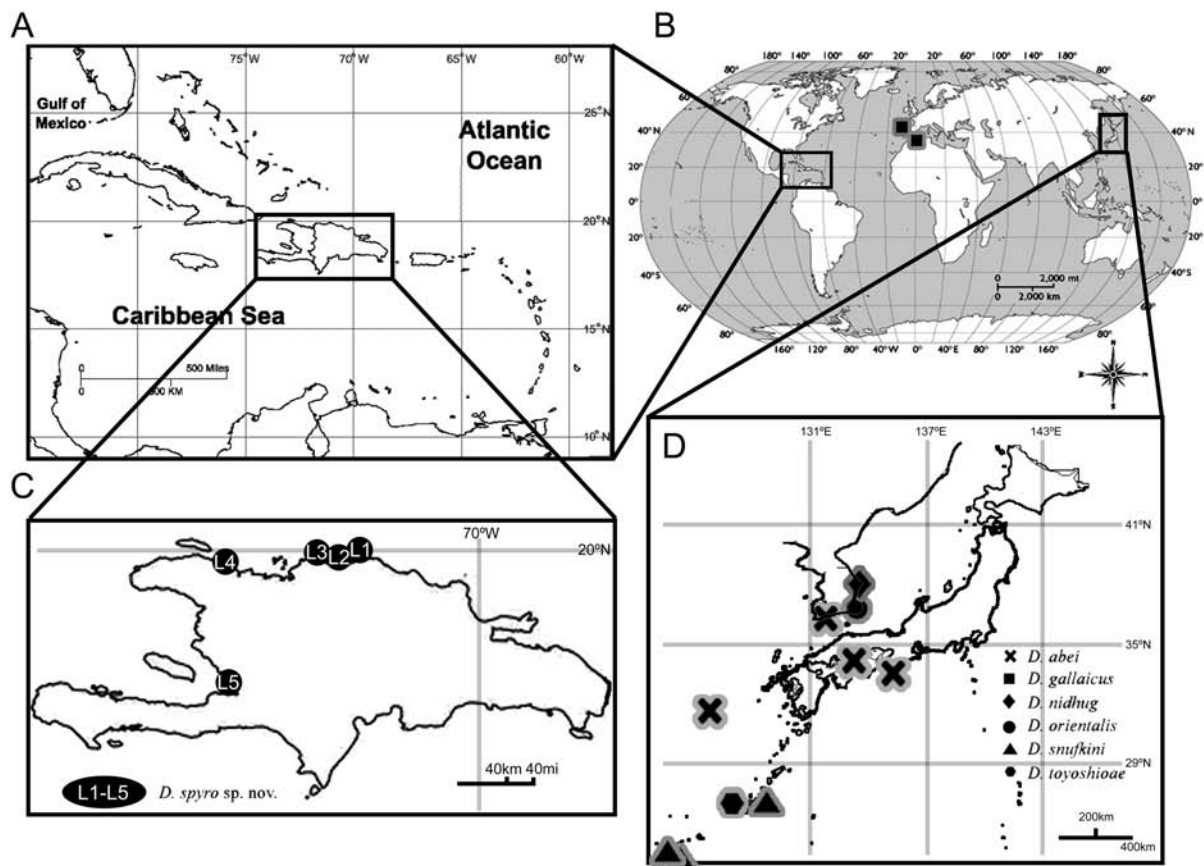
488 **Fig. 2.** Light micrographs showing trunk overview and details in the head and the
 489 sexual dimorphism of female holotype USNM1480327 (A-G) and male paratype
 490 USNM140333 (H) of *Dracoderes spyro* sp. nov.. (A) Ventral overview of head and
 491 trunk; (B) Mouth cone, showing the outer oral styles; arrow indicates the median area
 492 bushy fringe tips; (C) Neck, showing the placids; arrowhead indicates cuticular folds;
 493 (D) Introvert, showing the scalids; arrow indicates the filiform fringes of the basal
 494 region; (E) middorsal, paradorsal, subdorsal and laterodorsal regions of tergal plates of
 495 segments 2-7 (F) lateroventral, ventrolateral and ventromedial regions of tergal and
 496 sternal plates of segments 2-10 (G) lateroventral, ventrolateral and ventromedial
 497 regions of tergal and sternal plates of segments 10-11; (H) posterior end of the trunk,
 498 showing the sexually dimorphic male penile spines. Abbreviations: bp, basal part of
 499 outer oral style; hde, hook-like distal end of outer oral style; las, lateral accessory spine;
 500 lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal
 501 spine; pds, paradorsal spine; pl, placid; ps, penile spines; sbp, scalid basal part; sdp,
 502 scalid distal part; sus, subcuticular line; te, tergal extension; ts, trichoscalid; sensory

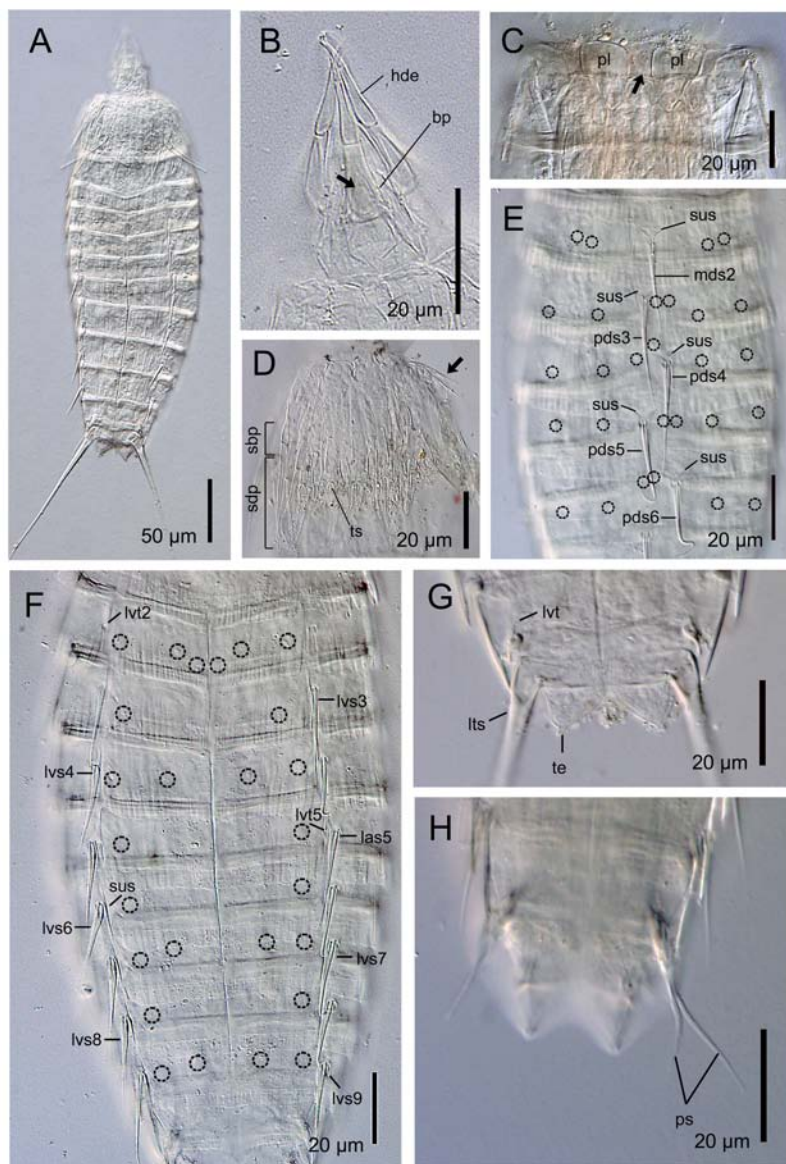
503 spots are marked as dotted-line circles; numbers after abbreviation indicate the
504 corresponding segment.

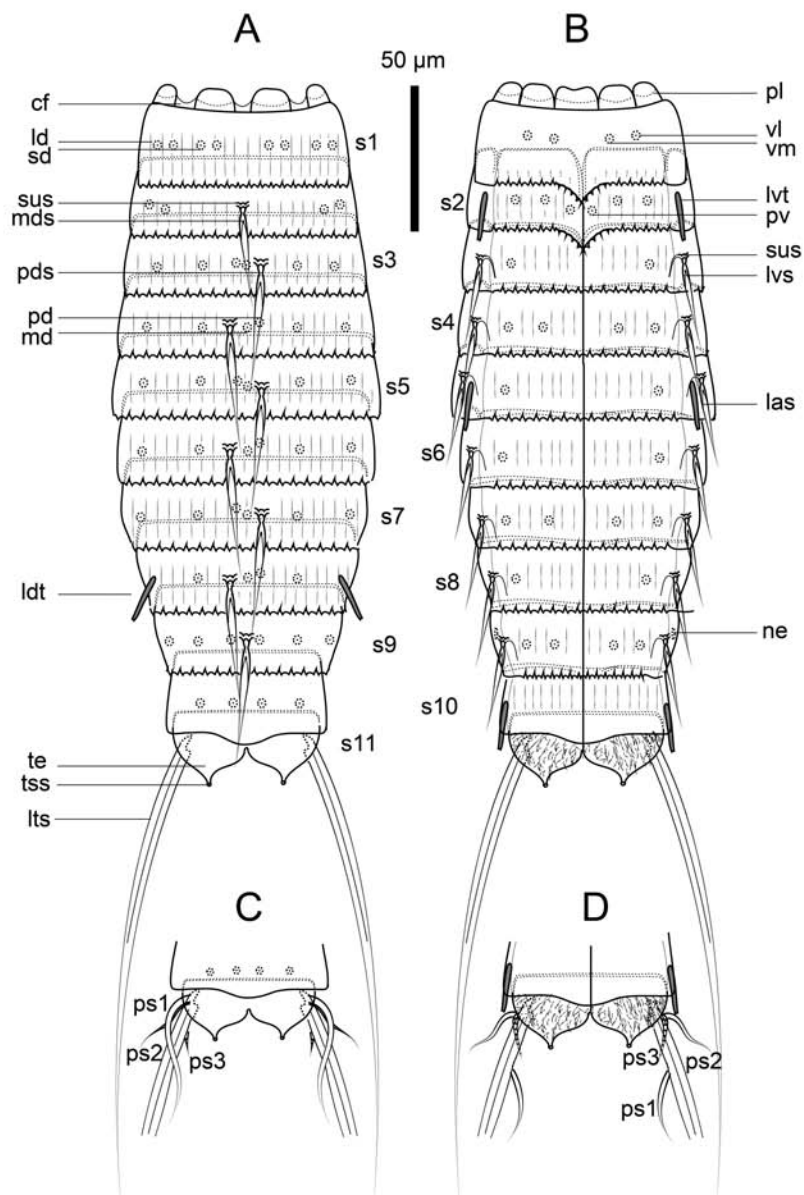
505 **Fig. 3.** Line-art illustrations of *Dracoderes spyro* sp. nov. (A) Female, dorsal view; (B)
506 Female, ventral view; (C) Male, segments 10–11, dorsal view; (D) Male, segments 10–
507 11, ventral view. Abbreviations: cf, cuticular folding; las, lateral accessory spine; ld,
508 laterodorsal sensory spot; ldt, laterodorsal tube; lts, lateral terminal spine; lvs,
509 lateroventral spine; lvt, lateroventral tube; md, middorsal sensory spot; mds, middorsal
510 spine; ne, nephridial pore; pd, paradorsal sensory spot; pds, paradorsal spine; pl, placid;
511 ps, penile spines followed by penile spine number; pv, paraventral sensory spot; s,
512 segment followed by segment number; sd, subdorsal sensory spot; sus, subcuticular
513 line; te, tergal extension; tss, terminal sensory spot; vm, ventromedial sensory spot; vl,
514 ventrolateral sensory spot.

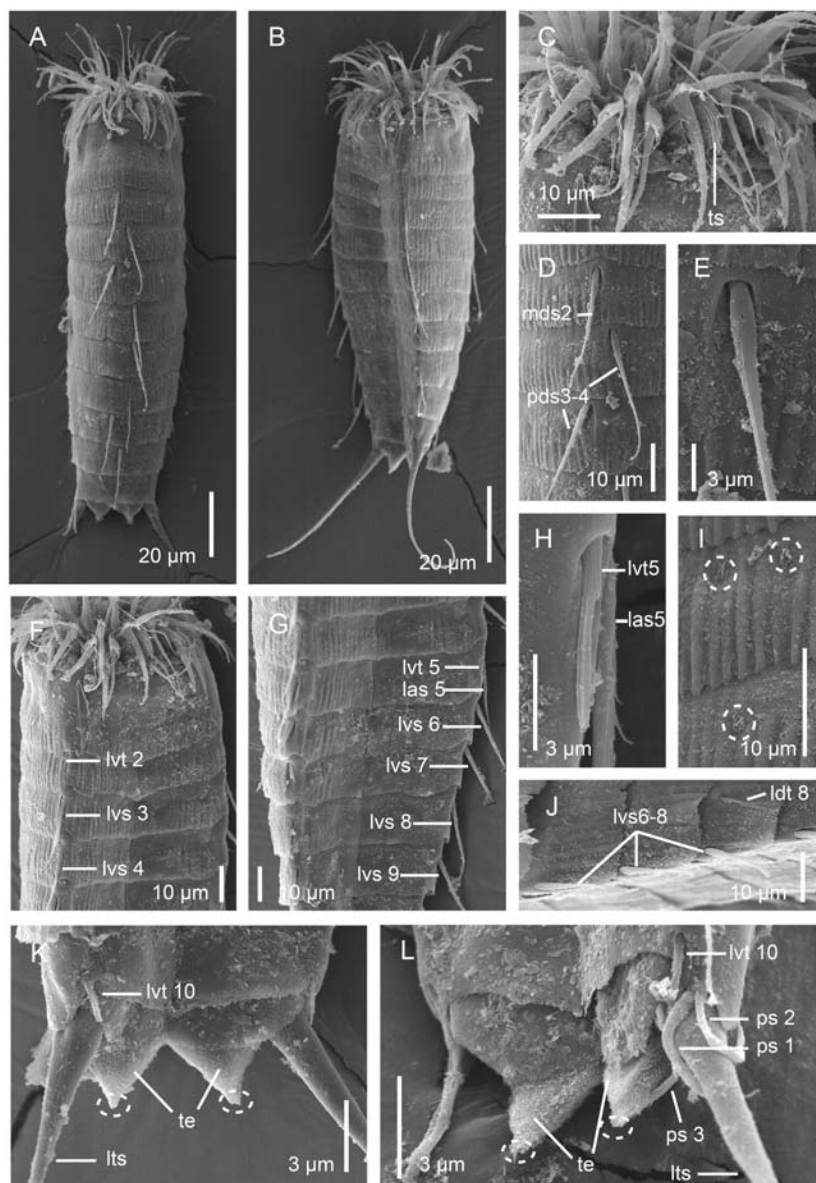
515 **Fig. 4.** Scanning electron micrographs showing overviews and details in the cuticular
516 trunk morphology of a non-type male (A, C–J and L) and a non-type female (B and K)
517 of *Dracoderes spyro* sp. nov. (A) Dorsal overview of trunk; (B) lateral and ventral
518 overviews of trunk; (C) introvert partially everted, showing some scalids; (D) middorsal
519 and paradorsal regions of tergal plates of segments 2–4; (E) detail of a paradorsal spine
520 of segment 3; (F) lateroventral, ventrolateral and ventromedial regions of tergal and
521 sternal plates of segments 1–4; (G) lateroventral, ventrolateral and ventromedial regions
522 of tergal and sternal plates of segments 5–9; (H) detail of a lateroventral tube and a
523 lateral accessory spine of segment 5; (I) detail of subddorsal and laterodorsal sensory
524 spots of segments 2–3; (J) laterodorsal and lateroventral regions of tergal plates of
525 segments 6–8; (K) lateroventral, ventrolateral and ventromedial regions of tergal and
526 sternal plates of segments 10–11 of a female; (L) lateroventral, ventrolateral and
527 ventromedial regions of tergal and sternal plates of segments 10–11 of a male.
528 Abbreviations: las, lateral accessory spine; ldt, laterodorsal tube; lts, lateral terminal
529 spine; lvt, lateroventral tube; lvs, lateroventral spine; mds, middorsal spine; pds,
530 paradorsal spine; ps, penile spine; te, tergal extension; ts, trichoscalid; sensory spots are
531 marked as dotted-line circles; numbers after abbreviations indicate the corresponding
532 segment.

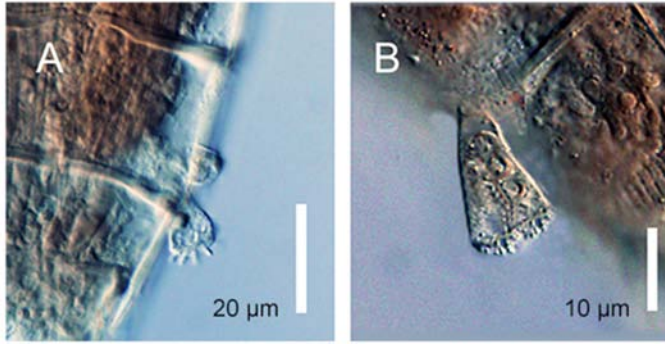
533 **Fig. 5.** Light micrographs showing details of epibiontic Ciliophora on the cuticle
534 surface of *Dracoderes spyro* sp. nov. on the laterodorsal position of segment 9. (A)
535 Cuticle of segment 9 showing the attached epibionts; (B) Detail of a epibiont.











ACCEPTED MANUSCRIPT