
First report of the family Zelinkaderidae (Kinorhyncha: Cyclorhagida) for the Caribbean Sea, with the description of a new species of *Triodontoderes* Sørensen and Rho, 2009 and an identification key for the family

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Abstract :

A new species of Kinorhyncha, *Triodontoderes lagahoo* sp. nov., is described from Tobago Island, Caribbean Sea (western Atlantic Ocean) from a coastal, sandy habitat using both light and scanning electron microscopy. The species is characterized by the presence of middorsal acicular spines on segments 1–11 (that on segment 10 crenulated in males), laterodorsal crenulated spines on segment 10 only in males, lateroventral acicular spines on segments 3–4 and 6–8 (lateroventral spines also on segment 10 in females), lateroventral cuspidate spines on segments 5 and 9, lateral accessory acicular spines on segments 5 and 9, lateral accessory cuspidate spines on segment 8, ventrolateral acicular spines on segment 2 and ventrolateral cuspidate spines on segment 2. Females furthermore possess short papillae in ventrolateral position on segment 8 and ventromedial position on segment 9. The absence of cuspidate spines in lateral accessory position on segment 6 easily distinguishes *T. lagahoo* sp. nov. from the single known congener, *T. anulap*. Moreover, also the arrangement of female papillae and sensory spots differ between the species. The finding of a new species of *Triodontoderes* in the Caribbean Sea is the first report of the genus for American waters and the Atlantic Ocean since its original description. Additionally, a dichotomous key for identification of the family Zelinkaderidae to species level, as well as systematic remarks on some morphological characters of the new species are included herein.

Keywords : Kinorhynchs, Biodiversity, Meiofauna, Morphology, Taxonomy, *Triodontoderes lagahoo* sp. nov.

38 1. Introduction

39 Kinorhynchs are small-sized, holobenthic, free-living, marine invertebrates that inhabit
40 sandy and muddy sediments (Higgins and Thiel, 1988; Neuhaus, 2013; Sørensen and
41 Pardos, 2008). Currently, the phylum comprises near 300 species distributed worldwide
42 and arranged in two classes, Allomalorhagida and Cyclorhagida (Sørensen et al. 2015).
43 The cyclorhagid family Zelinkaderidae was originally erected by Higgins (1990) to
44 accommodate the newly described species *Zelinkaderes floridensis* Higgins, 1990 from
45 Fort Pierce, Florida (western Atlantic Ocean) and the reassigned *Cateria submersa*
46 (Gerlach, 1969), originally described from the North Sea. Not much later, *Zelinkaderes*
47 *klepali* Bauer-Nebelsick, 1995 was described from the Red Sea and, more recently,
48 *Zelinkaderes brightae* Sørensen et al., 2007 also from Fort Pierce. Two years later, the
49 second genus of the family was erected with the description of *Triodontoderes anulap*
50 Sørensen and Rho, 2009 from the Chuuk Islands, Micronesia (western Pacific Ocean).
51 Finally, *Zelinkaderes yong* Altenburger et al., 2015 was described from the Korean
52 Peninsula (western Pacific Ocean).

53 Zelinkaderid kinorhynchs are morphologically characterized by having an
54 introvert with one ring of spinoscalids followed by three or four regular scalids rings,
55 fourteen or sixteen distally tripartite placids, trunk vermiform and conspicuously
56 circular in cross-section, at least segments 5 to 11 composed of a single tergal plate with
57 midventral joint, acicular spines present in dorsal and lateral positions, cuspidate spines
58 present in lateral position on some segments, segment 11 with lateral terminal, lateral
59 terminal accessory and midterminal spines, at least some large and oval sensory spots
60 with two pores in the anterior body region, scale-like cuticular hairs medially depressed
61 and males with crenulated spines on segment 10 (Sørensen and Rho, 2009). In the
62 present contribution, a new *Triodontoderes* species, *Triodontoderes lagahoo* sp. nov., is
63 described from Tobago Island (Caribbean Sea) using light and scanning electron
64 microscopes. This finding is the first report of the genus for American waters and the
65 western Atlantic Ocean since its original description from the Chuuk Archipelago,
66 Pacific Ocean (Sørensen and Rho, 2009). Additionally, a key to species level
67 identification for Zelinkaderidae is included.

68

69 2. Material and methods

70 Specimens of *Triodontoderes lagahoo* sp. nov. were collected at Tyrrel's Bay, Tobago
71 Island, Caribbean Sea (western Atlantic Ocean): 11°18'00"N, 60°30'00"W (Fig. 1).
72 The Archipelago of Trinidad and Tobago is situated at the verge of the Lesser Antilles
73 (Fig. 1) and is part of the so-called Southern Caribbean marine ecoregion. Sampling was
74 originally done on 13 May 1991 by Dr R. P. Higgins using a meiobenthic dredge
75 (Higgins and Thiel, 1988) at 5 m depth in very fine sand. After sampling, meiofauna
76 was extracted from sediment using the bubble and blot method defined by Higgins
77 (1964). Meiofaunal specimens were fixed in 4% formalin, preserved in Carosafe[®] and
78 deposited in unsorted vials at the Smithsonian National Museum of Natural History
79 (NMNH), Washington.

80 The aforementioned vials were loaned to the authors for the present study. Fixed
81 kinorhynchs were picked up under a Motic[®] SMZ-168 stereo zoom microscope with the
82 help of an Irwin loop and washed with distilled water in order to remove formalin. For
83 light microscopy (LM), specimens were dehydrated through a graded series of 25%,
84 50%, 75% and 100% glycerin and finally mounted on a glass slide in Fluoromount G[®]
85 sealed with Depex[®]. Mounted specimens were studied and photographed using an
86 Olympus[®] BX51-P microscope equipped with differential interference contrast (DIC)
87 optics and an Olympus[®] DP-70 camera. Morphological measurements were obtained
88 with Olympus cellSens[®] software. For scanning electron microscopy (SEM), specimens
89 were transferred to 70% ethanol and then progressively dehydrated through a series of
90 80%, 90%, 95% and 100% ethanol. Specimens were sonically cleaned during 5–7 s.
91 Hexamethyldisilazane (HMDS) was used for chemical drying through a HMDS-ethanol
92 series. Specimens were coated with gold and mounted on aluminium stubs to be
93 examined with a JSM 6335-F JEOL SEM at the ICTS Centro Nacional de Microscopía
94 Electrónica (Complutense University of Madrid, Spain). Line drawings, images and
95 plates plates composition were done using Adobe[®] Photoshop CC-2014 and Illustrator
96 CC-2014 software.

97

98 **3. Results**

99 *Taxonomic account*

100 Class **Cyclorhagida** (Zelinka, 1896) Sørensen et al., 2015

101 Order **Kentrorhagata** Sørensen et al., 2015

102 Family **Zelinkaderidae** Higgins, 1990

103 Genus **Triodontoderes** Sørensen and Rho, 2009

104 ***Triodontoderes lagahoo*** sp. nov.

105 (Figs. 2–6 and Tabs. 1–3)

106 The species was registered in Zoobank under: zoobank.org:pub:7699F0E0-3F1B-451C-
107 8E43-EB548773D1C0.

108 *3.1 Type material*

109 Holotype, adult female, collected on 13 May 1991 at Tyrrel's Bay, Tobago Island,
110 western Atlantic Ocean: 11°18'00"N, 60°30'00"W at 5 m depth in very fine sand;
111 mounted in Fluoromount G[®], deposited at NMHN under accession number: XXXXX.
112 Paratypes, seven adult males and four adult females, all of them with same collecting
113 data as holotype, mounted in Fluoromount G[®], deposited at NMHN under accession
114 numbers: XXXXX–XXXXX.

115 *3.2 Non-type material*

116 Five additional specimens with same collecting data as holotype and paratypes,
117 mounted for SEM, deposited at the Invertebrates Collection of the Meiofaunal
118 Laboratory at the Universidad Complutense de Madrid (UCM), Spain.

119 *3.3 Diagnosis*

120 *Triodontoderes* with middorsal acicular spines on segments 1–11 (that on segment 10
121 crenulated in males), laterodorsal crenulated spines on segment 10 only in males,
122 lateroventral acicular spines on segments 3–4 and 6–8 (lateroventral spines also on
123 segment 10 in females), lateroventral cuspidate spines on segments 5 and 9, lateral
124 accessory acicular spines on segments 5 and 9, lateral accessory cuspidate spines on
125 segment 8, ventrolateral acicular spines on segment 2 and ventrolateral cuspidate spines
126 on segment 2. Females with short papillae in ventrolateral position on segment 8 and
127 ventromedial position on segment 9. Neck and trunk segments superficially covered by
128 small, scale-like, medially depressed cuticular hairs arranged in slightly irregular
129 longitudinal bands. Primary pectinate fringe short on segment 1, strongly serrated with

130 bifid tips on the remaining trunk segments. Dorsal extensions of segment 11 elongated,
131 distally pointed, horn-like; ventral extensions of segment 11 short, wide, distally
132 rounded.

133 *3.4 Etymology*

134 The species is named after the mythical shapeshifting monster “Lagahoo” (also known
135 as “Ligahoo” or “Lugarhou”) from the folklore of Trinidad and Tobago, the location
136 where the species was found. According to the legend, Lagahoo can shapeshift into
137 various creatures, which resembles the different trunk shapes reported herein for the
138 species.

139 *3.5 Description*

140 See Tables 1–2 for measurements and dimensions, and Table 3 for summary of acicular,
141 crenulated and cuspidate spines, papillae and sensory spots location.

142 Head with narrow, retractable mouth cone and introvert with five rings plus an
143 extra ring of trichoscalids attached to the neck (Figs. 3 and 4A-H). Mouth cone
144 presumably with four rings of oral styles, incompletely observed (Fig. 3). Ring of
145 helioscalids and the first ring of inner oral styles (rings -03 and -02) barely visible in the
146 examined specimens. Second ring of inner oral styles (ring -01) with ten styles (Fig. 3).
147 Observed inner oral styles of ring -01 composed of a single unit, with a trapezoidal,
148 enlarged base bearing a short fringe and a triangular, hook-like, inwards-pointed, distal
149 tip (Fig. 4C). Ring 00 with nine equally-sized outer oral styles that morphologically
150 resemble the inner oral styles but much longer and flexible at their distal tips, with a
151 fringe and paired spines arising from their bases (Figs. 3, 4C-D and 6B). Outer oral
152 styles composed of a single unit, located anterior to each introvert sector, except in the
153 middorsal section 6 where a style is missing (Fig. 3). Triangular, cuticular thickenings
154 flanking the outer oral styles' bases (Fig. 4D). Posterior part of mouth cone elongated,
155 forming a long tube (Fig. 4A-B).

156 Heads were only everted in the holotype (mounted for LM) and one paratype,
157 (mounted for SEM), which disabled precise examination of the arrangement and
158 morphology of scalids in the remaining specimens. Ring 01 with ten primary
159 spinoscalids (Fig. 3) composed of a basal sheath and a distal elongated end-piece; basal
160 sheath equipped with a median dense fringe with long tips (Fig. 4E-F). Tips of the

161 fringe slightly protrude outwards when the introvert is retracted inside the trunk, and lay
162 on top of the primary spinoscalids when the introvert is completely everted (Fig. 4F).
163 Ring 02 with fifteen regular-sized scalids, arranged as two in the odd-numbered sectors
164 and one in the even-numbered sectors (Figs. 3 and 4G-H). Scalids on this and remaining
165 rings are composed of a basal sheath and a distal, elongated, hook-like end-piece (Fig.
166 4G-H). Ring 03 with fifteen regular-sized scalids, arranged as one in the odd-numbered
167 sectors and two in the even-numbered sectors (Figs. 3 and 4G-H). Ring 04 similar to
168 ring 02 (Figs. 3 and 4G-H). Ring 05 similar to ring 03 (Figs. 3 and 4G-H). The location
169 of scalids in rings 01–05 follows a strict pattern around the introvert, and each sector
170 carries six scalids, five following a quincunx arrangement plus a single scalid that
171 appears anterior (in even-numbered sectors) or posterior (in odd-numbered sectors)
172 (Figs. 3 and 4G-H).

173 Neck with fourteen inconspicuous, elongated, distally tripartite, soft placids of
174 uniform size; placids are fused with the segment 1 and a transverse articulation between
175 placids and segment 1 is missing (Figs. 2A-B, 4A-B and 6A, C). Fourteen small,
176 triangular trichoscalids attached to the neck, whose occurrence is directly associated
177 with the placids position (Figs. 3 and 4E). Trichoscalid plates absent.

178 Trunk vermiform, circular in cross-section, spindle-shaped, composed of eleven
179 segments (Figs. 2A-B, 4A-B and 6A). Body outline variable from longer and slender to
180 shorter and chubby (Figs. 2A-C and 4A-B, J-L). Cuticle along the whole trunk thin, soft
181 and flexible, making the intersegmental junctions barely visible. First trunk segment
182 with one tergal and one sternal plate (Fig. 2A-B); segments 2–4 with one tergal and two
183 sternal plates with lateroventral and midventral joints (Fig. 2A-B); remaining segments
184 with a single tergal plate with midventral joint (Fig. 2A-B, D-E). Segment 1 fused with
185 the neck, without distinct articulation (Figs. 2A-B, 5A and 6A, C). Neck and all trunk
186 segments superficially covered by small, scale-like, medially depressed cuticular hairs
187 arranged in slightly irregular longitudinal bands (Figs. 2A-B, D-E and 6D, G, I);
188 cuticular hairs absent at ventrolateral and ventromedial regions of trunk (Fig. 2B, E).
189 Trunk segments with longitudinal folds on the dorsal and lateral sides that are most
190 certainly a fixation artefact (Figs. 2A, C, D, 4A-B, 5A-B, D-E, G-H and 6A). Posterior
191 margin of segments straight, with long primary pectinate fringes (except that of segment
192 1 that is conspicuously shorter); primary pectinate fringes with very weak serration on
193 first segment, with strong serration and bifid tips on remaining segments (Figs. 2A-B,

194 D-E and 4I). Secondary pectinate fringes on segments 2–11 less conspicuous than
195 primary ones but also long, ventrally extending near the posterior margin of segment,
196 also serrated and with bifid tips (Figs. 2A-B, D-E and 4I).

197 Segment 1 with a small, very short, extremely flexible acicular spine in
198 middorsal position (Figs. 2A and 5A). Acicular spines on this and following segments
199 are composed of a single flexible, elongated piece with pointed tip that basally
200 articulates in a swollen cuticular thickening (Figs. 2A-B, D-E, 4I, 5A-K and 6A, D-F,
201 H, J); basal swollen articulation of acicular spines with paired cuticular protuberances
202 that flank the spine (Figs. 2A and 5A). Paired sensory spots in paradorsal position, on
203 top of the protuberances beside the spine's basal articulation (Figs. 2A and similar to
204 6D). Sensory spots on this and most following segments are composed of an oval patch
205 of numerous micropapillae surrounding a central pore (similar to 6G).

206 Segment 2 with acicular spine in middorsal position (Figs. 2A and 5A); paired
207 small, very short, extremely flexible acicular spines in ventrolateral position (Figs. 2B
208 and 5B). Paired cuspidate spines also in ventrolateral position, but located between
209 tergosternal junction and acicular spine (Figs. 2B and 5B). Cuspidate spines on this and
210 following segments are composed of a single syringe-like piece with broadened base, of
211 which the latter constitutes more than 50% of the spine dimension, basally articulated
212 (Figs. 2B, E, 5B, E, H and 6E). Paired sensory spots in paradorsal position, similar to
213 those of the precedent segment (Figs. 2A and 5A).

214 Segment 3 with acicular spine in middorsal position and paired acicular spines in
215 lateroventral position (Figs. 2A-B and 5A-B). Paired sensory spots in paradorsal,
216 laterodorsal and ventrolateral positions (Figs. 2A-B and 5A-B).

217 Segment 4 with acicular spine in middorsal position and paired acicular spines in
218 lateroventral position (Figs. 2A-B and 5D-E). Paired sensory spots in paradorsal,
219 laterodorsal, midlateral and ventrolateral positions (Figs. 2A-B, 5D and 6G). Midlateral
220 sensory spots on this and following segments are composed of an oval patch of
221 numerous micropapillae surrounding two pores (similar to Fig. 6I).

222 Segment 5 with acicular spine in middorsal position and paired acicular spines in
223 lateral accessory position (Figs. 2A-B, 5D-E and 6E); paired cuspidate spines in
224 lateroventral position (Figs. 2B, 5E and 6E). Paired sensory spots in paradorsal,
225 laterodorsal, midlateral and ventrolateral positions (Figs. 2A-B, 5D-E and 6G).

226 Segment 6 with arrangement of spines and sensory spots similar to segment 4
227 (Figs. 2A-B, 5D-E and 6F, I).

228 Segment 7 with arrangement of spines and sensory spots similar to segments 4
229 and 6 (Figs. 2A-B, 5D, H and 6F).

230 Segment 8 with acicular spine in middorsal position and paired acicular spines in
231 lateroventral position (Figs. 2A-B, D-E, 5G-H and 6D, F); paired cuspidate spines in
232 lateral accessory position (Figs. 2B, E and 5H). Paired sensory spots in paradorsal,
233 laterodorsal and midlateral positions (Figs. 2A-B, D-E, 5G and 6D). Females with
234 paired, small papillae in ventrolateral position (Figs. 2B and 5H); papillae on this and
235 following segment are rounded areas with a minute tubular structure carrying a basal
236 collar of short, flexible hairs.

237 Segment 9 with acicular spine in middorsal position and paired acicular spines in
238 lateral accessory position (Figs. 2A-B, D-E and 5G-H); paired cuspidate spines in
239 lateroventral position (Figs. 2B, E and 5H). Paired sensory spots in paradorsal,
240 subdorsal and laterodorsal positions (Figs. 2A, D and 5G). Females with paired, small
241 papillae in ventromedial position (Fig. 2B and 5H).

242 Segment 10 differing between males and females. Males with an unpaired,
243 crenulated spine in middorsal position and paired, crenulated spines in laterodorsal
244 position (Figs. 2D, 5J and 6H). Females with an unpaired, acicular spine in middorsal
245 position and paired acicular spines in lateroventral position (Figs. 2A-B and 5G-H).
246 Females with paired, large, strongly cuticularized, rounded gonopores at the
247 intersegmental junction between segments 10 and 11 (Fig. 5I). Both males and females
248 with paired sensory spots in paradorsal and subdorsal positions (Figs. 2A, D and 5G).

249 Segment 11 tapering to the base of the midterminal spine, with acicular spine in
250 middorsal position and paired lateral terminal and lateral terminal accessory spines
251 (Figs. 2A-B, D-E, 5C, F, G, I-K and 6A, J). Tergal plate of segment 11 carrying two
252 elongated, distally pointed, horn-like dorsal extensions (Figs. 2A, D, 5F and 6J) as well
253 as two short, wide, distally rounded ventral extensions (Figs. 2B, E and 5I). Paired
254 sensory spots arranged on top of the paired cuticular protuberances beside the middorsal
255 spine's basal articulation, in paradorsal position (Figs. 2A, D, 5G-J and 6J). Two pairs
256 of type 3 sensory spots in subdorsal position, one posterior to the paradorsal sensory
257 spots, another near the posterior margin of segment (Figs. 2A, D, 5C, J and 6J). Two

258 pairs of sensory spots in laterodorsal position, one near the base of the dorsal cuticular
259 extensions, another near the basal insertion of the lateral terminal spines (Figs. 2A, D
260 and 6J), barely visible under LM.

261

262 **4. Discussion**

263 *4.1 Remarks on morphological features*

264 *Triodontoderes lagahoo* sp. nov. fits well into the genus *Triodontoderes* by the
265 combination of the following characters: oral styles of mouth cone composed of a single
266 piece; neck composed of fourteen soft, elongated, inconspicuous, equally-sized, distally
267 tripartite placids fused with segment 1; neck and trunk with small, scale-like, medially
268 depressed cuticular hairs irregularly arranged in longitudinal bands; segment 1 with one
269 tergal and one sternal plate, segments 2–4 with one tergal and two sternal plates and
270 remaining segments with a single tergal plate with midventral joint; unpaired middorsal
271 spines on all trunk segments; segment 2 with paired, small, very flexible acicular spines
272 in ventrolateral position plus paired cuspidate spines also in ventrolateral position;
273 segments 3–9 with lateral acicular and/or cuspidate spines; males with middorsal and
274 paired laterodorsal crenulated spines on segment 10; females with paired, lateroventral
275 acicular spines on segment 10 and paired ventral papillae on some segment from 7 to 9;
276 segment 11 with midterminal, lateral terminal and lateral terminal accessory spines
277 (Sørensen and Rho, 2009).

278 Until now, the genus *Triodontoderes* was composed of a single species, *T.*
279 *anulap*, from the Chuuk Archipelago, Micronesia, western Pacific Ocean (Sørensen and
280 Rho, 2009). The main morphological discrepancies between the two congeners are
281 summarized in Table 4. Both species may be easily distinguished by their patterns of
282 spines, female papillae and sensory spots. *Triodontoderes anulap* is characterized by
283 having paired cuspidate spines in lateral accessory position on segment 6 (Sørensen and
284 Rho, 2009), absent in *T. lagahoo* sp. nov. Moreover, females of *T. anulap* have paired
285 papillae in ventrolateral position on segments 7–8 and in ventromedial position on
286 segment 9 (Sørensen and Rho, 2009), while females of *T. lagahoo* sp. nov. possess
287 papillae in ventrolateral position only on segment 8 and in ventromedial position on
288 segment 9. Additionally, the main differences between both species in sensory spot are
289 the presence of paired sensory spots in laterodorsal position on segments 3–9 and 11 in

290 *T. lagahoo* sp. nov. (only on segment 10 in *T. anulap*), in midlateral position on
291 segments 4–8 (only on segment 2 in *T. anulap*) and in ventrolateral positions on
292 segments 3–7 (displaced to ventromedial position and on segments 4, 6–8 and 10–11 in
293 *T. anulap*) (see Sørensen and Rho, 2009, for complete sensory spots arrangement of *T.*
294 *anulap*).

295 Another morphological discrepancy between both species refer to the trunk
296 pectinate fringes and cuticular hairs. *Triodontoderes anulap* only possesses serrated
297 posterior margin of segments with long pectinate fringes on segments 7–11 (Sørensen
298 and Rho, 2009), whereas *T. lagahoo* sp. nov. has serrated posterior margin of segments
299 and long pectinate fringes on segments 2–11. Moreover, *T. anulap* is characterized by
300 having several wavy secondary pectinate fringes composed of tiny scales mixed with
301 slightly longer aciculae from segment 2 (Sørensen and Rho, 2009), while *T. lagahoo* sp.
302 nov. has a single straight secondary pectinate fringe strongly serrated and with bifid
303 tips, also from segment 2. Finally, *T. anulap* has cuticular hairs arranged all over the
304 integument (Sørensen and Rho, 2009), whereas those of *T. lagahoo* sp. nov. are absent
305 at ventrolateral and ventromedial regions of trunk.

306 A striking morphological feature of *T. lagahoo* sp. nov. is the presence of two
307 different body outlines. Of the seventeen examined specimens, twelve belong to the
308 slender body outline and five to the chubby one. Both females and males were found in
309 the two different body outlines. Specimens with short and chubby body outline possess
310 the same number of trunk segments and arrangement of cuticular structures than those
311 with long and slender body outline (Fig. 4J). Moreover, these specimens also possess
312 developed gonads and, in case of females, conspicuous gonopores (Fig. 4L). Though the
313 abundance of the slender specimens were higher than that of the chubby ones, the latter
314 body outline could be an artefact of the fixation process. As both types of body outlines
315 were found in the vial containing non-mounted animals (Fig. 4K), the chubby shape is
316 not result of the mounting process for LM. Nevertheless, two possibilities must be
317 considered. On the one hand, the species may have the ability of kindly modifying its
318 body outline due to the soft cuticle that characterizes this genus. This could be related to
319 the proposed hypothesis by Yamasaki (this issue) of thin-cuticle body kinorhynchs, as
320 this kind of cuticle would allow the animal being more flexible to seep through
321 sediment interstices more easily and absorbing physical damage when sand grains are
322 disturbed. On the other hand, the chubby specimens may correspond to the latest

323 juvenile stages of the species. Though both chubby females and males were found with
324 completely developed gonads, and gonopores in case of females (Fig. 4L), the latest
325 juvenile stages of kinorhynchs often begin to develop gonads (Neuhaus, 2013).

326 4.2 Remarks on systematic features

327 *Triodontoderes*, together with the genus *Zelinkaderes*, belongs to the family
328 Zelinkaderidae, whose monophyly was supported by a total-evidence analysis
329 (Sørensen et al. 2015). This family is morphologically characterized by possessing an
330 introvert with one ring of primary spinoscalids followed by three or four rings of regular
331 scalids, a trunk conspicuously circular in cross-section, at least segments 5 to 10
332 composed of a single tergal plate with midventral joint, acicular spines present in dorsal
333 and lateral positions, cuspidate spines present on some segments, a segment 11 with
334 lateral terminal, lateral terminal accessory and midterminal spines, at least some large,
335 oval sensory spots with two pores in the anterior trunk region, scale-like cuticular hairs
336 with a medial depression and male sexually dimorphic crenulated spines on segment 10
337 (Sørensen and Rho, 2009).

338 The introvert of Zelinkaderidae is characterized by the reduction of, at least, one
339 ring of scalids. Regular scalids are completely absent on rings 02–03 in *Z. brightae* and
340 *Z. klepali* (Bauer-Nebelsick, 1995; Sørensen et al. 2007); on ring 06 in *T. anulap* and *T.*
341 *lagahoo* sp. nov. (Sørensen and Rho, 2009; this paper); on rings 05–06, odd sectors of
342 ring 03 and even sectors of ring 02 in *Z. floridensis* (Higgins, 1990); and on ring 02,
343 even sectors of ring 06 and odd sectors of ring 03 in *Z. yong* (Altenburger et al. 2015).
344 In summary, species of *Zelinkaderes* generally shows a strong reduction of the introvert
345 scalids, as this reduction involves more than a single ring, whereas *Triodontoderes* only
346 shows scalid reduction in the last ring. Additionally, *Zelinkaderes* seems to show more
347 variability in the scalid arrangement (Sørensen et al. 2007) than the genus
348 *Triodontoderes*, with identical disposition of scalids in the two known species
349 (Sørensen and Rho, 2009; this paper). The only other cyclorhagid genus with a
350 considerably lower number of scalids is *Cateria* Gerlach, 1956, that, besides the ten
351 primary spinoscalids, possesses 35 regular scalids (Herranz et al., this issue; Neuhaus
352 and Kegel, 2015). Furthermore, a newly described genus of Franciscideridae also
353 possesses a reduction in the number of scalids, lacking these structures in ring 06 and
354 the even-numbered sectors of ring 05 (Yamasaki, this issue). It seems that *Cateria*,
355 *Triodontoderes* and the new genus of Franciscideridae lost its more posterior scalid

356 rings (Herranz et al., this issue; Sørensen and Rho, 2009; Yamasaki, this issue), whereas
357 *Zelinkaderes* reduced the scalids in its more anterior rings (Altenburger et al. 2015;
358 Sørensen et al. 2007). The reduction of scalids could have occurred independently in the
359 four genera, as also proposed by Herranz et al. (this issue). However, this hypothesis
360 cannot be tested until a more complete systematic analysis of Kentrorhagata is
361 performed.

362 The presence of distally tripartite placids seems also to be a synapomorphic
363 feature of the family Zelinkaderidae (Sørensen and Rho, 2009), with the exception of *Z.*
364 *yong* that has very reduced placids (Altenburger et al. 2015). Both species of
365 *Triodontoderes* also share the former feature (Sørensen and Rho, 2009; this paper).
366 According to the most recent phylogenetic analysis (Sørensen et al. 2015), it is likely
367 that the plesiomorphic condition for placid morphology in Zelinkaderidae is the
368 possession of distally tripartite placids. Then, *Z. yong* would have suffered a reversion
369 of the character state through the placid reduction as an autapomorphy of the species.
370 Again, this hypothesis cannot be tested until more morphological, and especially
371 molecular phylogenetic data is available for the whole family.

372 One of the important morphological differences between species of
373 *Triodontoderes* and *Zelinkaderes* is the number and arrangement of both acicular and
374 cuspidate spines. The former genus is characterized by having middorsal acicular spines
375 along all trunk segments (Sørensen and Rho, 2009; this paper), whereas the latter has
376 middorsal spines on segments 4, 6 and 8–11 (Sørensen et al. 2007). Additionally, lateral
377 acicular and/or cuspidate spines are present on segment 2 and 4–9 in *Zelinkaderes*
378 (Altenburger et al. 2015; Bauer-Nebelsick, 1995; Higgins, 1990; Sørensen et al. 2007),
379 while they are present in at least one sex on segments 2–10 in *Triodontoderes* (Sørensen
380 and Rho, 2009; this paper). Thus, a greater number of dorsal and lateral spines
381 characterizes the genus *Triodontoderes* within the family Zelinkaderidae. However, it is
382 still too early to infer an evolutionary trend towards increasing or decreasing the number
383 of spines in Zelinkaderidae.

384 4.3 Key to species of Zelinkaderidae

385 1. Segment 1 composed of one tergal and one sternal plate; segments 2 to 4 composed
386 of one tergal and two sternal plates; segments 5 to 11 composed of a single plate with
387 midventral joint; neck consisting of 14 distally tripartite placids; middorsal spines

388 present on all trunk segments; cuticular hairs irregularly arranged in scattered bands ...
389 2 (genus *Triodontoderes*)

390 - Segments 1 to 2 composed of one closed cuticular ring; segments 3 to 11 composed of
391 a single plate with midventral joint; neck consisting of 16 entire or distally tripartite
392 placids; middorsal spines present on segments 4, 6 and 8 to 11; cuticular hairs regularly
393 arranged in longitudinal bands ...3 (genus *Zelinkaderes*)

394 2. Lateral accessory cuspidate spines present on segment 6; female, sexually dimorphic
395 papillae present in ventrolateral position on segments 7 to 8 and in ventromedial
396 position on segment 9; long, conspicuous pectinate fringes on segments 7 to 11 ... *T.*
397 *anulap*

398 - Lateral accessory cuspidate spines absent on segment 6; female, sexually dimorphic
399 papillae present in ventrolateral position on segment 8 and in ventromedial position on
400 segment 9; long, conspicuous pectinate fringes on segments 2 to 11 ... *T. lagahoo* sp.
401 nov.

402 3. Spines present in various lateral positions on segment 2 ... 4

403 - Spines absent on segment 2 ... *Z. floridensis*

404 4. Lateroventral or lateral accessory acicular spines present on segment 9 ... 5

405 - Lateroventral or lateral accessory acicular spines absent on segment 9 ... *Z. yong*

406 5. Cuspidate spines present in lateral series on segments 4 and 6 ... 6

407 - Cuspidate spines absent in lateral series on segments 4 and 6 ... *Z. klepali*

408 6. Cuspidate spines present in lateroventral position on segment 7... *Z. submersus*

409 - Cuspidate spines absent in lateroventral position on segment 7 ... *Z. brightae*

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455

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462 The authors declare no conflicts of interest.

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479 TABLES

480 Table 1. Measurements of body size, lateral terminal, lateral terminal accessory and
 481 midterminal spines of adult *Triodontoderes lagahoo* sp. nov., including number of
 482 measured specimens (*n*), mean of data and standard deviation (SD). There were no
 483 remarkable differences in sizes or dimensions between the two sexes. Abbreviations:
 484 LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; MTS, midterminal
 485 spine; S, segments lengths (number after S indicates the corresponding segment); TL,
 486 total length of trunk.

Character	Range	Mean (SD; <i>n</i>)
TL (μm)	319.0–540.2	428.0 (62.0; 12)
S1 (μm)	35.5–72.8	51.1 (13.1; 12)
S2 (μm)	21.2–57.4	43.1 (12.0; 12)
S3 (μm)	25.4–62.9	47.4 (11.3; 12)
S4 (μm)	29.8–63.8	52.3 (11.9; 12)
S5 (μm)	29.4–67.2	55.4 (12.8; 12)
S6 (μm)	39.5–63.7	52.1 (7.8; 12)
S7 (μm)	37.5–65.9	53.4 (8.8; 12)
S8 (μm)	47.8–76.0	56.6 (12.0; 12)
S9 (μm)	31.5–76.2	58.4 (12.4; 12)
S10 (μm)	34.3–71.2	56.7 (11.9; 12)
S11 (μm)	26.0–51.1	43.8 (11.6; 12)

LTS (μm)	52.8–78.8	60.8 (6.9; 12)
LTS/TL (%)	10.6–21.5	14.5 (3.1; 12)
LTAS (μm)	33.7–42.4	39.7 (3.8; 12)
LTAS/TL (%)	8.2–13.3	9.5 (1.9; 12)
LTAS/LTS (%)	55.4–74.4	65.6 (4.5; 12)
MTS (μm)	117.6–288.2	214.8 (51.7; 9)
MTS/TL (μm)	27.8–72.3	39.5 (27.5; 9)

487

488 Table 2. Measurements of middorsal, laterodorsal, lateral accessory and lateroventral
 489 spines of adult *Triodontoderes lagahoo* sp. nov., including number of measured
 490 specimens (*n*), mean of data and standard deviation (SD). Abbreviations: ac, acicular
 491 (spine); cr, crenulated (spine); cu, cuspidate (spine); f, female condition of sexually
 492 dimorphic character; LAS, lateral accessory spine; LDS, laterodorsal spine; LVS,
 493 lateroventral spine; m, male condition of sexually dimorphic character; MDS, middorsal
 494 spine.

Character	Range	Mean (SD; <i>n</i>)
MDS 1 (ac) (μm)	5.0–10.5	7.5 (1.8; 11)
MDS 2 (ac) (μm)	14.3–34.2	24.9 (7.6; 12)
MDS 3 (ac) (μm)	24.5–53.2	38.9 (7.4; 11)
MDS 4 (ac) (μm)	32.5–57.7	46.1 (8.6; 11)
MDS 5 (ac) (μm)	37.6–60.5	48.9 (7.9; 12)
MDS 6 (ac) (μm)	42.5–64.5	53.3 (8.4; 12)
MDS 7 (ac) (μm)	41.3–71.9	58.6 (9.0; 12)
MDS 8 (ac) (μm)	47.9–71.1	60.8 (7.9; 12)
MDS 9 (ac) (μm)	39.3–73.4	59.9 (10.5; 11)
MDS 10 (cr, m; ac, f) (μm)	22.3–65.9	42.8 (13.2; 12)
MDS 11 (ac) (μm)	25.4–51.7	46.0 (7.6; 12)
LDS 10 (cr, m) (μm)	26.1–34.8	31.6 (3.3; 7)
VLS 2 (ac) (μm)	11.4–22.0	16.1 (4.9; 12)
VLS 2 (cu) (μm)	13.6–24.2	18.3 (5.2; 12)
LVS 3 (ac) (μm)	19.9–50.0	34.0 (8.8; 12)
LVS 4 (ac) (μm)	31.0–55.6	41.9 (7.6; 11)
LVS 5 (cu) (μm)	18.8–27.4	23.4 (3.1; 12)
LAS 5 (ac) (μm)	32.3–55.6	43.2 (8.4; 12)
LVS 6 (ac) (μm)	36.1–56.1	48.9 (6.4; 12)
LVS 7 (ac) (μm)	40.0–65.7	54.8 (8.6; 12)
LVS 8 (ac) (μm)	38.2–47.5	42.7 (2.9; 12)
LAS 8 (cu) (μm)	20.5–30.5	26.0 (3.5; 12)

LVS 9 (cu) (μm)	22.5–31.7	28.2 (2.5; 12)
LAS 9 (ac) (μm)	34.9–50.4	43.1 (6.0; 12)
LVS 10 (ac, f) (μm)	21.7–28.1	24.0 (2.8; 5)

495

496 Table 3. Summary of nature and arrangement of sensory spots, papillae and spines in
 497 *Triodontoderes lagahoo* sp. nov. Abbreviations: ac, acicular spine; cr, crenulated spine;
 498 cu, cuspidate spine; f, female condition of sexually dimorphic character; LA, lateral
 499 accessory; LD, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal
 500 spine; LV, lateroventral; m, male condition of sexually dimorphic character; MD,
 501 middorsal; mt, midterminal spine; ML, midlateral; pa, papilla; PD, paradorsal; SD,
 502 subdorsal; ss, sensory spot; ss3, type 3 sensory spot; VL, ventrolateral; VM,
 503 ventromedial.

Segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1	ac	ss							
2	ac	ss						cu, ac	
3	ac	ss		ss			ac	ss	
4	ac	ss		ss	ss		ac	ss	
5	ac	ss		ss	ss	ac	cu	ss	
6	ac	ss		ss	ss		ac	ss	
7	ac	ss		ss	ss		ac	ss	
8	ac	ss		ss	ss	cu	ac	pa(f)	
9	ac	ss	ss	ss		ac	cu		pa (f)
10	cr (m)/ac (f)	ss	ss	cr (m)			ac (f)		
11	ac, mt	ss	ss3, ss3	ss, ss		ltas	lts		

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505 Table 4. Summary of main morphological differences between *Triodontoderes anulap*
 506 and *T. lagahoo* sp. nov.

Character	<i>T. anulap</i>	<i>T. lagahoo</i> sp. nov.
Cuspidate spines in lateral accessory position on segment 6	Present	Absent
Female papillae arrangement	Ventrolateral on segments 7–8 and ventromedial on segment 9	Ventrolateral on segment 8 and ventromedial on segment 9
Laterodorsal sensory spots	Segment 10	Segments 3–9 and 11
Midlateral sensory spots	Segment 2	Segments 4–8
Ventral sensory spots	Ventromedial on segments 4, 6–8 and 10–11	Ventrolateral on segments 3–7

Long and conspicuous trunk Segments 7–11

Segments 2–11

pectinate fringes

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516 FIGURE LEGENDS

517 **Fig. 1.** Map showing the sampling locality on Tobago Island (Trinidad and Tobago),
518 Lesser Antilles, Caribbean Sea (western Atlantic Ocean).

519 **Fig. 2.** Line art illustrations of *Triodontoderes lagahoo* sp. nov. (A) Female, dorsal
520 overview; (B) Female, ventral overview; (C) Female, dorsal overview showing the fat
521 shape of the species; (D) Male, segments 8-11, dorsal overview; (E) Male, segments 8-
522 11, ventral overview. Abbreviations: de, dorsal extension (of segment 11); dpl, dorsal
523 placid; f, female condition of sexually dimorphic feature; go, gonopore; laac, lateral
524 accessory acicular spine; lacu, lateral accessory cuspidate spine; ldcr, laterodorsal
525 crenulated spine; ldss, laterodorsal sensory spot; ltas, lateral terminal accessory spine;
526 lts, lateral terminal spine; lvac, lateroventral acicular spine; lvcu, lateroventral cuspidate
527 spine; m, male condition of sexually dimorphic feature; mdac, middorsal acicular spine;
528 mdcr, middorsal crenulated spine; mlss, midlateral sensory spot; mts, midterminal
529 spine; mvj, midventral junction; pdss, paradorsal sensory spot; ppf, primary pectinate
530 fringe; S, segment followed by number of corresponding segment; sdss, subdorsal
531 sensory spot; sdss3, subdorsal type 3 sensory spot; spf, secondary pectinate fringe; tsj,
532 tergo-sternal junction; ve, ventral extension (of segment 11); vlac, ventrolateral acicular
533 spine; vlcu, ventrolateral cuspidate spine; vlpa, ventrolateral papilla; vlss, ventrolateral
534 sensory spot; vmpa, ventromedial papilla; vpl, ventral placid.

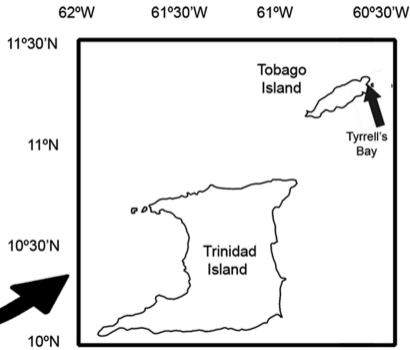
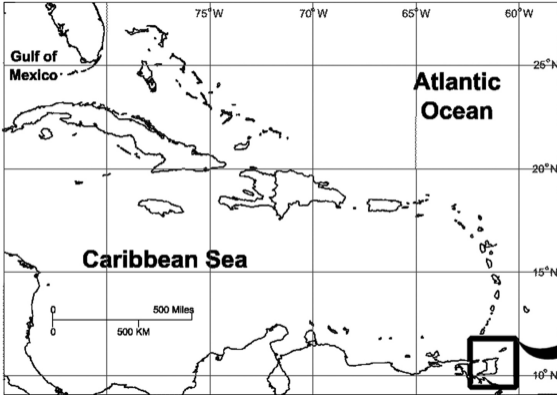
535 **Fig. 3.** Diagram of mouth cone, introvert and trichoscalids in *Triodontoderes lagahoo*
 536 sp. nov., with indication of oral style, scalid and trichoscalid arrangement. The
 537 outermost bold lines refers to the placids.

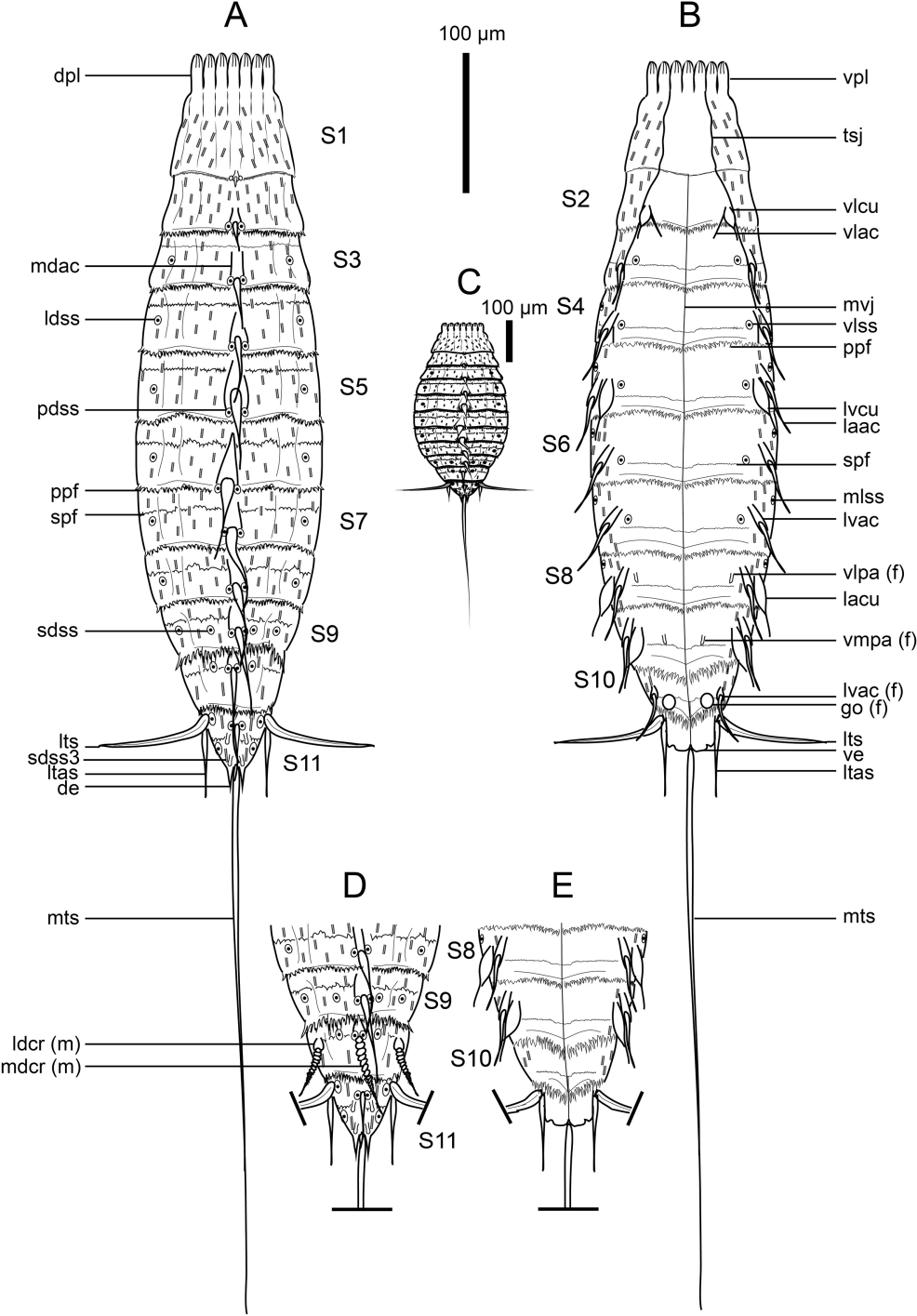
538 **Fig. 4.** Light micrographs (A-J, L) and stereomicroscope photo (K) showing trunk
 539 overviews and details in the mouth cone, introvert and general cuticular trunk characters
 540 of the female holotype NMNH XXXXX (A-I), a male paratype NMNH XXXXX (J), a
 541 female paratype NMNH XXXXX (L) and non-mounted additional specimens (K) of
 542 *Triodontoderes lagahoo* sp. nov. (A) Dorsal overview of trunk; (B) ventral overview of
 543 trunk; (C) mouth cone, with detail of the last ring of inner oral styles (ring -01); (D)
 544 mouth cone, with detail of the ring of outer oral styles (ring 00); (E) introvert, showing
 545 the first ring of primary spinoscalids (ring 01) and trichoscalids; (F) detail of a primary
 546 spinoscalid, showing the rigid spine that extends from its basal plate; (G) sector 5 of
 547 introvert, with detail of scalids of rings 02-05; (H) sector 6 of introvert, with detail of
 548 scalids of rings 02-05; (I) midlateral and lateroventral regions on right half of tergal
 549 plate of segments 8-10, with detail of primary and secondary pectinate fringes; (J)
 550 ventral overview of a chubby body outline male; (K) slender body outline (right) and
 551 chubby body outline (left) non-mounted specimens; (L) ventral view of segments 7-11
 552 of a chubby body outline female, showing the gonads and the gonopores .
 553 Abbreviations: bs, basal sheath; dp, distal piece; f, female condition of sexually
 554 dimorphic character; g, gonad; go, gonopore; ios, inner oral style; oos, outer oral style;
 555 ppf, primary pectinate fringe; psc, primary spinoscalid; r, ring; S; segment followed by
 556 number of corresponding segment; sp, spine; sc, scalid; spf, secondary pectinate fringe;
 557 tct, triangular cuticular thickening; ts, trichoscalid.

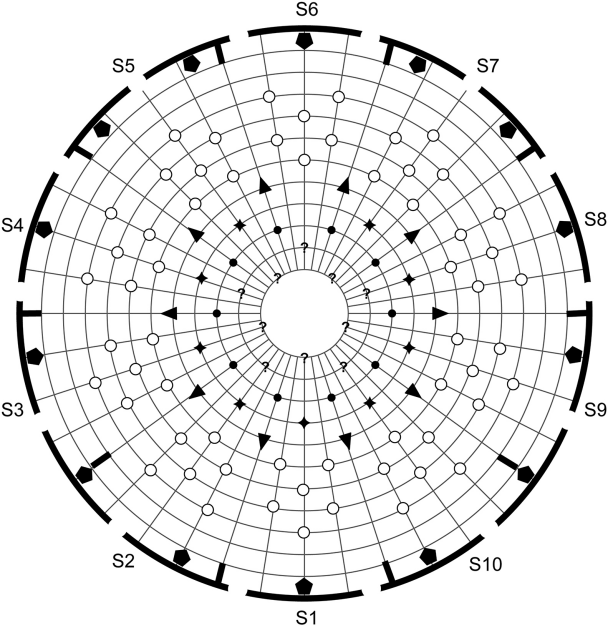
558 **Fig. 5.** Light micrographs showing details of cuticular trunk characters of female
 559 holotype NMNH XXXXX (A-I, K) and male paratype NMNH XXXXX (J) of
 560 *Triodontoderes lagahoo* sp. nov., with main focus on spines, sensory spots, sexually
 561 dimorphic features and segment 11 cuticular extensions. (A) Dorsal view of segments 1-
 562 3; (B) lateral view of right half of segments 2-3; (C) dorsal view of segment 11,
 563 showing the two pairs of type 3 sensory spots; (D) dorsal view of segments 4-7; (E)
 564 lateral accessory to ventromedial regions on right half of tergal and sternal plates of
 565 segments 4-6; (F) dorsal view of segment 11, showing the tergal extensions (in arrows);
 566 (G) dorsal view of segments 8-11; (H) lateral accessory to ventromedial regions on right
 567 half of tergal plates of segments 7-10; (I) ventral view of segment 11, showing the

568 sternal extensions (in arrows) and the female gonopores; (J) lateral view of right half of
 569 a male segment 11; (K) ventral view of segment 11, showing the midterminal spine.
 570 Abbreviations: f, female condition of sexually dimorphic character; go, gonopore; laac,
 571 lateral accessory aciculate spine; lacu, lateral accessory cuspidate spine; ldcr,
 572 laterodorsal crenulated spine; ltas, lateral terminal accessory spine; lts, lateral terminal
 573 spine; lvac, lateroventral acicular spine; lvcu, lateroventral cuspidate spine; m, male
 574 condition of sexually dimorphic character; mdac, middorsal acicular spine; mdcr,
 575 middorsal crenulated spine; mts, midterminal spine; pa, papilla; vlac, ventrolateral
 576 acicular spine; vlcu, ventrolateral cuspidate spine; sensory spots are marked as
 577 continuous circles and papillae as dotted circles; numbers after spines indicate the
 578 corresponding segment.

579 **Fig. 6.** Scanning electron micrographs showing general overview and details of the
 580 cuticular trunk morphology of non-type specimens of *Triodontoderes lagahoo* sp. nov.
 581 (A) Dorsal overview of trunk; (B) mouth cone, showing the outer oral styles; (C) dorsal
 582 view of neck, showing the distally tripartite placids; (D) detail of middorsal spine of
 583 segment 8, showing the swollen cuticular thickenings of its basal articulation with the
 584 paired paradorsal sensory spots; (E) lateroventral and lateral accessory regions on right
 585 half of tergal plates of segment 5; (F) middorsal and paradorsal regions of tergal plates
 586 of segments 6-8; (G) laterodorsal region on left half of tergal plates of segments 4-5;
 587 (H) dorsal view of a male segment 10, showing the crenulated middorsal and
 588 laterodorsal spines; (I) detail of midlateral sensory spot of segment 6; (J) lateral view of
 589 left half of segment 11 tergal plate, showing all sensory spots on left side.
 590 Abbreviations: de, dorsal extension (of segment 11); laac, lateral accessory acicular
 591 spine; ldcr, laterodorsal crenulated spine; ldss, laterodorsal sensory spot; lvcu,
 592 lateroventral cuspidate spine; m, male condition of sexually dimorphic character; mdac,
 593 middorsal acicular spine; mdcr, middorsal crenulated spine; pdss, paradorsal sensory
 594 spot; sdss3, subdorsal type 3sensory spot; sensory spots are marked as continuous
 595 circles; numbers after spines indicate the corresponding segment.







Oral style and scalid arrangement

By ring:

- Ring -03: ? helioscalids } ?
- Ring -02: ? inner oral styles •
- Ring -01: 10 inner oral styles ◆
- Ring 00: 9 outer oral styles ▲
- Ring 01: 10 primary spinoscalids ○
- Ring 02: 15 scalids }
- Ring 03: 15 scalids }
- Ring 04: 15 scalids }
- Ring 05: 15 scalids }
- Ring 06: / }
- Trichoscalid row: 14 trichoscalids ●

By sector:

Odd sectors: 6 scalids



Even sectors: 6 scalids



