

1 **Crossing the Polar front – Antarctic species discovery in the**
2 **nudibranch genus *Tritoniella* (Gastropoda)**

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Declarations

22 **Funding** JM postdoctoral fellowship and microscopy analyses were supported by the Alexander von Humboldt
23 Foundation (Germany). Funds for field research were provided by the German Research Foundation (DFG
24 SCHR667/3,4,15 to MS) and National Science Foundation, USA (ANT-1043749 to NGW).

25 **Conflicts of interest/Competing interests** The authors declare that they have no conflict of interest.

26 **Availability of data and material** Material examined during this study including type material is deposited at the
27 SNSB-Bavarian State Collection of Zoology (ZSM, Munich, DE) and the Benthic Invertebrate Collection at
28 Scripps Institution of Oceanography (SIO-BIC, La Jolla, CA, USA).

29 **Code availability** Not applicable.

30 **Authors' contributions** MS and NGW collected specimens. MS and JM contributed to resources and work in the
31 conceptualization. PMS and JM performed lab work and wrote the original draft. All authors reviewed and edited
32 the final version of the manuscript.

33

Acknowledgements

34 We would like to thank the crews and science parties on the R/V *Polarstern* (AWI, Germany) during the EASIZ
35 II and the 2000 cruises, and of the R/V *Nathaniel B. Palmer* (NSF, USA) during the 2011 and 2013 cruises. Special
36 thanks go to Amy Moran (UH, Manao) and Peter Brueggeman for providing live pictures of *T. belli* specimens,
37 and to Greg Rouse (SIO, UCSD) for field support and photography. We appreciate Andreia Salvador (NHM, UK)
38 and Charlotte Seid (BIC-SIO, USA) for helping provide type- and specimen material. Many thanks to Heike
39 Wägele (ZFMK, Germany) for providing valuable information on her previous work. We thank Dirk Schories
40 (DLR, Germany) for providing specimens and live pictures from his SCUBA-dives and Roland Melzer (ZSM,
41 Germany) for helping with the SEM imaging. Additional thanks go to Irina Ekimova (MSU, Russia) for providing
42 us with the elusive Minichev (1972) publication. Special thanks to Morgan Oberweiser (LMU, Germany) for
43 proofreading the draft before submission. We also thank all people involved in providing low cost, open access
44 and open-source software. JM postdoctoral fellowship and microscopy analyses were supported by the Alexander
45 von Humboldt Foundation (Germany). Funds for field research and sequencing was provided by the German
46 Research Foundation (DFG SCHR667/3,4,15 to MS) and National Science Foundation, USA (ANT-1043749 to
47 NGW).

Abstract

49 *Tritoniella belli* is the only valid species of a nudibranch genus endemic to the Southern Ocean. Recent exhaustive
50 sampling and molecular analyses led to the discovery of several new lineages. A total of 69 specimens were
51 collected from 25 sites across the Weddell and Scotia Seas, from 5 to 751 m depth. In this study, we provide
52 morphological and anatomical characters to describe five new *Tritoniella* species, namely *T. gnocchi* n. sp., *T.*
53 *prinzess* n. sp., *T. gnathodontata* n. sp., *T. schoriesi* n. sp., *T. heideae* n. sp. Detailed descriptions of colouration,
54 external morphology, digestive and reproductive organs, distribution, and ecology are presented in a systematic
55 context. These are compared to the type material from the Ross Sea of *T. belli* and its synonym *T. sinuata*, whose
56 status requires additional sampling to be solved. Discrete differences in external characters, including the shape of
57 dorsal notum ridge and mantle edges, support the species hypotheses delimited by Moles, Berning, et al. (2021).
58 Moreover, detailed scanning electron microscopy images of the masticatory border of the jaws, radula teeth, and
59 penial papilla were provided and their differences were discussed. The gut content of all species revealed sclerites
60 of Primnoidae gorgonians as their preferred prey. Pseudo-cryptic radiations along the Scotia Arc, explained by the
61 combination of distribution reduction due to glacial cycles and the existence of refugia, enhanced by their
62 ‘supposed’ direct development, could explain the allopatric speciation events in *Tritoniella* species.

63 **Keywords** Mollusca, Scotia Arc, Southern Ocean, species discovery, taxonomy, Tritoniidae

Introduction

65 The Southern Ocean (SO) surrounds Antarctica and encompasses unique ecosystems that have evolved through
66 isolation and extreme environmental conditions, providing the means for speciation and rich biodiversity (Lee et
67 al., 2011). SO isolation is driven by the largest ocean jet, the Antarctic Circumpolar Current, which limits water
68 exchange through temperature, salinity, and water density differences (Moore et al., 2018). Due to such density
69 and temperature clines, the Polar Front is seen as a barrier to the distribution of even long-distance dispersers
70 (Clarke et al., 2005; Thornhill et al., 2008). The SO is characterized by extreme temperatures and seasonal ice
71 regimes. Historically speaking, during glacial maxima the ice shelves reached far and deep into the SO making the
72 seabed below uninhabitable (Convey et al., 2009; Goehring, 2019). Thus, species could only survive in refugia
73 and the deep sea, out of reach of the ice shelves (Rex & Etter, 2010; Strugnell et al., 2008). In periods of ice-shelf
74 retreat, refugia lead to subsequent radiations and thus speciation particularly of slow dispersers (Baird et al., 2011;
75 Hawkins et al., 2018; Thatje et al., 2005; Wilson et al., 2009). Island patchiness along the Scotia Arc acted as
76 another driver for speciation. Distance between islands limits gene flow between populations and leads to

77 speciation, commonly cryptic (Moles, Derkarabetian, et al., 2021; Wilson et al., 2009). Overall, these factors
78 describe the Antarctic biodiversity pump phenomenon (Clarke & Crame, 1989, 1992; Rogers, 2007), showing
79 how, unlike the Arctic, Antarctica has a high species richness comparable to temperate and tropical regions (Gray,
80 2001).

81 Molluscs are one of the most species-rich phyla of marine life, and the biodiversity of the SO is steadily
82 increasing with new species being described regularly (Fassio et al., 2020; Layton et al., 2019; Moles et al., 2019).
83 Due to advances in molecular tools and sampling efforts in the SO, the systematics of mollusc taxa are in constant
84 flux, by the many major taxonomic revisions and species discoveries in the last decades (Levicoy et al., 2021;
85 Moles et al., 2018; Moles, Berning, et al., 2021; Moles, Derkarabetian, et al., 2021). Some of these new species
86 discoveries have unearthed previously unrecognized cryptic species complexes, further increasing the estimated
87 biodiversity of the SO (Linse et al., 2007; Moles et al., 2019; Wilson et al., 2013). Within Nudibranchia, Tritoniidae
88 is represented in the SO by two genera: *Tritonia* Cuvier, 1798 with three described species and *Tritoniella* Eliot,
89 1907 with currently only one valid species. *Tritoniella* can be differentiated from *Tritonia* by a wide dorsal ridge
90 and lack of foliaceous tufts (gills) (Eliot, 1907; Rossi et al., 2021; Wägele, 1989b). The genus *Tritoniella* was first
91 described from shallow waters in the Ross Sea with the two sympatric species *T. belli* Eliot, 1907 and *T. sinuata*
92 Eliot, 1907, based on five specimens and one specimen, respectively. Eliot differentiated the two groups by
93 dentition, jaws, reproductive organs, and stomach plates. These characters were not considered specific by later
94 authors (Odhner, 1934; Wägele, 1989b), and subsequently led to the synonymy of *T. sinuata* with *T. belli* by
95 Wägele (1989b). This revision utilized intermediate states of many characters after more specimens were examined
96 from the B.A.N.Z.A.R. Expedition (Kerguelen and MacRobertson Islands and Enderby Land) and several stations
97 from the ANT I, II, and III expeditions across the Weddell Sea and Scotia Arc of the German R/V *Polarstern*.
98 Only recently, a molecular phylogeny of the Tritoniidae based on partial nuclear H3 and the mitochondrial 16S
99 and COI markers by Moles, Berning, et al. (2021) revealed the presence of six species of *Tritoniella* in the SO and
100 adjacent waters. Thus, the main aims of this study are threefold: to (1) describe the newly delimited species of
101 *Tritoniella*, (2) ascertain the taxonomy of *T. belli* and *T. sinuata* by reassessing the type material, and (3) provide
102 a morpho-anatomical and ecological background for all *Tritoniella* species.

103 **Material and Methods**

104 **Specimen Collection**

105 A total of 69 specimens were collected by Agassiz trawl, bottom trawl, Rauschert dredge, and SCUBA diving in
106 the Scotia Sea and the eastern Weddell Sea. Expeditions included the 1998 EASIZ II (W. E. Arntz) and 2000
107 EASIZ III (W. E. Arntz) cruises of the R/V *Polarstern* (Alfred Wegener Insitute, Bremerhaven, Germany), the
108 2011 and 2013 (N. Wilson, G. Rouse) cruises of the R/V *Nathaniel Palmer* (Unites States National Science
109 Foundation, Punta Arenas, Patagonia), and other independent dive expeditions (Fig. S1). The specimens were
110 collected at depths between 5 and 751 m at 25 different stations. A colour-coded distribution map (Fig. 1) was
111 designed in Arc-GIS Pro version 2.7.3 (Esri, Redlands, CA, USA). Most specimens were photographed alive
112 before being preserved in 70% or 96% EtOH or 10% formalin in seawater for molecular and morphological
113 analyses. Voucher specimens were deposited in the SNSB-Bavarian State Collection of Zoology (ZSM, Munich,
114 Germany) and the Benthic Invertebrate Collection at Scripps Institution of Oceanography (SIO-BIC, La Jolla, CA,
115 USA). Additionally, the holotype and paratypes of *T. belli* (Fig. 2) and *T. sinuata* (Fig. 3) were requested from the
116 Marine Gastropoda and Historical Mollusca Collections of the Natural History Museum of London (NHM,
117 London) and received as high-quality photographs with scales (taken by Kevin Webb, NHMUK Photographic
118 Unit).

119 Morphological Documentation

120 Photographs of preserved animals were taken with a Nikon 1 V1 with LEICA Z16 APO and a LEICA 10445930
121 1.0x microscope lens with ring light type illumination. Specimen length and width were recorded by a millimetre
122 scale next to the animal and measured using Adobe Photoshop CS2 analysis tools. Specimens were dissected
123 sagittally and cut open laterally with fine forceps under a stereomicroscope. Radulae and jaws were removed from
124 the buccal bulb and the surrounding soft tissue was removed with forceps. The gut content was removed from the
125 gut and intestine with a pipette. The remaining tissue was dissolved in a solution of 10% NaOCl for the radulae
126 and 50% NaOCl for the jaws and gut contents and later rinsed in distilled water. The reproductive system was
127 depicted, the penial papilla extracted and dried stepwise by immersion in 100% EtOH and subsequently in 25%,
128 33%, 50% and 100% solutions of 1,1,1,3,3,3-Hexamethyldisilazane (HMDS) for 30min each. The final HMDS
129 was slowly evaporated overnight under a hood at room temperature. The cleaned jaws, radulae, gut contents, and
130 penial papillae were mounted on stubs with carbon sticky-tabs and coated in gold with a Polaron SC510 sputter
131 coater. Images were taken with a Carl Zeiss LEO 1430VP scanning electron microscope (SEM) at the ZSM. All
132 resulting images were adjusted for brightness, contrast, and colour. For non-detail images, the background was
133 removed using the lasso tool implemented in Adobe Photoshop CS2. Schematic drawings were made as vector
134 graphics in Inkscape version 1.0.

135 Descriptions of morphological traits are written in detail for the type species *T. belli*. For clarity reasons,
136 only morphological deviations of other species are described herein, while leaving out identical characters unless
137 otherwise stated. Character states and measurements of more than one specimen of a given species are reported as
138 a range between lowest and highest measurement.

139 **Results**

140 Systematic Descriptions

141 Class: Gastropoda Cuvier, 1795

142 Subclass: Heterobranchia Burmeister, 1837

143 Order: Nudibranchia Cuvier, 1817

144 Suborder: Cladobranchia

145 Family: Tritoniidae Lamarck, 1809

146 Genus: *Tritoniella* Eliot, 1907

147 Type species: *Tritoniella belli* Eliot, 1907

148 (Figs. 2–7)

149 *Tritoniella belli* Eliot (1907): 5–29, figs. 1–8 & pl. A&B; Odhner (1934): 287–292, figs. 54, 56a, 57–60 & pl. III:
150 figs. 30–33; Minichev (1972): 358–382, fig. 5; Vicente & Arnaud (1974): 537–539, figs. 3&4; Wägele (1989b):
151 235–243, figs. 1a, c, d, 4–8, Brueggeman (1998): 28–36.

152 *Tritoniella sinuata* Eliot (1907): 10–29, figs. 9–11 & pl. C; Odhner (1934): 537–539, figs. 55, 56b & pl. III: figs.
153 34–37; Vicente & Arnaud (1974): 292–293, fig. 4.

154 **Type locality** Hut Point & McMurdo Bay, McMurdo Sound, Ross Sea; 7–15 m depth.

155 **Diagnosis** Colour white. Central ridge broad, without knobs, between rhinophoral sheaths thicker. Notum broad,
156 sparsely covered by knobs. Notal margins smooth. Jaws oval, spike subterminal. Vas deferens short, penial papilla
157 elongated, tip pointed.

158 **Material examined** Hut Point, Winter Quarters, 45–55 m depth, 3 spcs., NHMUK1906.7.5.1 (holotype *T. belli*);
159 NHMUK1919.9.16.3 (holotype *T. sinuata*); NHMUK1906.7.5.2 (paratype *T. belli*); 4–18 m, 3 spcs.,
160 NHMUK1906.7.5.4 (paratype *T. belli*); NHMUK1906.7.5.5 (paratype *T. belli*); NHMUK1906.7.5.6 (paratype *T.*
161 *belli*). Kapp Norvegia, Weddell Sea, 71.1916° S 12.2611° W, 309–318 m depth, 1 spc., ZSM 20012172, *L* = 23
162 mm, *W* = 10 mm, *H* = 7 mm, COI barcode MW444337; 71.1308° S 11.4528° W, 73–137 m depth, 1 spc., 1
163 dissected, ZSM 20012253, COI barcode MW444339; 71.1292° S 11.4678° W, 80 m depth, 3 spcs., 1 dissected,
164 ZSM 20012255, *L* = 26 mm, *W* = 12 mm, *H* = 11 mm, COI barcode MW444340, ZSM 20090522, *L* = 27 mm, *W*
165 = 17 mm, *H* = 9 mm, COI barcode MW444342. Austasen Bank, Eastern Weddell Sea, 70.8444° S 10.5889° W,
166 226–266 m depth, 1 spc., ZSM 20012249, COI barcode MW444338.

167 **External morphology** (Fig. 4) Body 23–27 mm long, 10–17 mm wide, 7–11 mm high; elongated, massive. Colour
168 beige to milky white in preserved specimens (Fig. 4a–c), living specimens completely white (Fig. 4d). Dorsal
169 mantle surface with thick, longitudinal, central ridge, straight or crooked, sometimes with side ridge on right side
170 at ½ of length, running close towards end of tail; with knobs and tubercles, interspersed all over notum but the
171 ridges, one knob or small head ridge central on head, not connected to central ridge; central ridge, body margins,
172 and knobs usually with white pigmentation (subepithelial). Notal margin with 5 to 7 extensions per side.
173 Rhinophores with central club, surrounded by many feather-like plumes; rhinophoral sheath large, sometimes
174 extended laterally and connected to the notal margin, margin smooth (Fig. 4a, c). Velum single-lobed or slightly
175 bilobed after preservation; velar margin smooth or with up to 14 extremely short processes; tentacles ear-shaped,
176 small. Lips oval to round, thick (Fig. 4e). Foot ½ to ⅔ of notum in width; propodium rounded (Fig. 4b). Genital
177 papilla on right side at 1/3 of body length. Nephroproct and anal opening close together at ½ of body length (Fig.
178 4c).

179 **Jaws and radula** (Fig. 5a–d) Jaws oval, light yellow; masticatory border amber; distal ends translucent.
180 Masticatory border long, smooth. Spike subterminal, smooth. Radular formula 41 x 23.1.1.1.23. Rachidian tooth
181 longer than broad; cusp protruding, large. First lateral tooth with extremely short cusp. Lateral teeth progressively
182 hook-shaped, smooth.

183 **Digestive system** Oral tube short, muscular. Pharynx muscular, dorsally connected to oesophagus. Salivary glands
184 running ventrolaterally to oesophagus, tilted towards left side. Esophagus thin, without cuticular lining, internally
185 folded. Stomach connecting oesophagus with intestine; internally folded; three openings to the digestive glands;
186 stomach plates absent. Digestive gland massive, with two types of glandular structures: (1) small, granular, orange

187 in colour, (2) larger, bubble-like, transparent, visibly interconnected through ducts. Intestine, connected dorsally
188 to stomach, making loop to right, below stomach, then loop to left above stomach, ultimately shaping an eight,
189 leading to anal aperture. Anus opens through the epidermis laterally on right side.

190 **Reproductive system** (Figs. 5e, f, 6a, 7) Gonad thick, of granular structure, covering digestive gland. Ampulla
191 wide, compactly folded; splitting into vas deferens and vaginal duct. Vas deferens (Fig. 6a) long with 9–13
192 compact folds. Penial sheath muscular, folded longitudinally inside, embedded in tegument. Penis conical with
193 circular enlargement close to tip. Mucous gland white with plicated folds, capsule gland smaller with reticulated
194 structure. Vaginal opening in a slit ventral to penial opening. Seminal receptacle club-shaped, thick, compactly
195 folded posterior of ampulla; with long duct.

196 **Ecology** Occurs at depths from 4 to 318 m (Eliot, 1907; this study). Scales and spicules of soft corals were present
197 in gut content of dissected specimens (Wägele, 1989b). Specimens studied from the Ross Sea ingest and store
198 chimyl alcohol as a chemical defence against sea star predators (Bryan et al., 1998; McClintock & Baker, 1997),
199 although this tactic is proven ineffective against the sympatric anemone *Isotealia antarctica* Carlgren, 1899
200 (McClintock & Baker, 1997). The placement of the egg ribbons is not substrate-specific (Bryan et al., 1998). Egg
201 mass displayed in bands, spiral in shape, diameter 60 mm, height 8–10 mm, 400 eggs per 5 mm of band length,
202 with a reinforced mucous layer (Wägele, 1989a). Eggs transparent, oval to round, diameter 600 µm, surrounded
203 by a soft, jelly-like hull. Embryos at veliger state light orange, giving colour to egg mass (Wägele, 1989a).

204 **Distribution** Ross and Weddell Seas (Eliot, 1907; Wägele, 1989b; this study).

205 **Remarks** Two of the specimens depicted by Wägele (1989b; T2 and T11) could not be identified to any of the
206 species described here. While T11 (fig. 2a therein) could be a specimen of *T. gnathodentata* n. sp. a closer look at
207 the material is needed. Specimen T2 (Wägele 1989b, fig. 1b) looks exceedingly different from all the specimens
208 examined especially due to the number of knobs interspersed all over the notum and might be a new species
209 altogether. *Tritoniella belli* differs from other species by its thick ventral ridge in combination with its smooth
210 notal margin and, generally, a milky, white colouration. The species is only known from high-latitude Antarctica.
211 We found some incongruencies while examining specimens from previous studies, that were attributed to *T. belli*.
212 Most *T. belli* specimens show more similarities to the *T. sinuata* holotype than to the *T. belli* holotype. This could
213 infer, that – in case *T. belli* and *T. sinuata* are two distinct species – the original *T. belli* is the rarer of the two. We
214 suspect that the validation of the two species might change with broader sampling in both the Weddell and (most
215 importantly) the type locality, the Ross Sea.

216 *Tritoniella gnocchi* n. sp.

217 (Figs. 6b, 8–9)

218 *Tritoniella* sp. 1 Moles, Berning, et al. (2021).

219 **ZooBank registration** urn:lsid:zoobank.org:act:0A027FAA-5B9A-4A0E-AEDB-660A65489119

220 **Type locality** Burdwood Bank East, South Falkland Islands, 54.4666° S 55.6808° W; 561–572 m depth.

221 **Diagnosis** Colour white. Notum bloated, central ridge only anterior, faint. Notal margin with serrated extensions.

222 Jaws subquadrangular, spike terminal. Rachidian with linear, lateral grooves. First lateral pointing upwards.

223 Subsequent laterals with sharp tips, curved inwards. Vas deferens short, penial papilla stout, tip flattened.

224 **Material examined** Burdwood Bank East, South Falkland Islands, 54.4666° S 55.6808° W. 561–572 m depth: 1

225 spc., sequenced and dissected, SIO-BIC M13502 (holotype), $L = 21$ mm, $W = 10$ mm, $H = 11$ mm, COI barcode

226 MW444343.

227 **Etymology** The name stems from the fact that this species externally reminds of the Italian gnocchi, especially

228 after preservation.

229 **External morphology** (Fig. 8) Body 21 mm long, 10 mm wide, 11 mm high; bloated. Colour beige in preserved

230 specimen (Fig. 8a), living specimen translucent white (Fig. 8d). Mantle surface smooth, bloated; lacking knobs

231 and tubercles; ridge faint, only seen on anterior part of mantle, connecting rhinophores. Notal margin with up to

232 15 extremely short, serrated extensions per side. Rhinophoral sheath extended, laterally connected to notal margin,

233 margin smooth (Fig. 8a). Velum single-lobed; velar margin with 4 extremely short processes; tentacles conical,

234 small, pointing outwards. Lips round (Fig. 8e). Foot $\frac{1}{3}$ of notum in width (Fig. 8b).

235 **Jaws and radula** (Fig. 9a–d) Jaws subquadrangular, amber in colour, darker at masticatory border. Masticatory

236 border long, coarse. Spike terminal, reaching farther than rest of jaws, coarse. Radular formula 71 x 62.2.1.2.62.

237 Rachidian tooth as long as broad; cusp pointing upwards; with linear grooves laterally. First two lateral teeth with

238 blunt cusp, curved upwards. Subsequent outer lateral teeth progressively hook-shaped, smooth, pointing

239 downwards; inner lateral teeth with sharp tip curved inward.

240 **Male reproductive system** (Figs. 6b, 9e, f) Specimen probably early adult. Vas deferens short, 4 folds. Penial

241 papilla flat, cone-shaped, densely ciliated.

242 **Ecology** Occurs at depths from 561–572 m (this study). Plates, spindle sclerites and inner axis of gorgonian present
243 in gut content of the dissected specimen, belonging to the gorgonian family Primnoidae (Fig. 9g–h). Plate shape
244 elongated-squarish, oval or arrow-like, with tubercles on inner side and a longitudinal central crest (Fig. 9g).
245 Spindles spherical, rod-like – straight or curved – or irregular; tuberculated (Fig. 9h).

246 **Distribution** The singleton was found at Burdwood Bank east, south of the Falkland Islands (this study).

247 **Remarks** *Tritoniella gnocchi* differs from its congeners by a faint, anterior central ridge and a short and bloated
248 body. Internally, this is the only species with a terminal spike in the jaws.

249 *Tritoniella prinzeß n. sp.*

250 (Figs. 6c, 10–11)

251 *Tritoniella* sp. 2 Moles, Berning, et al. (2021).

252 **ZooBank registration** urn:lsid:zoobank.org:act:9B67C543-4B1D-4201-AF6B-F9EF47DCC39E

253 **Type locality** Ardley Island, King George Island, South Shetland Islands, 62.2103° S 58.9139° W; 20–40 m depth.

254 **Diagnosis** Colour translucent white with white knobs, central ridge comprised of single knobs, mantle margin with
255 continuous large knobs. Jaws subquadrangular, spike subterminal. Vas deferens short (juvenile), penial papilla
256 elongated.

257 **Material examined** Ardley Island, King George Island, South Shetland Islands, 62.2103° S 58.9139° W, 20–40
258 m depth: 1 spc., sequenced and dissected, ZSM 2041002 (holotype), $L = 17$ mm, $W = 10$ mm, $H = 6$ mm, COI
259 barcode MW444344.

260 **Etymology** This species is named after the oldest German confectionary Café Prinzess (1686, Regensburg,
261 Germany) that sells chocolates in the form of molluscs. The species name is to be considered as a noun in
262 apposition for nomenclature.

263 **External morphology** (Fig. 10) Body 17 mm long, 10 mm wide, 6 mm high. Colour milky white in live and
264 preserved specimens, with distinct white pigmentation in apex of dorsal knobs and mantle margin. Central ridge
265 straight, mainly composed of knobs. Head ridge and ridge between rhinophoral sheaths absent. Notal margin lined
266 with knobs, with 4 extensions per side. Rhinophoral sheath laterally connected to notal margin, margin with

267 tubercles (Fig. 10a). Velum bilobed, velar margin with 10 extremely short processes. Lips oval (Fig. 10d). Foot $\frac{1}{4}$
268 of notum in width (Fig. 10e).

269 **Jaws and radula** (Fig. 11a–d) Jaws subquadrangular; light brown; yellow to amber at masticatory border.
270 Masticatory border short, coarse. Spike subterminal, coarse. Radular formula 49 x 60.1.1.1.60. Rachidian tooth as
271 long as broad; cusp extremely short, with fine ridge in the middle. First lateral tooth not visible on the SEM images.
272 Outer lateral teeth progressively hook-shaped, thick, smooth.

273 **Male reproductive system** (Fig. 6c) The specimen is a juvenile. Vas deferens (Fig. 6c) very short, 2 folds. Penial
274 papilla short, conical, without any characteristic features yet developed.

275 **Ecology** Occurs at depths from 20–40 m (this study). Spindle sclerites of gorgonians were present in gut content
276 of dissected specimen, belonging to Primnoidae (Fig. 11e–f). Spindle rod-like, straight, curved, or irregular;
277 usually densely tuberculated (Fig. 11f).

278 **Distribution** This singleton was found only off King George Island (this study).

279 **Remarks** *Tritoniella prinzei* differs from its congeners by thick and white-sparkled knobs constructing the central
280 ridge, also lining the notal margin.

281 ***Tritoniella gnathodontata* n. sp.**

282 (Figs. 6d, 12–13, S2)

283 *Tritoniella* sp. 3 Moles, Berning, et al. (2021).

284 **ZooBank registration** urn:lsid:zoobank.org:act:E238FCB4-8036-414D-8B10-F51776F66C1E

285 **Type locality** South Georgia, 53.8069° S 37.2170° W; 140–144 m depth.

286 **Diagnosis** Colour white, body conical, anteriorly broad. Central ridge slim, notum with few knobs. Notal margin
287 with many extensions. Jaws quadrangular, spike subterminal, masticatory border with rows of denticles.
288 Consecutive laterals very thin. Vas deferens long, penial papilla stout, flattened.

289 **Material examined** South Georgia, 53.8069° S 37.2170° W, 140–144 m, 2 spcs., 1 dissected, SIO-BIC M12606
290 (holotype), $L = 24$ mm, $W = 10$ mm, $H = 8$ mm, COI barcode MW444345, SIO-BIC M12648 (paratype), $L = 42$
291 mm, $W = 22$ mm, $H = 15$ mm, COI barcode MW444348; 55.0515° S 35.3955° W, 119 m depth, 2 spcs., 1 dissected

292 and sequenced, SIO-BIC M12939 (paratype), $L = 33\text{--}35$ mm, $W = 13\text{--}14$ mm, $H = 9\text{--}11$ mm, COI barcode
293 MW444349. Shag Rocks, 53.4240° S 42.0177° W 149–160 m depth: 1 spc., SIO-BIC M12618B, $L = 32$ mm, W
294 $= 10$ mm, $H = 9$ mm, COI barcode MW444347; 53.4532° S 42.0579° W, 169–186 m depth: 9 spcs., SIO-BIC
295 M12609, $L = 12\text{--}26$ mm, $W = 5\text{--}12$ mm, $H = 3\text{--}8$ mm, COI barcode MW444346; 53.7211° S 41.4627° W, 180 m
296 depth: 2 spcs., SIO-BIC M13488, $L = 22\text{--}26$ mm, $W = 9$ mm, $H = 7\text{--}8$ mm, COI barcode MW444350; 53.5343°
297 S 41.6339° W, 132–133 m depth: 2 spcs., 1 dissected and sequenced, SIO-BIC M13489, $L = 20\text{--}21$ mm, $W = 8$
298 mm, $H = 6\text{--}8$ mm, COI barcode MW444351. Discovery Bank, 60.1457° S 34.9199° W, 427–751 m depth, 1 spc.,
299 SIO-BIC M13492, $L = 38$ mm, $W = 10$ mm, $H = 9$ mm, COI barcode MW444352.

300 **Etymology** The name indicates the diagnostic presence of dentition on the masticatory border of the jaws.

301 **External morphology** (Fig. 12) Body 12–42 mm long, 5–22 mm wide, 3–15 mm high; elongated, often conical
302 with a broad head. Living specimens milky white to translucent pink. Dorsal mantle surface with central ridge,
303 straight or wavy, often broken, sometimes with side ridge on right side at $\frac{1}{2}$ of length, running to $\frac{3}{4}$ of the total
304 length; with few knobs. One knob or small head ridge central on head, not connected to central ridge; body margins,
305 and knobs with white pigmentation (subepithelial). Notal margin with 5 to 7 extensions per side. Rhinophoral
306 sheath large, sometimes extended laterally and connected to notal margin, margin smooth (Fig. 12a, c). Foot $\frac{1}{2}$ of
307 notum in width (Fig. 12b).

308 **Jaws and radula** (Figs. 13a–d, S2a–d) Jaws subquadrangular to quadrangular; amber in colour; masticatory border
309 darker. Masticatory border long; with several rows of conspicuous denticles. Spike internal, with denticles. Radular
310 formula 47–53 x 54–63.1.1.1.54–63. Rachidian tooth as long as broad; cusp very distinct, acute; with a lateral
311 small cusps per side. First lateral tooth with thick, short cusp. Outer lateral teeth very thin, progressively hook-
312 shaped, smooth.

313 **Male reproductive system** (Figs. 6d, 13e, f, S2e, f) Vas deferens long, 15 folds. Penial papilla short; with broad,
314 flat tip.

315 **Ecology** Occurs at depths from 119–751 m (this study). Plates and spindle sclerites of gorgonians present in the
316 gut content of dissected specimens, belonging to Primnoidae (Fig. 13g–h). Plates elongated squarish, oval or
317 irregular; thick or thin; dorsally with tubercles on inner side, sometimes with longitudinal central crest; ventrally
318 smooth (Fig. 13g–h). Spindles spherical, rod-like, or irregular; generally tuberculated (Fig. 13g).

319 **Distribution** Shag Rocks and South Georgia (this study); 119–751 m depth.

320 **Remarks** *Tritoniella gnathodentata* externally differs from its congeners by a conical body shape, faint dorsal
321 ridge, and prominent margin knobs. Internally, this is the only species with denticles on the masticatory border
322 (found in all three specimens dissected from South Georgia and Shag Rocks).

323 *Tritoniella schoriesi* n. sp.

324 (Figs. 6e, 14–15)

325 *Tritoniella* sp. 4 Moles, Berning, et al. (2021).

326 **ZooBank registration** urn:lsid:zoobank.org:act:11869CAF-3AA3-4541-8219-408B66CE49D6

327 **Type locality** Coronation Island, South Orkney Islands, 60.5509° S 45.1761° W; 222–278 m depth.

328 **Diagnosis** Colour white to bright orange. Central ridge slim, elevated, notum broad with many knobs. Notal margin
329 with many extensions, strongly serrated. Jaws subquadrangular, spike subterminal. Vas deferens long, penial
330 papilla elongated, tip pointed.

331 **Material examined** Coronation Island, South Orkney Islands, 60.5509° S 45.1761° W, 222–278 m depth: 1 spc.,
332 SIO-BIC M12599 (holotype), $L = 36$ mm, $W = 10$ mm, $H = 8$ mm, COI barcode MW444353. Ardley Island, King
333 George Island, Bransfield Strait, 62.2103° S 58.9139° W, 20–40 m depth: 1 spc., dissected and sequenced, ZSM
334 20110202-02 (paratype), $L = 54$ mm, $W = 26$ mm, $H = 27$ mm, COI barcode MW444354.

335 **Etymology** This species is named after Dirk Schories who collected and documented the analysed specimens
336 while SCUBA diving at King George Island.

337 **External morphology** (Fig. 14) Body 36–56 mm long, 10–26 mm wide, 8–27 mm high. Colour beige in preserved
338 specimens (Fig. 14a–c), living specimens translucent white to bright orange (Fig. 14d). Dorsal mantle surface with
339 faint longitudinal central ridge, straight, with a side ridge on the right side, at $\frac{1}{2}$ of body length; short head ridge
340 central on the head, not connected to central ridge; with subepithelial white pigmentation below knobs and
341 tubercles, interspersed all over notum. Notal margin with up to 11, strongly serrated extensions per side.
342 Rhinophoral sheath large, extended laterally and connected to notal margin; ridge between sheaths extremely
343 elevated, more than central ridge (Fig. 14a). Velum bilobed; velar margin with up to 12 extremely short processes;
344 oral tentacles large, ear-shaped, elongated laterally. Lips oval (Fig. 14e). Foot $\frac{1}{2}$ of notum in width (Fig. 14b).

345 **Jaws and radula** (Fig. 15a–d) Jaws subquadrangular; lower part pointed; amber in colour; masticatory border
346 darker. Masticatory border very long, coarse. Spike coarse. Radular formula 68 x 109.1.1.1.109. Rachidian tooth
347 as long as broad; with small lateral cusps on both sides of median cusp. First lateral tooth with blunt cusp. Outer
348 lateral teeth hook-shaped, smooth; inner lateral teeth with sharp tip curved inward.

349 **Male reproductive system** (Figs. 6e, 15e, f) Vas deferens very long, 25 folds. Penial papilla long, bud-shaped;
350 with circular enlargement close to the tip; tip cone-shaped.

351 **Ecology** Occurs at depths from 20–278 m (this study). Plates, spindle sclerites and inner axis of gorgonians were
352 present in the gut content of the dissected specimens, belonging to Primnoidae (Fig. 13g–h). Plates elongated
353 squarish or oval, with dense, coarse tubercles on inner side (Fig. 13g). Spindles rod-like, straight or bifurcated,
354 tuberculated (Fig. 13h).

355 **Distribution** Known from Ardley, King George, Coronation, and South Orkney Islands (this study); 20–278 m
356 depth.

357 **Remarks** *Tritoniella schoriesi* differs from its congeners by a thin, elevated central ridge, a strongly serrated and
358 wavy notal margin, and a bright orange colouration (even though this might be dietary dependent; Rossi et al.,
359 2021).

360 ***Tritoniella heideae* n. sp.**

361 (Figs. 6f, 16, 17, S3)

362 *Tritoniella* sp. 5 Moles, Berning, et al. (2021).

363 **ZooBank registration** urn:lsid:zoobank.org:act:95E0D612-CCE0-4C40-B7B9-66E6449E1FCC

364 **Type locality** Ardley Island, King George Island, Bransfield Strait, 62.2103° S 58.9139° W; 20–40 m depth.

365 **Diagnosis** Colour translucent white to pink, central ridge straight, broad. Notum and notal margins covered with
366 knobs. Jaws subquadrangular, spike subterminal. First lateral sometimes with median cusp, consecutive laterals
367 with sharp tip, curved inwards. Vas deferens long, penial papilla elongated, tip pointed.

368 **Material examined** Ardley Island, King George Island, Bransfield Strait, 62.2103° S 58.9139° W, 20–40 m depth:
369 7 spcs., 2 dissected and 5 sequenced, ZSM 20141003 (paratype), $L = 47$ mm, $W = 30$ mm, $H = 20$ mm, COI barcode

370 MW444366, ZSM 20141004 (paratype), $L = 53$ mm, $W = 34$ mm, $H = 21$ mm, COI barcode MW444367, ZSM
371 20141005 (paratype), $L = 26$ – 51 mm, $W = 11$ – 22 mm, $H = 9$ – 20 mm, COI barcode MW444368, ZSM 20110221-
372 06 (holotype), $L = 51$ mm, $W = 33$ mm, $H = 22$ mm, COI barcode MW444365, ZSM 20110202-01 (paratype), L
373 $= 53$ mm, $W = 21$ mm, $H = 17$ mm, COI barcode MW444364. Montagu Island, South Sandwich Islands, 58.3773°
374 S 26.2824° W, 153–420 m depth: 3 spcs., sequenced, SIO-BIC M12617A, $L = 29$ mm, $W = 11$ mm, $H = 11$ mm,
375 COI barcode MW444359, SIO-BIC M12617B, $L = 24$ mm, $W = 12$ mm, $H = 7$ mm, COI barcode MW444360,
376 SIO-BIC M12617C, $L = 23$ mm, $W = 14$ mm, $H = 7$ mm, COI barcode MW444361; 58.3845° S 26.2813° W, 147–
377 262 m depth: 1 spc., sequenced, SIO-BIC M12608, $L = 31$ mm, $W = 15$ mm, $H = 12$ mm, COI barcode MW444357;
378 59.3936° S 27.3227° W, 110–188 m depth: 2 spcs., 1 sequenced, SIO-BIC M13011, $L = 12$ – 26 mm, $W = 7$ – 11
379 mm, $H = 4$ – 8 mm, COI barcode MW444363. Bransfield Strait, 62.8695° S 57.2168° W, 150–247 m depth: 1 spc.,
380 sequenced, SIO-BIC M12593, $L = 28$ mm, $W = 9$ mm, $H = 6$ mm, COI barcode MW444356; 62.7529° S 57.3217°
381 W, 272–292 m depth: 1 spc., sequenced, SIO-BIC M12615, $L = 35$ mm, $W = 12$ mm, $H = 10$ mm, COI barcode
382 MW444358; 63.3228° S 59.8511° W, 197–199 m depth: 1 spc., sequenced, SIO-BIC M12581B, $L = 31$ mm, $W =$
383 18 mm, $H = 11$ mm, COI barcode MW444355.

384 **Etymology** This species is dedicated to Heide Schulz for her research enthusiasm and merits in marine
385 microbiology.

386 **External morphology** (Fig. 16) Body 23–53 mm long, 9–34 mm wide, 6–21 high. Living specimens from
387 transparent white, pink to light orange (Fig. 16d). Dorsal mantle surface with thick longitudinal central ridge, not
388 reaching end of tail, straight; with knobs and tubercles, interspersed all over notum; one large tubercle or small
389 head ridge central on head, not connected to central ridge. Central ridge, body margins, and knobs with white
390 pigmentation (subepithelial). Notal margin with 5 to 7 extensions per side. Rhinophoral sheath large, extended
391 laterally, connected to notal margin (Fig. 16a). Velum single-lobed, oral tentacles extended posterolaterally; velar
392 margin with 9 to 14 short processes (Fig. 16e).

393 **Jaws and radula** (Figs. 17a–d, S3a–d) Jaws subquadrangular; amber in colour, masticatory border darker.
394 Masticatory border short, coarse. Spike very coarse. Radular formula 55–64 x 95–101.1.1.1.95–101. Rachidian
395 tooth as long as broad; with lateral cusps on both sides of median cusp. First lateral tooth short, thick cusp, with
396 lateral cusps on median side. Outer lateral teeth progressively hook-shaped, smooth; inner lateral teeth with sharp
397 tip curved inward.

398 **Male reproductive system** (Figs. 6f, 17e, f, S3e, f) Vas deferens very long, 17 folds. Penial papilla long, cone-
399 shaped; with circular, broad enlargement close to tip; tip flat, cone-shaped.

400 **Ecology** Occurs at depths from 20–420 m (this study). Plates and spindle sclerites and inner axis of gorgonian
401 present in the gut content of the dissected specimens, belonging to Primnoidae (Fig. 17g–h). Plate elongated
402 squarish, oval or arrow-like, with dense tubercles on the inner side (Fig. 17g). Spindle spherical, rod-like (straight,
403 curved, bi- or trifurcated) or irregular; tuberculated (Fig. 17g).

404 **Distribution** Bransfield Strait, Ardley Island (King George Island) and Montagu Island (South Sandwich Islands)
405 (this study); 20–420 m depth.

406 **Remarks** *Tritoniella* resembles most features of *T. belli* although it appears slenderer, with a thinner, knob-
407 interspersed notum.

408

Discussion

409

Systematics and Taxonomy of *Tritoniella*

410 In this study, we describe five new species of *Tritoniella* and redescribe *T. belli* by providing a comparative
411 morpho-anatomical and ecological analysis. The newly described species were collected in the Weddell and the
412 Scotia Seas from the infralittoral to 751 m in depth. We also reassessed the type material of each of the two species
413 of *Tritoniella* described to date, *T. belli* and *T. sinuata*, maintaining their synonymy until additional material from
414 the type locality is gathered. *Tritoniella belli* and *T. sinuata* were originally described based on minor anatomical
415 differences in the dentition (rachidian and lateral teeth), jaw length, reproductive organs (tip of penial papilla), and
416 stomach ridges. These characteristics seem to be prone to substantial changes by fixation and intraspecific
417 variation, which makes differentiation of the two species impossible (Odhner, 1926, 1934; see discussion of
418 Wägele, 1989b). Odhner (1934) tried to distinguish the species by the shape of the rachidian, the first lateral teeth,
419 and the masticatory border, after emphasizing that differentiation by outer morphology and penis shape was
420 impossible (see discussion of Wägele, 1989b). Wägele (1989b) later argued that even those differences are caused
421 by fixation and individual variability, which led to the synonymy of both species. Here, the reassessment of the
422 type material and a thorough comparison with our five new species (delimited with molecular data) does not
423 provide evidence of the validity nor synonymy of *T. sinuata* to any of the species here described. Thus, we will
424 conservatively retain the synonymy of *T. sinuata* to *T. belli* until additional sampling in the type locality, the Ross
425 Sea, and molecular data suggest otherwise.

426 Here, we primarily provide external morphological descriptions to enable easier identification of live
427 *Tritoniella* species for future expeditions (see Table 1 for comparison), although further anatomical characters are
428 given for comparative purposes. *Tritoniella belli* can be identified by a broad central ridge that is especially
429 prominent between the rhinophoral sheaths (Eliot 1907; Wägele; this study 1989b). The notum in this species is
430 broad and sparsely, but evenly, covered by knobs, except for the central ridge and the relatively smooth notal
431 margin. *Tritoniella gnocchi* n. sp. shows a bloated body with an extremely faint ridge that can only be seen in the
432 anterior part of the smooth notum, with the caveat that we only had a single specimen at our disposal. The notal
433 margin shows several serrated extensions. *Tritoniella prinzeß* n. sp. shows the only central ridge that is composed
434 of single knobs. The notum shows few additional knobs with a particular white pigmentation (subepidermal
435 glands). The notal margin is continuously lined by these thick knobs. *Tritoniella gnathodentata* n. sp. shows a
436 conical body with a broad head that narrows posteriorly. The notum shows a slim central ridge and few knobs, and
437 the notal margin shows many extensions. *Tritoniella schoriesi* n. sp. has a white to bright orange body, a slim and
438 elevated central ridge, and knobs interspersed all over the broad notum. The notal margin is strongly serrated with
439 many extensions. *Tritoniella heideae* n. sp. has a translucent white to pink colouration and a thick and straight
440 central ridge. The notum and notal margins are covered by knobs. The shape of the jaws ranges from oval (*T.*
441 *belli*), to subquadrangular (*T. gnocchi* n. sp., *T. prinzeß* n. sp., *T. schoriesi* n. sp. and *T. heideae* n. sp.) to
442 quadrangular (*T. gnathodentata* n. sp.). Jaws are light yellow to amber in colour with darker colouration at the
443 masticatory border in all species. The spike of the masticatory border is either terminal (*T. gnocchi* n. sp.) or
444 subterminal (other species). The edges of the masticatory border are either smooth or coarse, with a clear
445 denticulation shown only in *T. gnathodentata* n. sp. Concerning the radula, the rachidian teeth generally have a
446 protruding, median cusp (which is absent in *T. gnocchi* n. sp., although it might be eroded, as it also presents lateral
447 linear grooves), and lateral cusps in some species (reported in *T. belli* by Wägele, 1989a but not observed in this
448 study, *T. gnathodentata* n. sp., *T. schoriesi* n. sp. and *T. heideae* n. sp.). The first laterals usually have a stout, short
449 cusp that can be blunt. *Tritoniella gnocchi* n. sp. also shows the first laterals pointing upwards and *Tritoniella*
450 *heideae* n. sp. has lateral cusps on the median side of the first lateral (ZSM 20110202-01). Subsequent lateral teeth
451 are generally progressively hook-shaped and have their tips curved sharply inward in *T. gnocchi* n. sp., *T. schoriesi*
452 *n. sp.* and *T. heideae* n. sp., especially in the inner laterals. Outer laterals are very thin in *T. gnathodentata* n. sp.
453 The reproductive system shows an overall similar organization in all species (see Fig. 7 for schematic
454 representation in *T. belli*). Major differences can be seen in the length and the number of loops of the vas deferens
455 (Fig. 6), although this may be related to age. Yet, the vas deferens is relatively short in *T. belli* and *T. gnathodentata*
456 n. sp., while elongated in *T. schoriesi* n. sp. and *T. heideae* n. sp. The shape of the penial papilla also ranges from

457 stout and flattened in *T. gnocchi* n. sp. and *T. gnathodentata* n. sp. to elongated with a pointed tip in the other
458 species. Both singleton species are either juvenile (*T. prinzeß* n. sp.) or sub-adult (*T. gnocchi* n. sp.) and show
459 only partly developed reproductive organs, so precise statements of their adult characteristics should be re-
460 evaluated once more adult specimens have been collected.

461 Biogeographic Patterns

462 The distribution of the *Tritoniella* species can be explained by their phylogeny (see Fig. 18). While in this study
463 *T. belli* was only found in the Ross and Weddell Seas, a circumpolar distribution seems plausible. Its congeners
464 however have only been recorded in the Scotia Arc, where *T. belli* presence was discarded by molecular analyses.
465 One of its closest related species, *T. schoriesi* n. sp. is distributed between King George and the South Orkney
466 Islands in relatively close vicinity to the Antarctic shelf. The other, *Tritoniella heideae* n. sp. is distributed between
467 King George and the South Sandwich Islands, a range encompassing the whole southern part of the Scotia Arc.
468 Sister to this triad of taxa, *T. gnathodentata* n. sp. ranges from Shag Rocks in the north to the Discovery Bank in
469 the south of the Scotia Sea. *Tritoniella prinzeß* n. sp. was only found at King George Island, while the sister group
470 to all other *Tritoniella* species – *T. gnocchi* n. sp. – was only found on the other side of the Scotia Arc and the
471 Polar Front, south of the Falkland Islands. Similarly, the single high-altitude Antarctic species of *Tritonia*, *T.*
472 *antarctica*, is also found circumpolar and its siblings are systematically found in the subantarctic islands of the
473 Scotia Arc (Moles, Berning, et al., 2021). This speciation event could be explained by ‘synopsis’ (Clarke & Crame,
474 1992); the combination of distribution range changes caused by glacial cycles, and the existence of refugia on the
475 continental shelf allow populations to survive (Fraser et al., 2012, 2014; Thatje et al., 2005). These surviving
476 populations were small, therefore favouring genetic drift, and in combination with their low dispersal could have
477 speciated before intermixing again with other surviving populations. These allopatric speciation events of cryptic
478 species are also known from other groups like Isopoda, Crinoidea and Mollusca (Held, 2003; Held & Wägele,
479 2005; Wilson et al., 2007). *Tritoniella* species may have followed the same patterns due to their direct development
480 in adherent egg clutches (Wägele, 1989a). Pseudocryptic speciation is one of the reasons why Antarctic mollusc
481 biodiversity is sharply increasing in recent years (Linse et al., 2007).

482 Conclusions

483 The detailed morphological revision of the genus *Tritoniella* has provided valuable insight into a seemingly cryptic
484 species complex in the SO and has unearthed the need to review old taxonomic groups with genetic data. Although
485 we provide a morpho-anatomical description of five species delimited by molecular data, the issue with *T. belli*

486 and *T. sinuata* is still not yet fully resolved, thus requiring more sampling and systematic work, especially in the
487 type locality (Ross Sea). Taxonomic work using a combination of both morphological and molecular methods is
488 important for the better estimation of the biodiversity of the SO and should be considered as the foundation that
489 chemical, ecological, reproductive, and population studies rely upon. Further, taxonomic work in geographic
490 locations that include thermal clines – like the fronts of the ACC – could help to understand future changes caused
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492

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607

608

Figure Captions

609 **Fig. 1** Map of the Southern Ocean with sampling stations across the Scotia and Weddell Seas depicted in Arc-GIS,
610 colour-coded by species. Yellow circles: *Tritoniella belli*; green crosses: *Tritoniella gnocchi* n. sp.; blue
611 diamonds: *Tritoniella prinze* n. sp.; purple triangles: *Tritoniella gnathodontata* n. sp.; red squares: *Tritoniella*
612 *schoriesi* n. sp.; orange stars: *Tritoniella heideae* n. sp.

613 **Fig. 2** Holotype of *Tritoniella belli* (NHMUK 1906.7.5.1). A, dorsal view. B, ventral view. C, lateral, left view.
614 D, lateral, right view. Pictures © by the Natural History Museum of London; taken by Kevin Webb, NHMUK
615 Photographic Unit. This image is not covered by the terms of the Creative Commons licence of this publication.
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617 **Fig. 3** Holotype of *Tritoniella sinuata* (NHMUK 1919.9.16.3). A, dorsal view. B, ventral view. C, lateral, left
618 view. D, lateral, right view. Pictures © by the Natural History Museum of London; taken by Kevin Webb, NHMUK
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621 **Fig. 4** Specimens of *Tritoniella belli* ZSM 20090522 (but live picture). A, dorsal view. B, ventral view. C, lateral
622 view. D, live picture of a specimen of *T. belli* from McMurdo Sound taken by Peter Brueggemann. E, ventral view
623 of the anterior part with velum

624 **Fig. 5** Characteristic body parts of *Tritoniella belli* specimen ZSM 20090522 (A–D) and ZSM 20012253 (E–F).
625 A, jaws. B, scanning electron micrograph (SEM) of the jaws showing masticatory border (mb) with a spike (sp).
626 C–D, SEM of radula showing rachidian (rh) teeth, first (fl) and subsequent (cl) lateral teeth. E, SEM of the penial
627 papilla. F, SEM close-up of the penial papilla showing the tip (t)

628 **Fig. 6** Schematic drawings of the male reproductive system showing vas deferens (vd) and penial papilla (pp). A,
629 *Tritoniella belli*. B, *T. gnocchi n. sp.* C, *T. prinzeß n. sp.*, pp was attached to penial sheath where parallel lines
630 are depicted D, *T. gnathodontata n. sp.*, ring surrounding pp depicting connective tissue E, *T. schoriesi n. sp.* F,
631 *T. heideae n. sp.*

632 **Fig. 7** Schematic drawing of the anterior part of the reproductive system of *Tritoniella belli*. Abbreviations: A,
633 ampulla; Fgl, female glands; Vdu, vaginal duct; Pes, penial sheath (including penial papilla); R, seminal receptacle;
634 Vd, vas deferens

635 **Fig. 8** Holotype of *Tritoniella gnocchi n. sp.* (SIO-BIC M13502). A, dorsal view. B, ventral view. C, lateral view.
636 D, live picture. E, ventral view of the anterior part with velum

637 **Fig. 9** Characteristic body parts of *Tritoniella gnocchi n. sp.* specimen SIO-BIC M13502 (holotype). A, jaws. B,
638 scanning electron micrograph (SEM) of jaws showing masticatory border (mb) with a spike (sp). C, SEM of the
639 radula showing rachidian (rh) teeth, first (fl) and subsequent (cl) lateral teeth. D, SEM of the radula showing a
640 lateral tooth. E, SEM of the penial papilla. F, SEM of the tip (t) of the penial papilla. G, SEM of the gut content,
641 showing plates and capstan sclerites. H, SEM of the gut content showing a gorgonian tuberculated spindle

642 **Fig. 10** Holotype of *Tritoniella prinzeß n. sp.* (ZSM 20141002). A, dorsal view. B, ventral view. C, lateral view.
643 D, live picture. E, ventral view of the anterior part with velum

644 **Fig. 11** Characteristic body parts of *Tritoniella prinzeß n. sp.* specimen ZSM 20141002 (holotype). A, jaws. B,
645 scanning electron micrograph (SEM) of the jaws showing masticatory border (mb) with a spike (sp). C, SEM of
646 the radula showing rachidian (rh) teeth, first (fl) and subsequent (cl) lateral teeth. D, SEM of the radula showing
647 lateral teeth. E, SEM of the gut content, showing rod-like and spindle sclerites. F, detail of the gut content showing
648 a spindle sclerite

649 **Fig. 12** Specimen SIO-BIC M13489 of *Tritoniella gnathodontata n. sp.* A, dorsal view. B, ventral view. C, lateral
650 view. D, live picture. E, ventral view of the anterior part with velum

651 **Fig. 13** Characteristic body parts of *Tritoniella gnathodentata* n. sp. specimen SIO-BIC M12648 (paratype). A,
652 jaws. B, scanning electron micrograph (SEM) of the jaws showing masticatory border (mb) with a spike (sp) with
653 indentation. C, SEM of the radula showing rachidian (rh) teeth, first (fl) and subsequent (cl) lateral teeth. D, SEM
654 of the radula showing lateral teeth. E, SEM of the penial papilla. F, SEM of the penial papilla showing tip (t). G–
655 H, SEM of the gut content, showing sclerites

656 **Fig. 14** Paratype of *Tritoniella schoriesi* n. sp. (ZSM 20110202-02). A, dorsal view. B, ventral view. C, lateral
657 view. D, live picture. E, ventral view of the anterior part with velum

658 **Fig. 15** Characteristic body parts of *Tritoniella schoriesi* n. sp. specimen ZSM 20110202-02 (paratype). A, jaws.
659 B, scanning electron micrograph (SEM) of the jaws showing masticatory border (mb) with a spike (sp). C, SEM
660 of the radula showing rachidian (rh) teeth, first (fl) and subsequent (cl) lateral teeth. D, SEM of the radula showing
661 lateral teeth. E, SEM of the penial papilla. F, SEM of the penial papilla showing tip (t). G, SEM of the gut content,
662 showing sclerites. H, SEM of the gut content showing a spindle sclerite

663 **Fig. 16** Paratype of *Tritoniella heideae* n. sp. (ZSM 20110202-01). A, dorsal view. B, ventral view. C, lateral
664 view. D, live picture. E, ventral view of the anterior part with velum

665 **Fig. 17** Characteristic body parts of *Tritoniella heideae* n. sp. specimen ZSM 20141005B (paratype). A, jaws. B,
666 scanning electron micrograph (SEM) of the jaws showing masticatory border (mb) with a spike (sp). C, SEM of
667 the radula showing rachidian (rh) teeth, first (fl) and subsequent (cl) lateral teeth. D, SEM of the radula showing
668 lateral teeth. E, SEM of the penial papilla. F, SEM of the penial papilla showing tip (t). G, SEM of the gut content,
669 showing sclerites. H, SEM of the gut content showing a gorgonian axis

670 **Fig. 18** Maximum likelihood tree based on concatenated markers COI, 16S, and H3 of all *Tritoniella* species
671 studied here calculated in IQTREE. Bootstrap support values are depicted on branches. The tree includes 35
672 specimens of the six *Tritoniella* species described and the two outgroups *Tochuina gigantea* and *Tochuina*
673 *nigritigris*. Scale bar indicates substitutions per site. For details see Moles, Berning, et al. (2021)

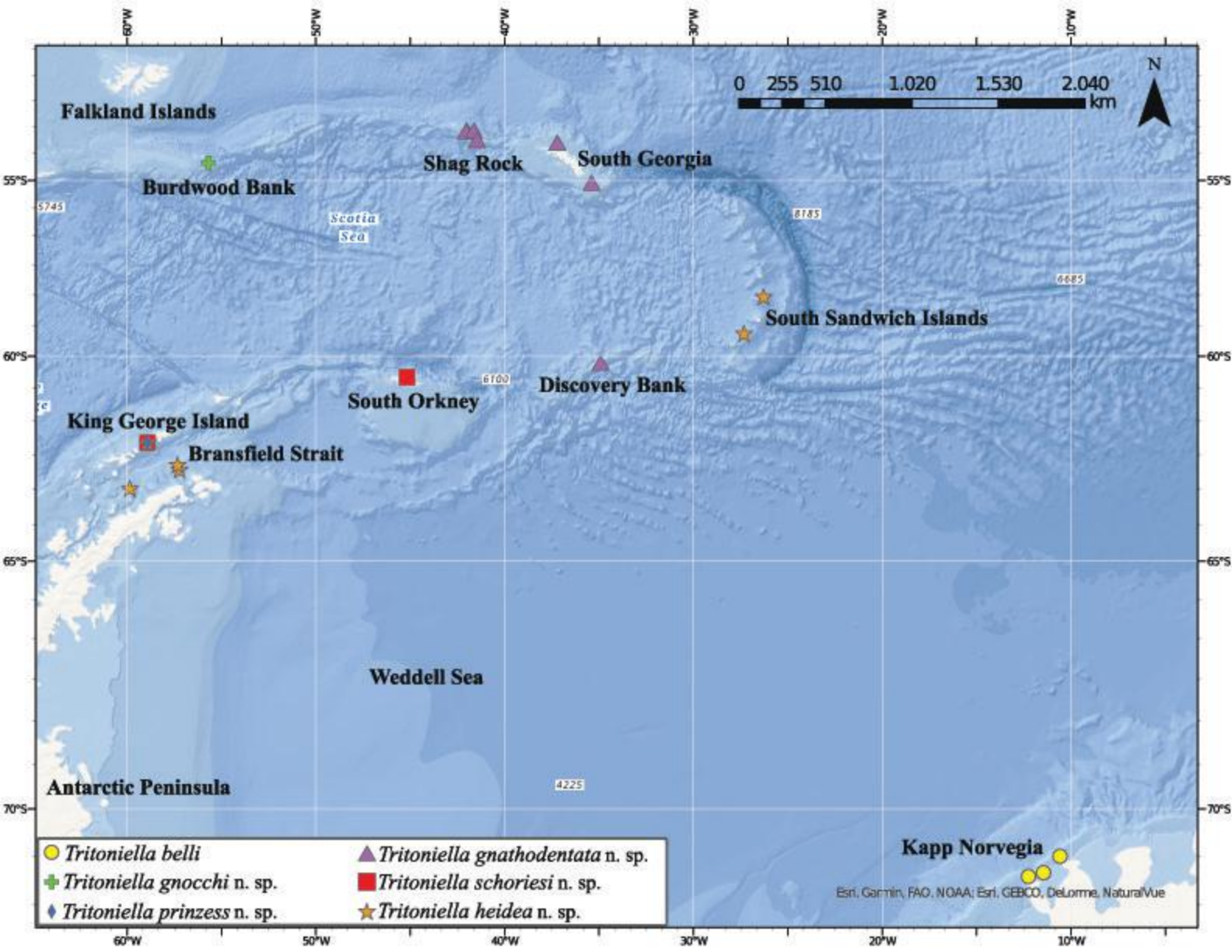
674 **Tab. 1** Diagnostic characters of *Tritoniella* species. Locations of new species as blue crosses on a schematic
675 depiction of the Scotia Arc

676
Supplementary Information

677 **Fig. S2** Characteristic body parts of *Tritoniella gnathodentata* n. sp. Specimen SIO-BIC M13939. A, jaw. B,
678 scanning electron micrograph (SEM) of jaw showing masticatory border (mb) with a spike (sp) with indentation.

679 C, SEM of radula showing rachidian (rh) teeth, first (fl) and subsequent (cl) lateral teeth. D, SEM of radula showing
680 lateral teeth. E, SEM of penial pulp. F, SEM of penial pulp showing tip(t). G, SEM of gut content showing plate
681 sclerite H, SEM of gut content showing spindle sclerite

682 **Fig. S3** Characteristic body parts of *Tritoniella heideae* n. sp. Specimen ZSM 20110202-01. A, jaws. B, scanning
683 electron micrograph (SEM) jaw showing masticatory border (mb) with a spike (sp). C, SEM of radula showing
684 rachidian teeth (rh), first (fl) and subsequent (cl) lateral teeth. D, SEM of radula showing lateral teeth. E, SEM of
685 penial pulp. F, SEM of penial pulp showing tip (t). G, SEM of gut content. H, SEM of gut content showing sclerite



A**B****C****D**

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B

0.5 cm

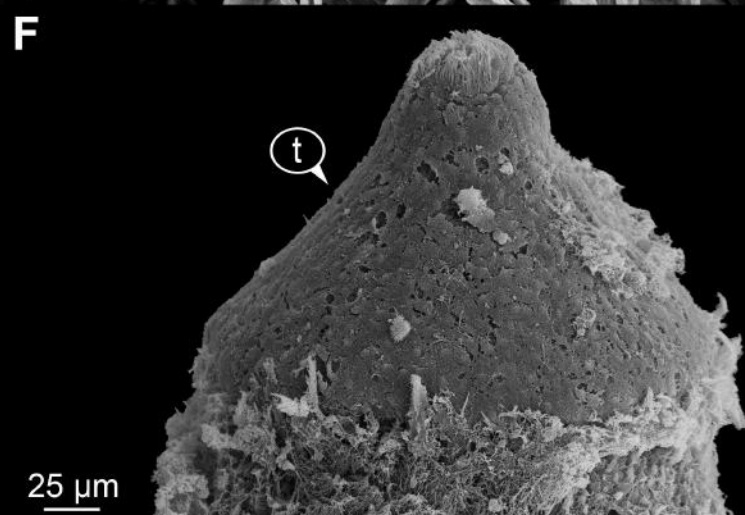
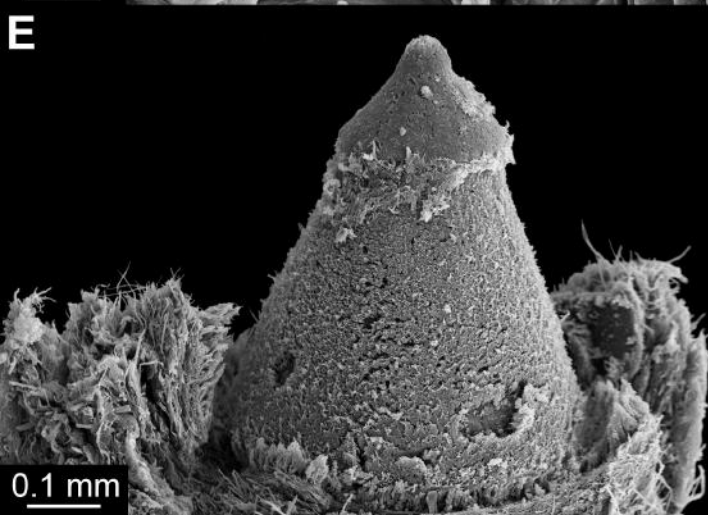
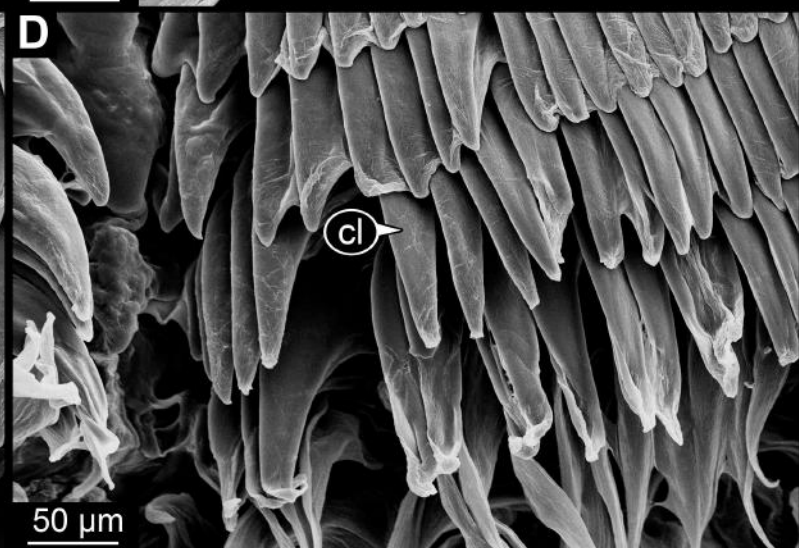
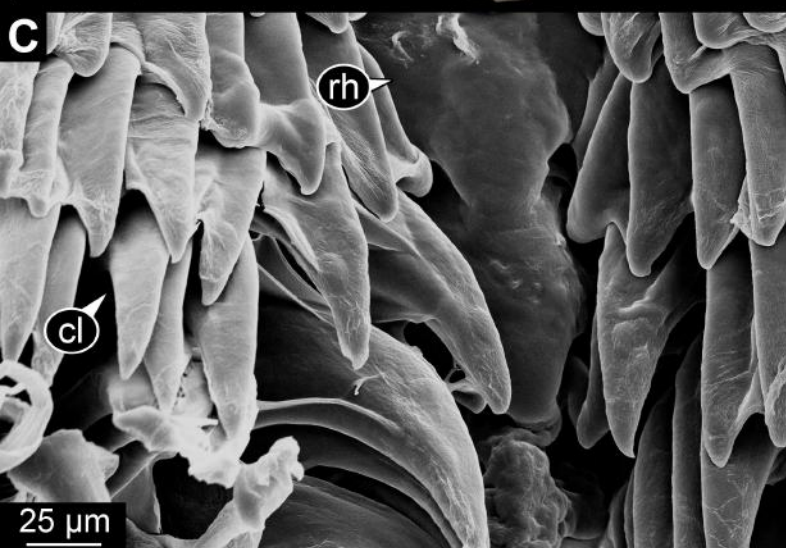
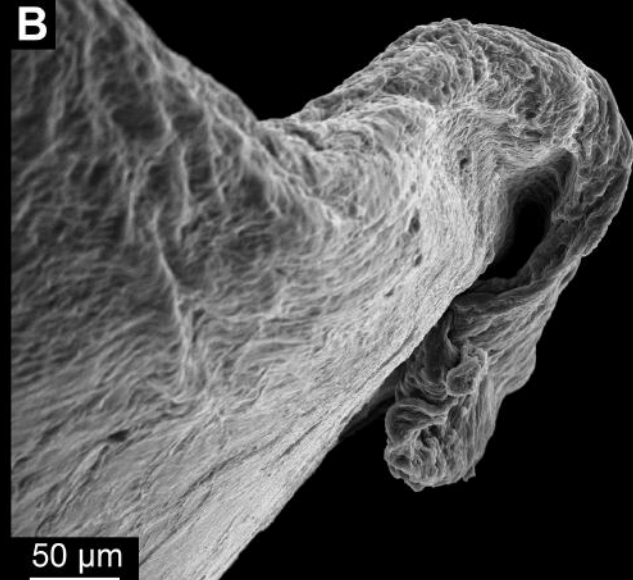
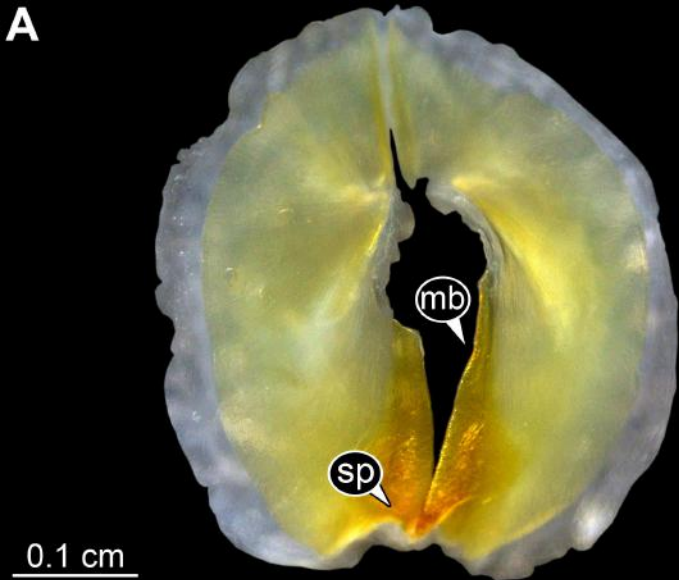
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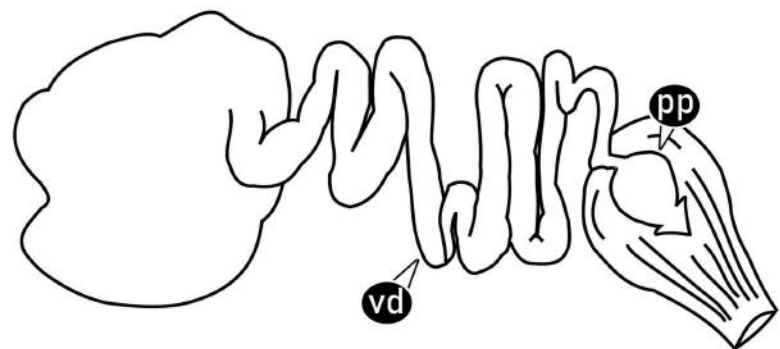
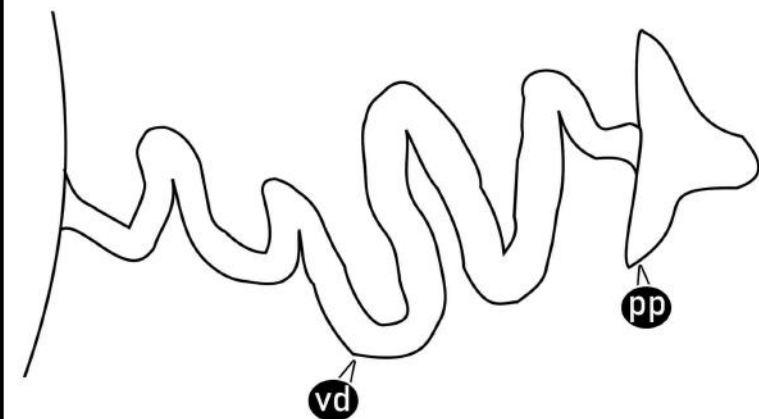
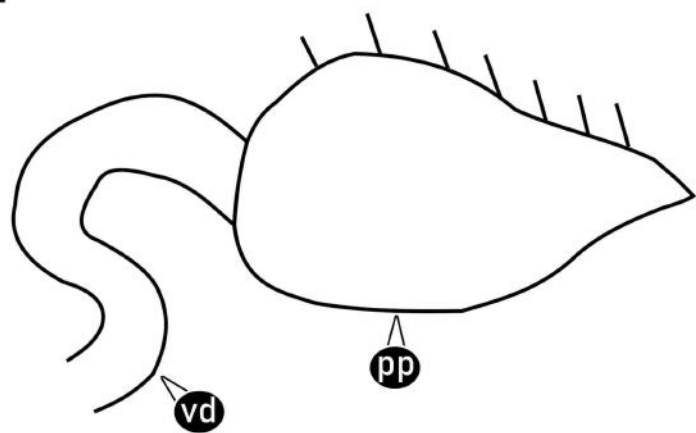
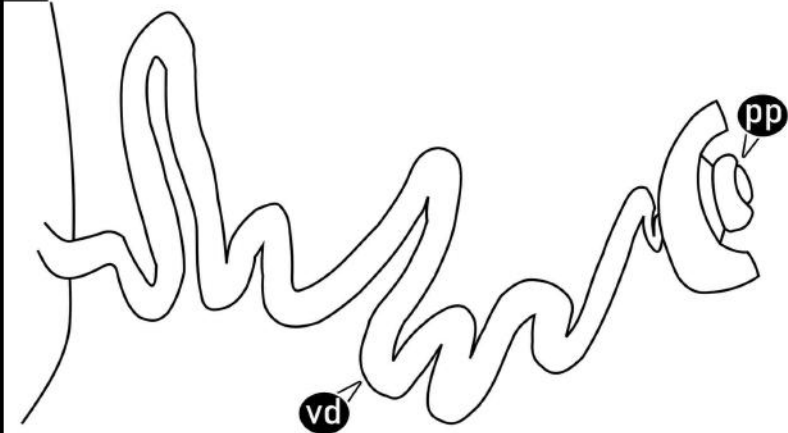
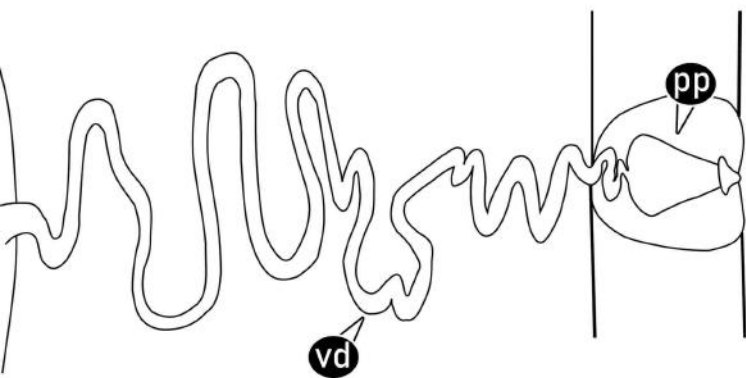
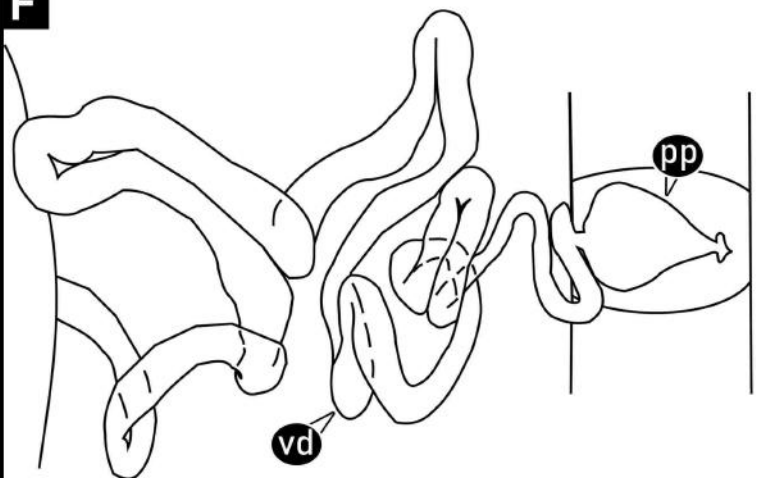
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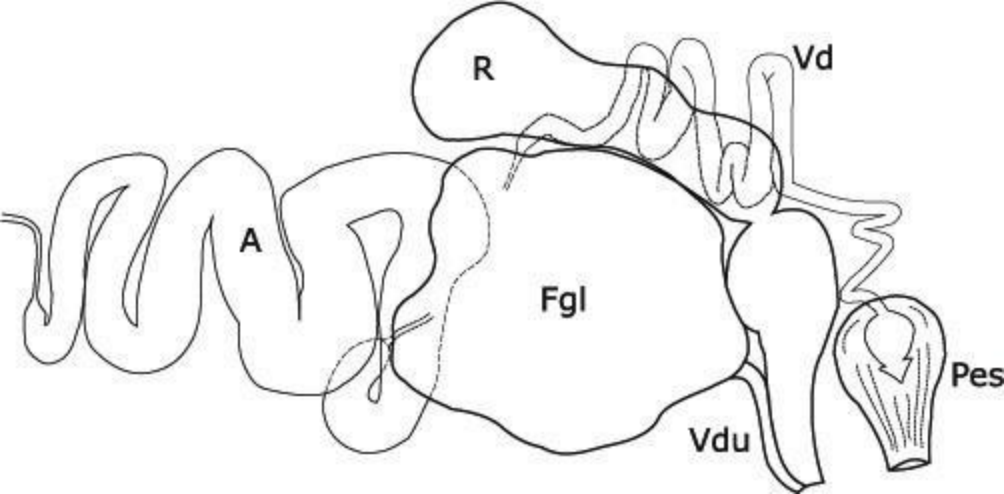
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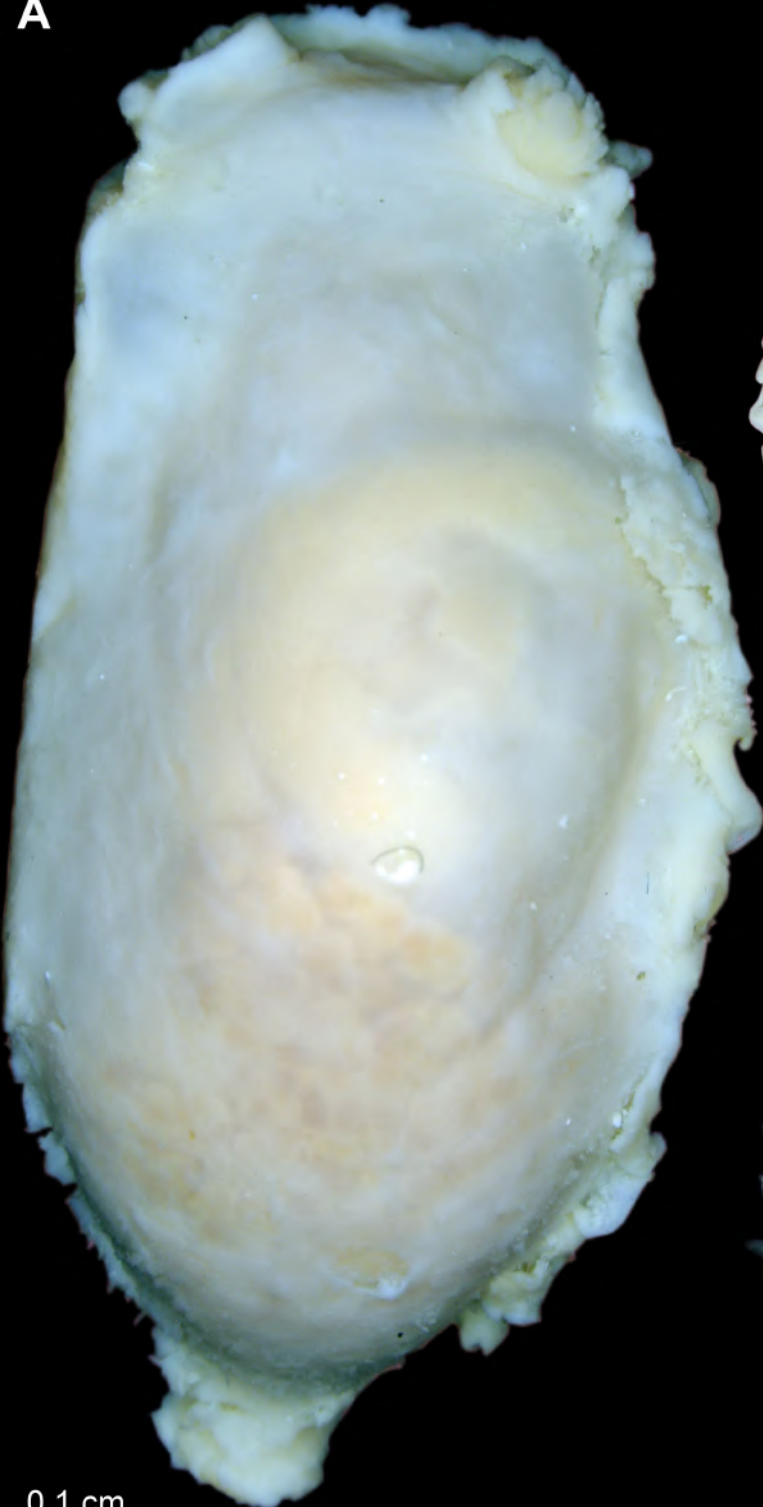
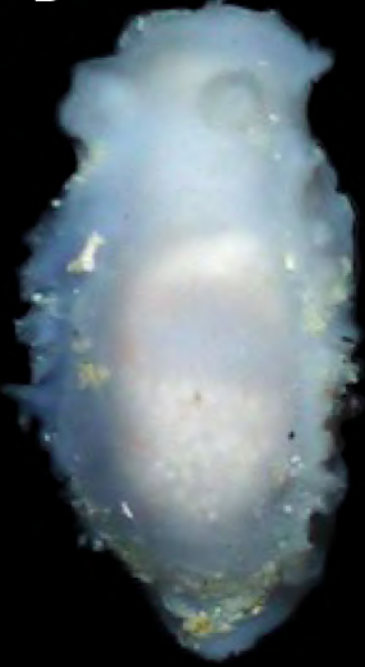
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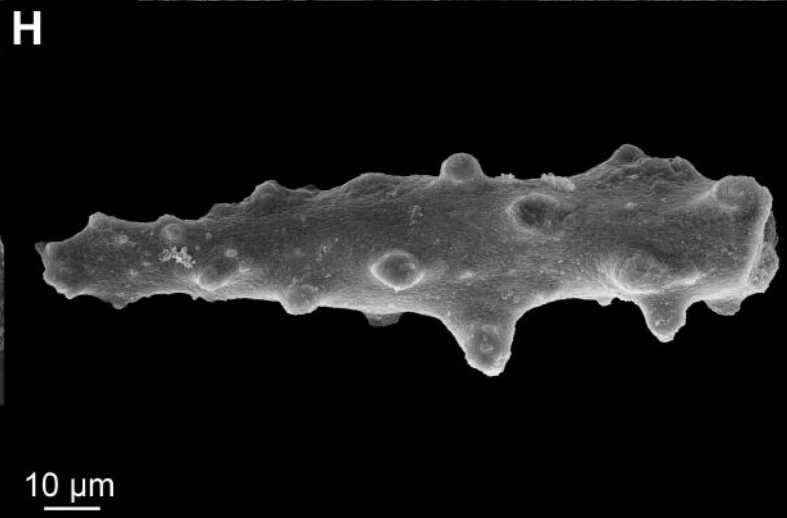
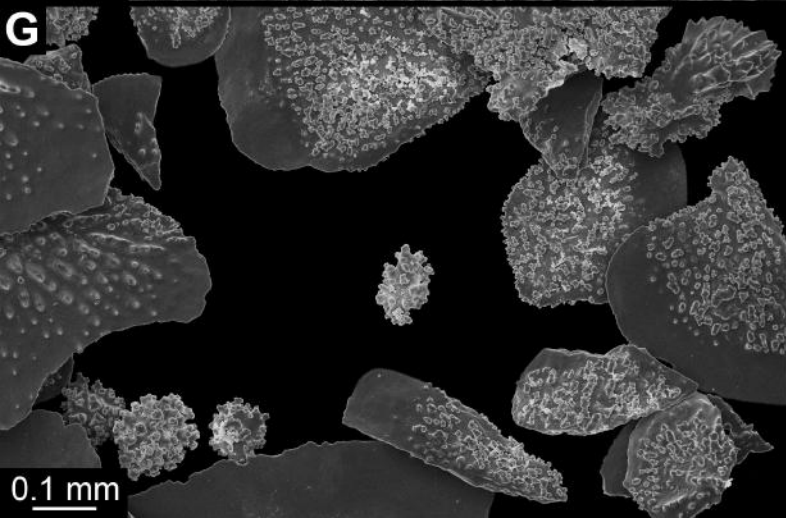
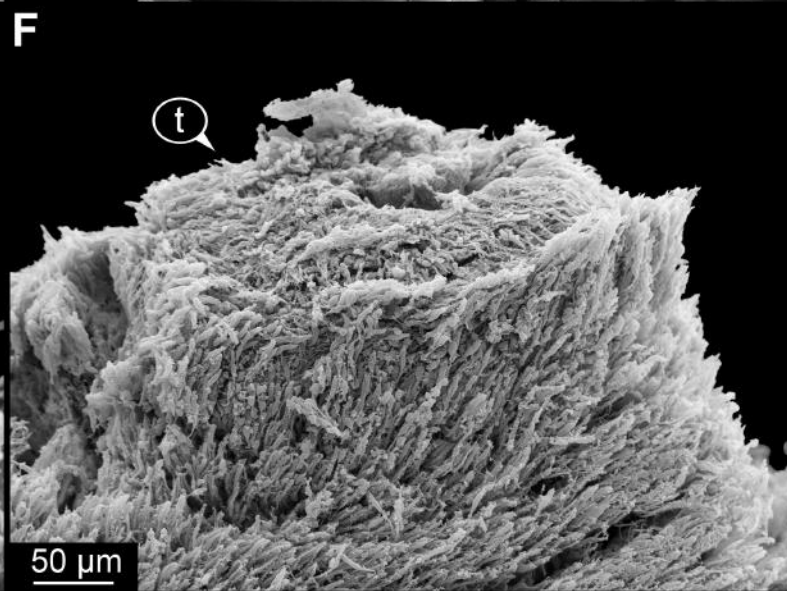
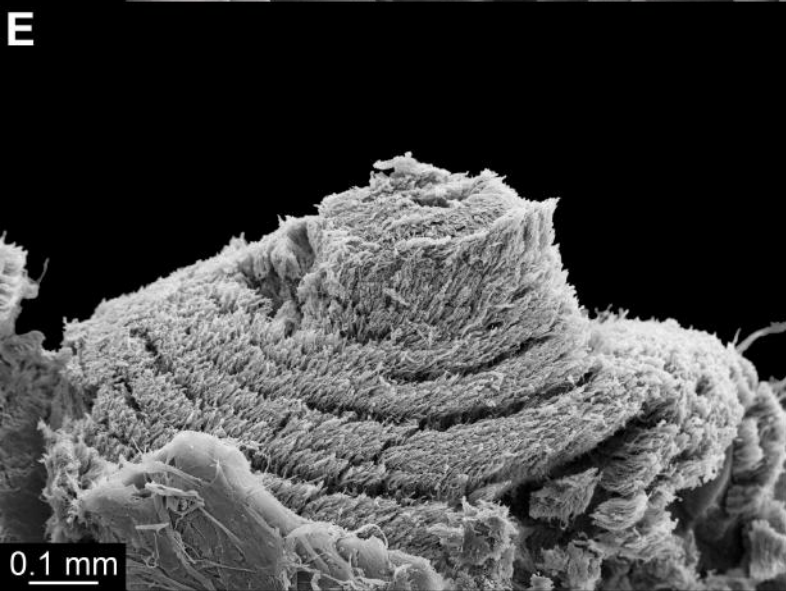
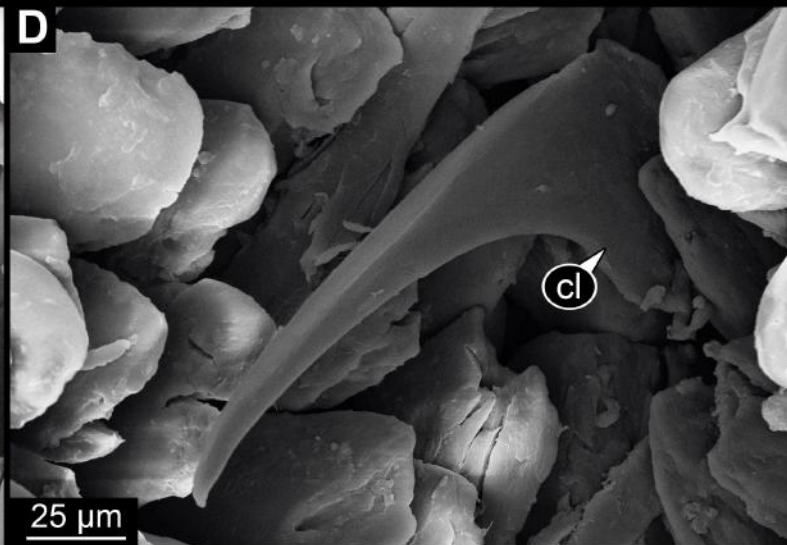
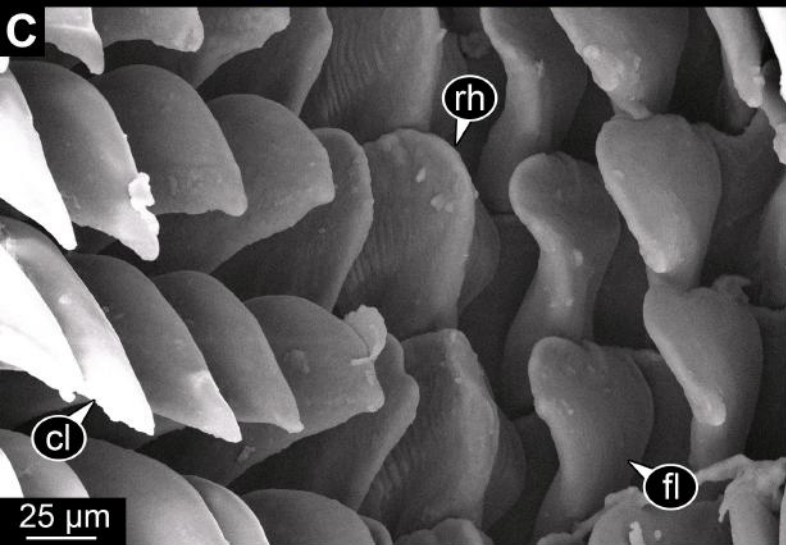
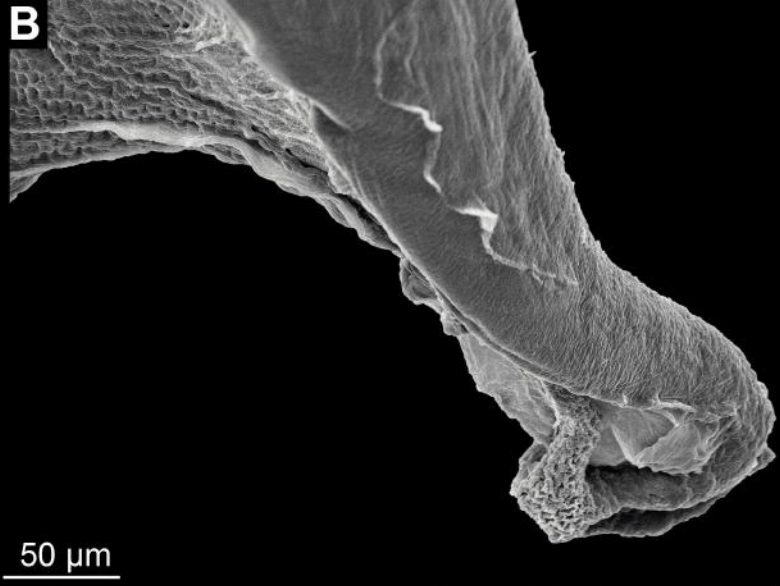
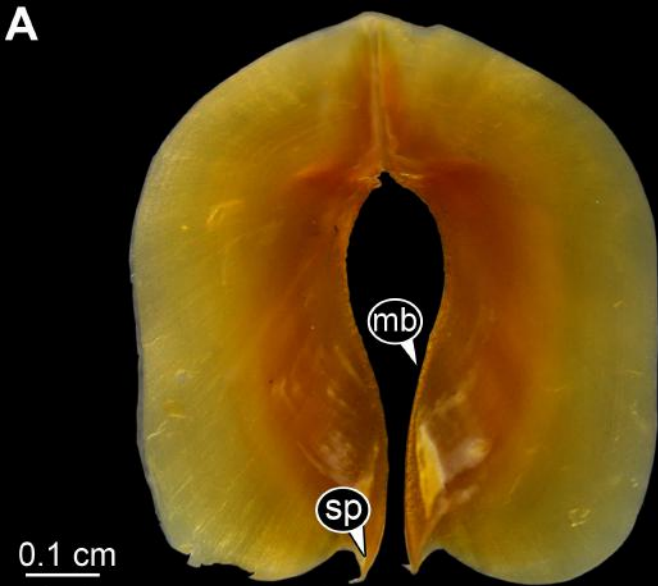
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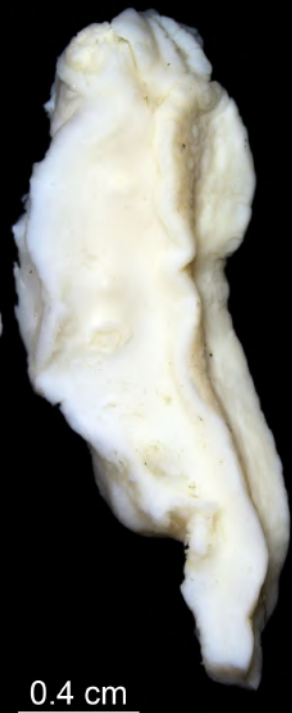


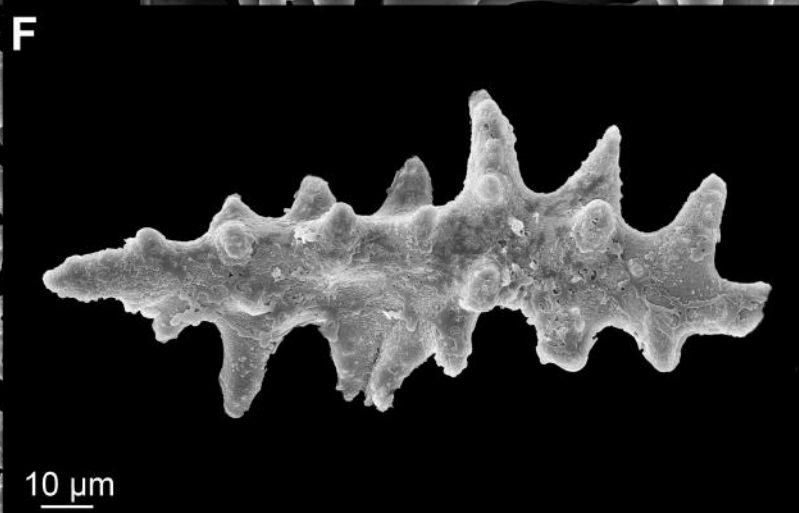
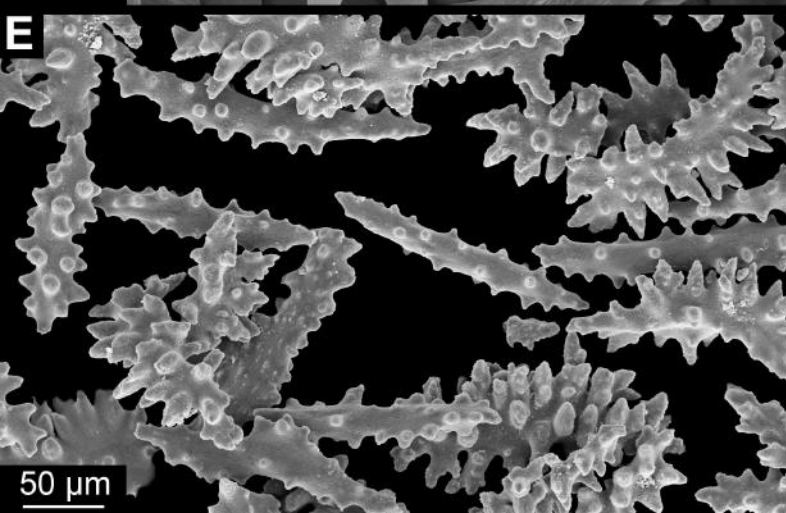
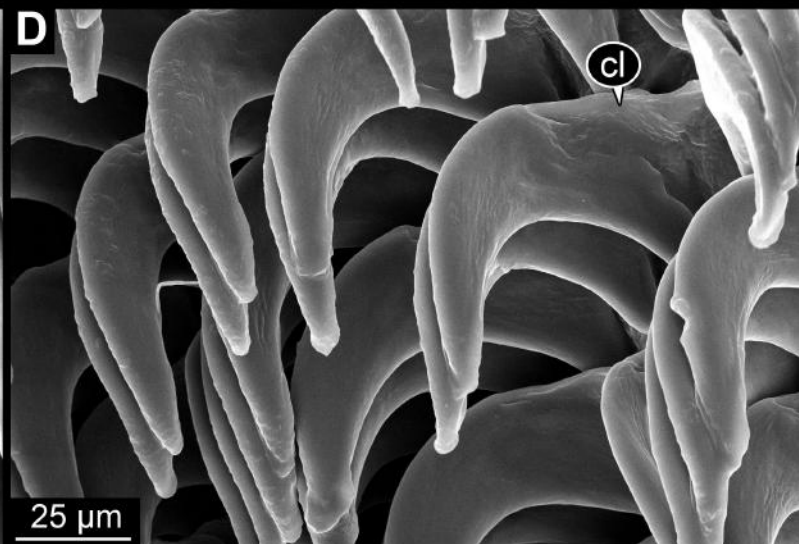
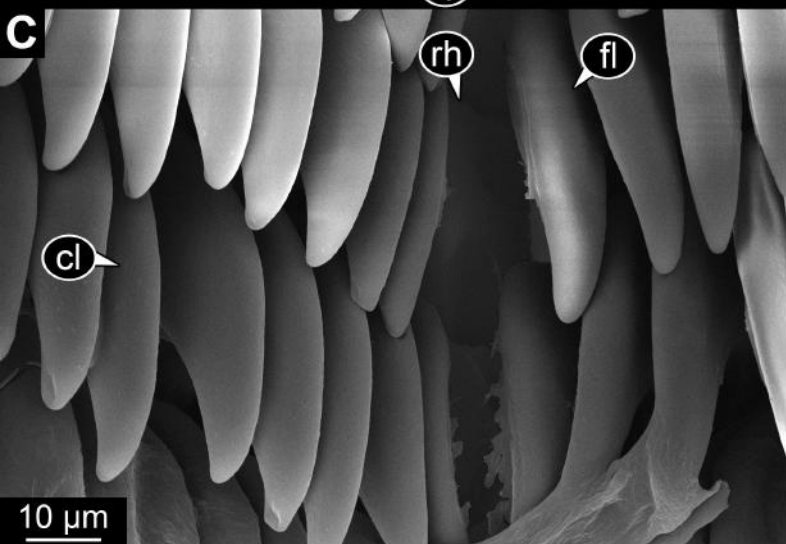
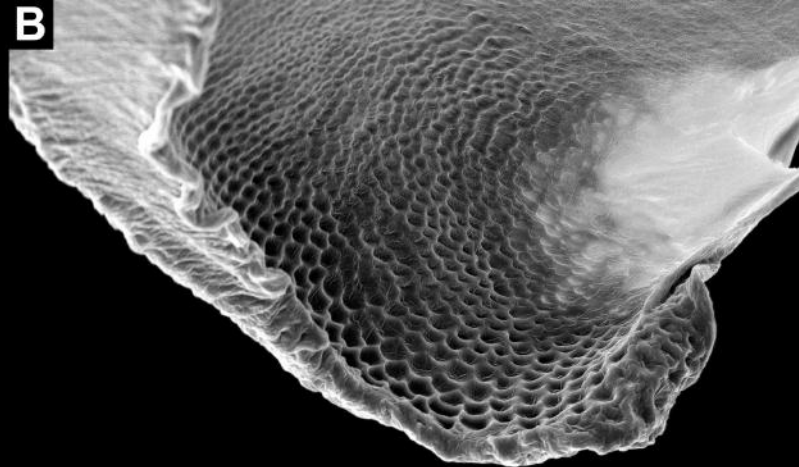
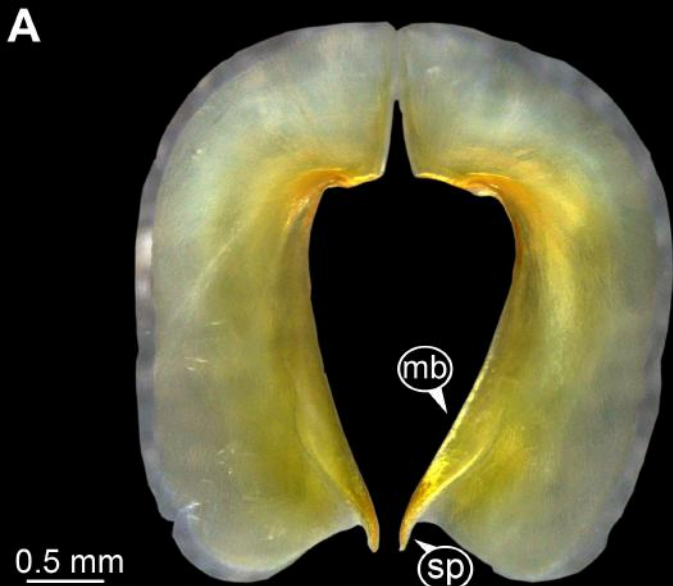
A**B****C****D****E****F**

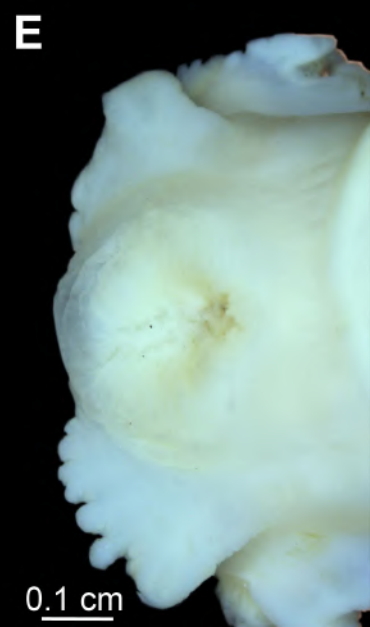
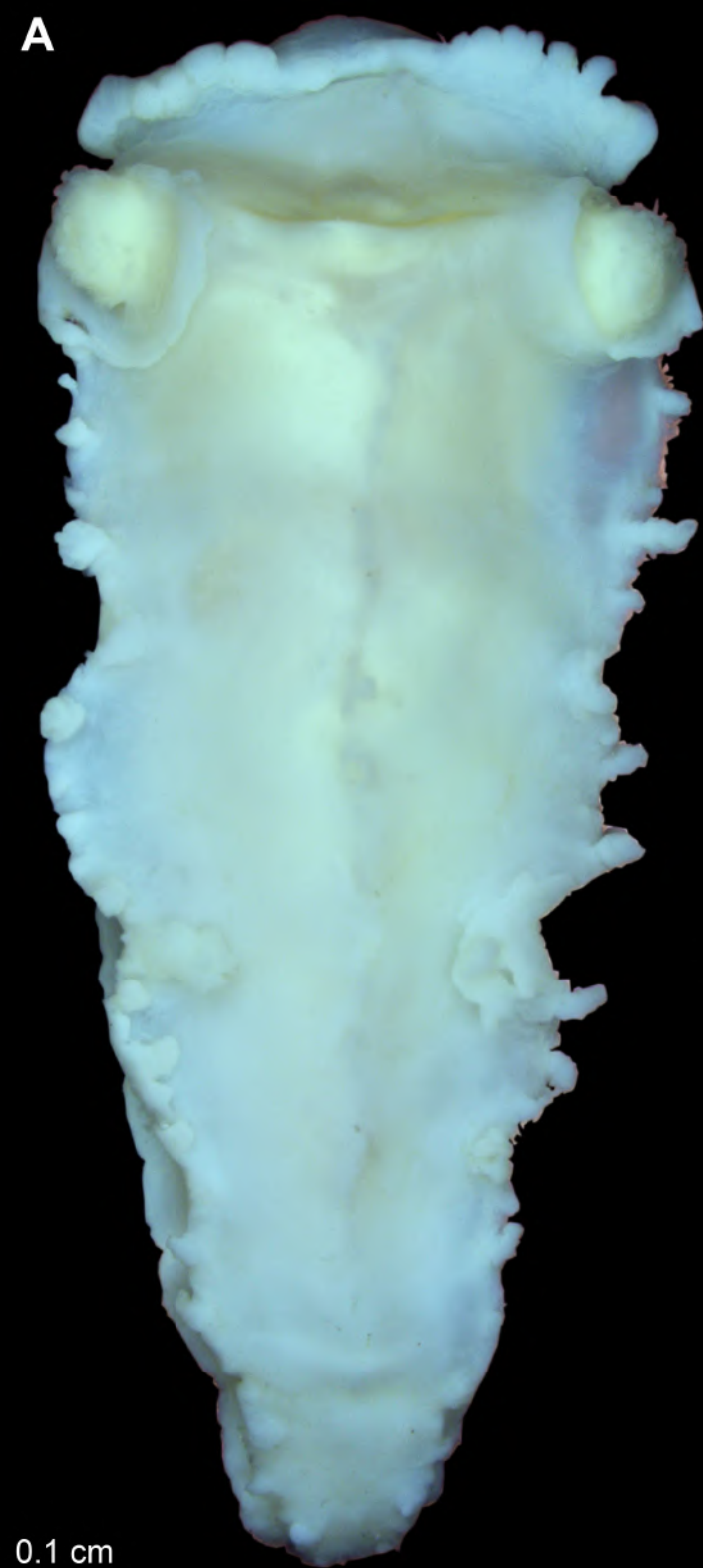


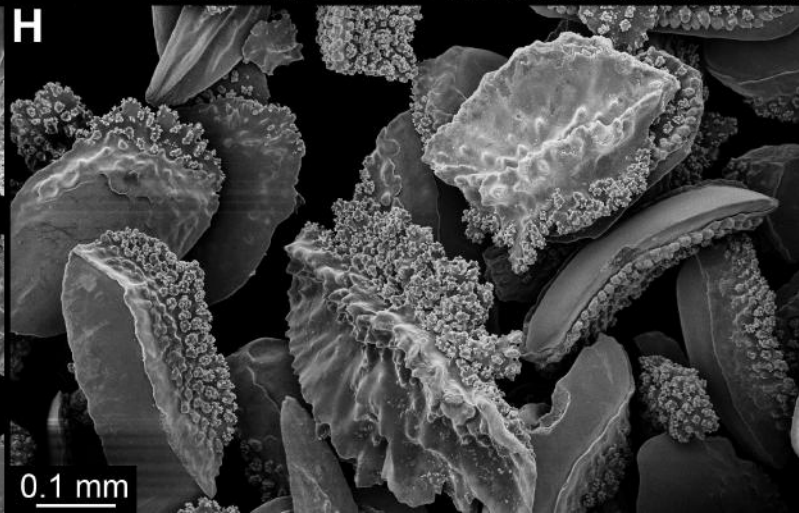
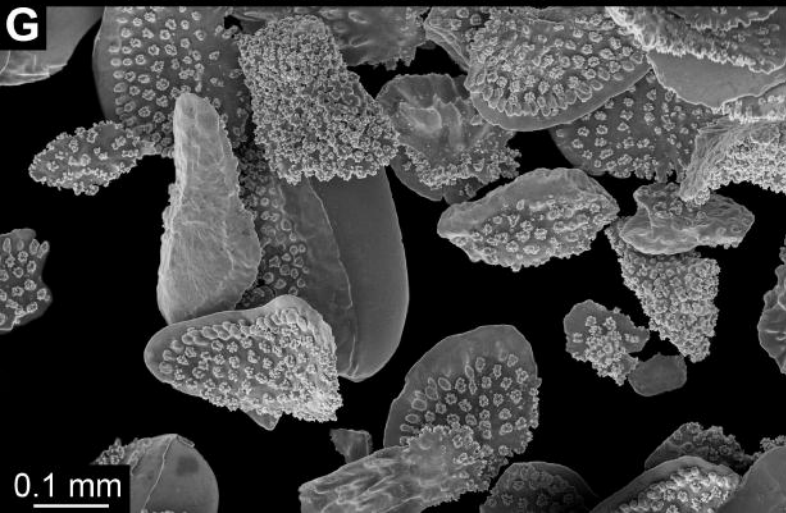
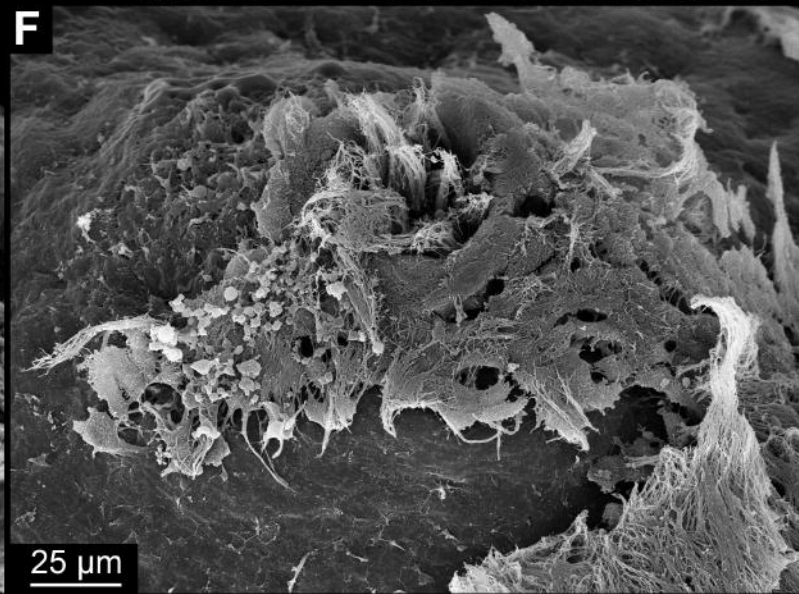
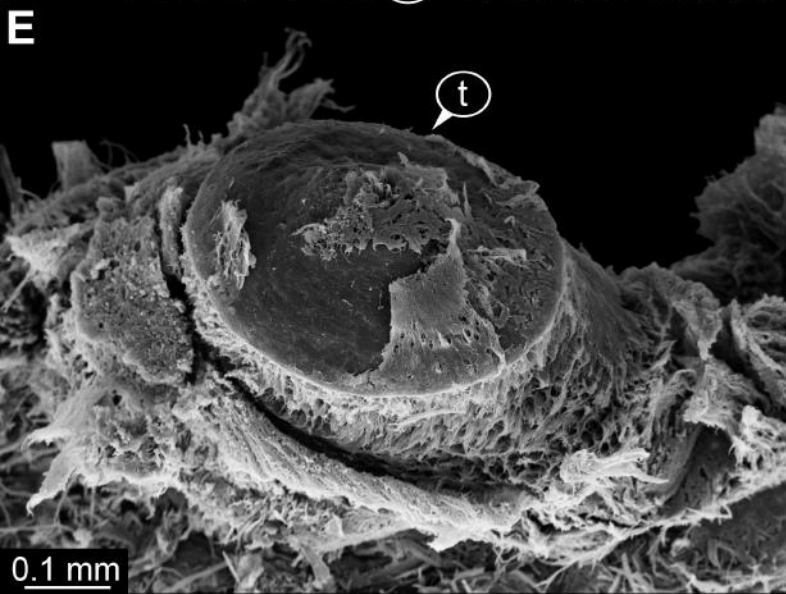
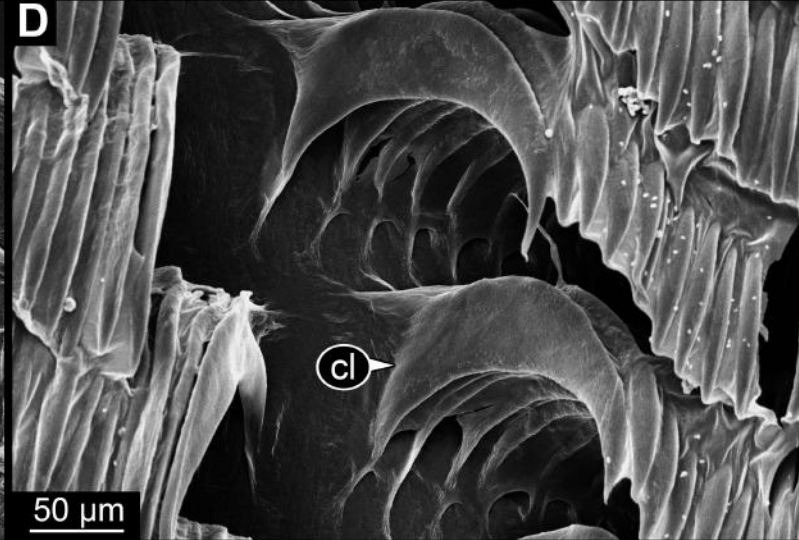
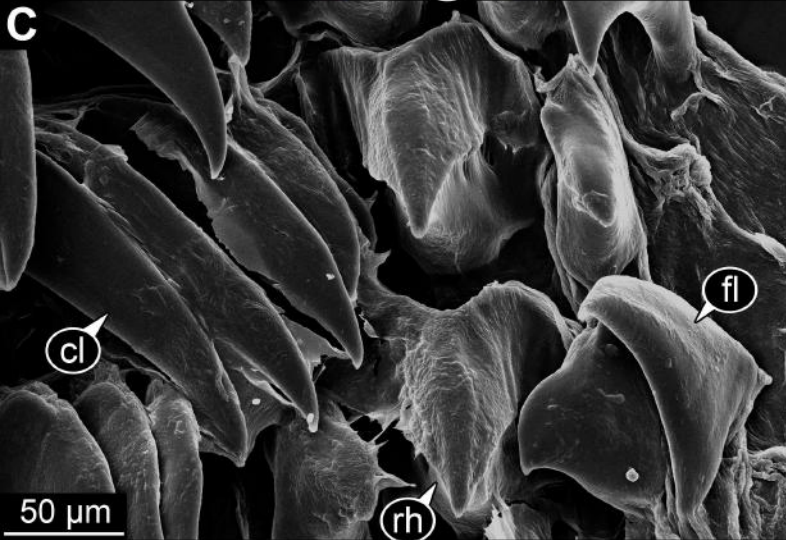
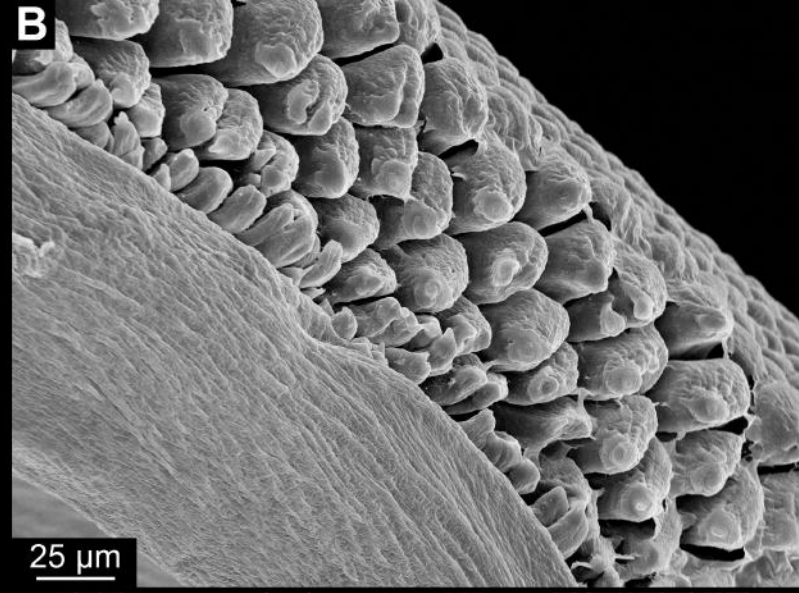
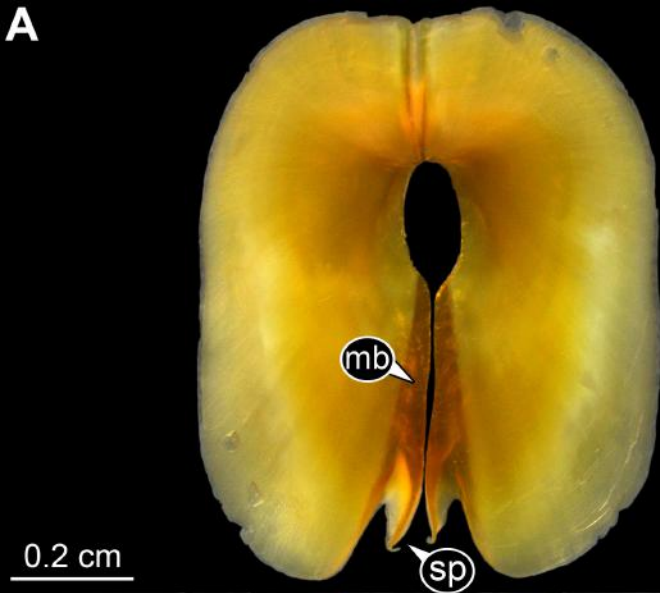
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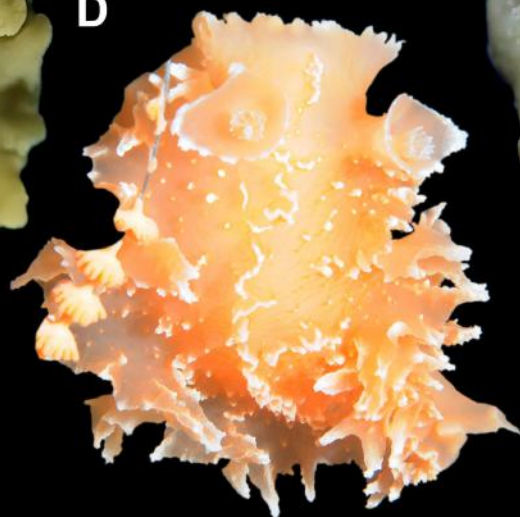


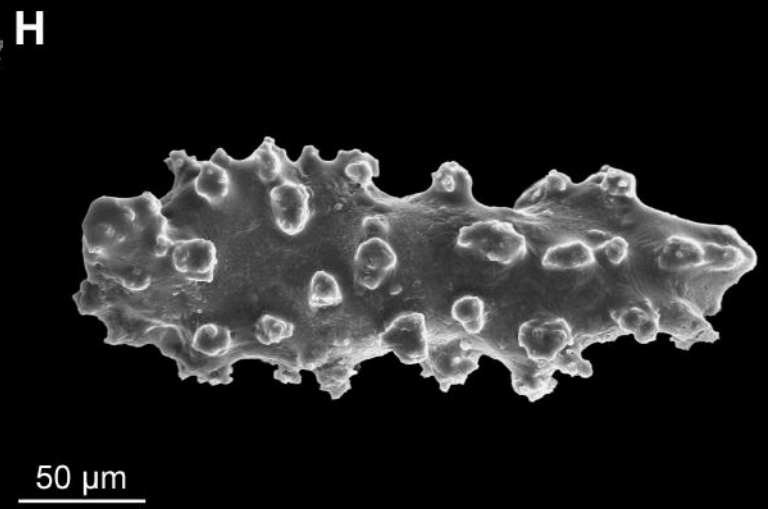
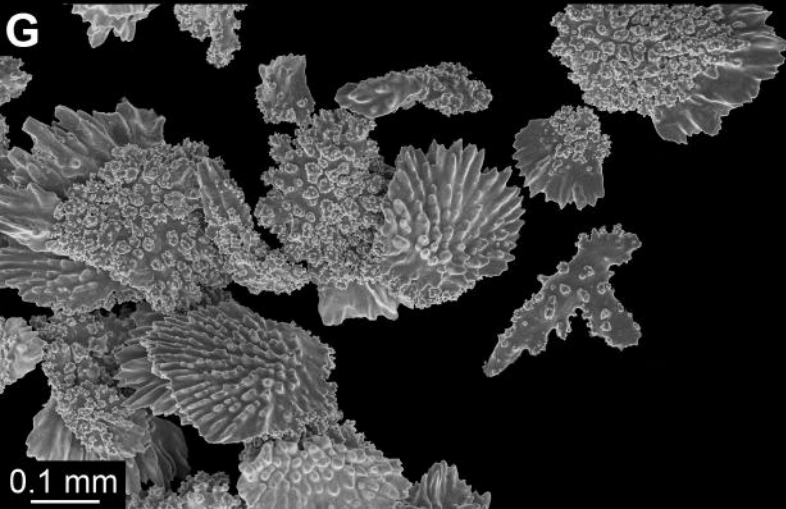
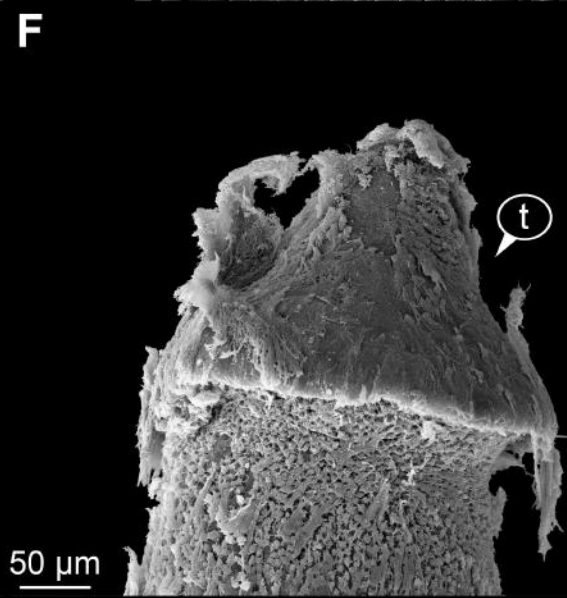
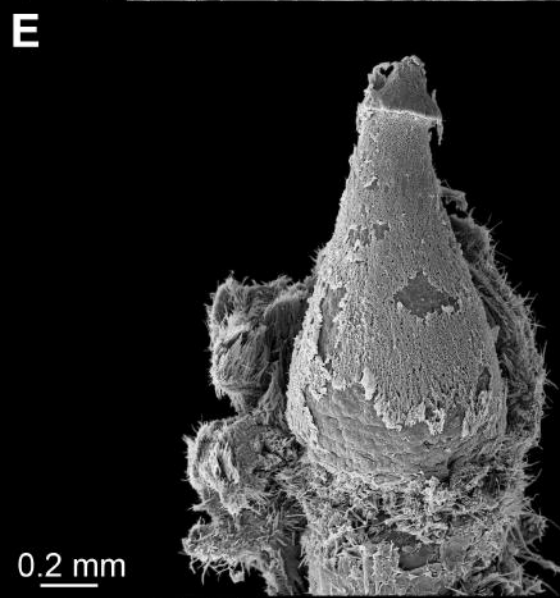
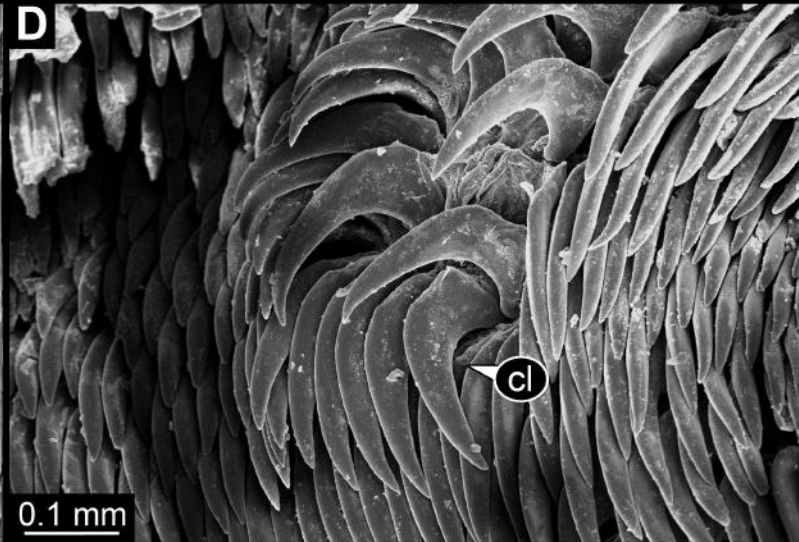
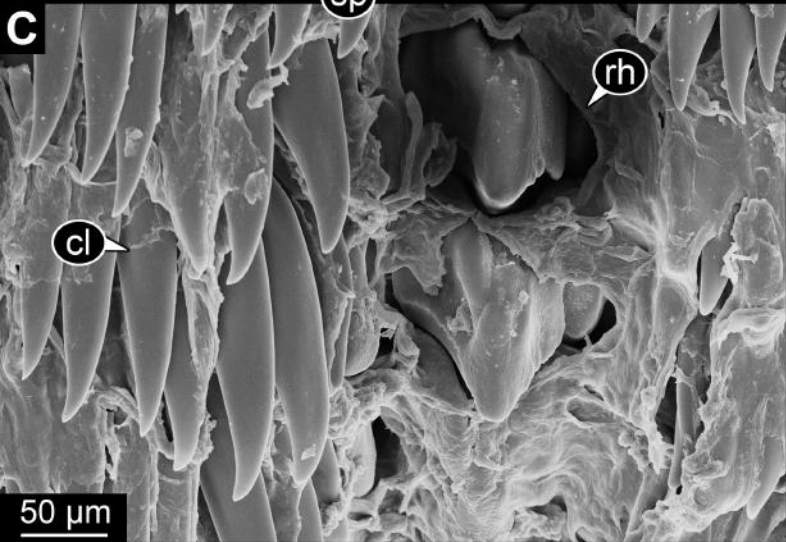
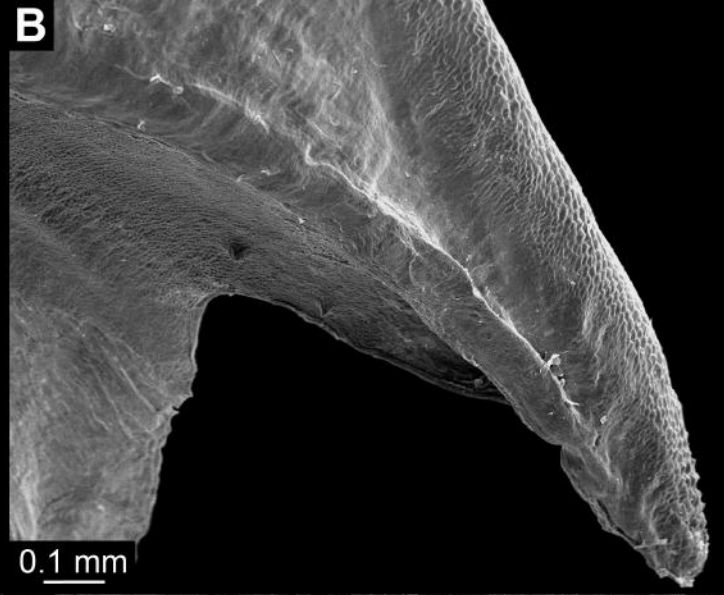
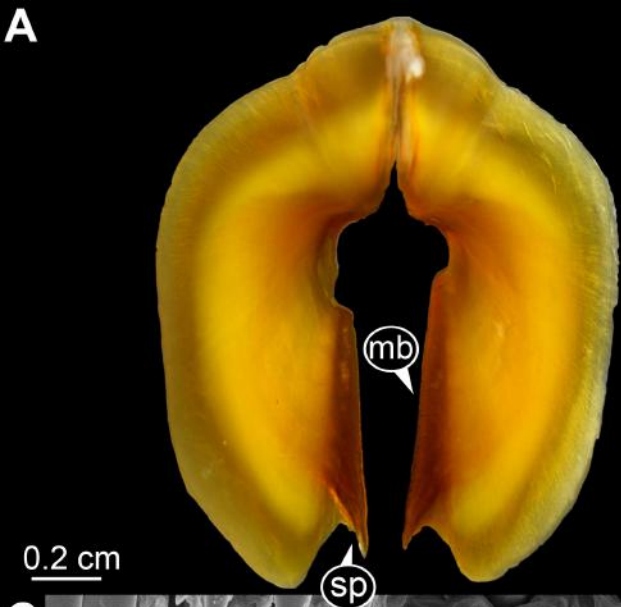
A**B****C****D****E**0.1 cm0.2 cm0.4 cm0.5 cm

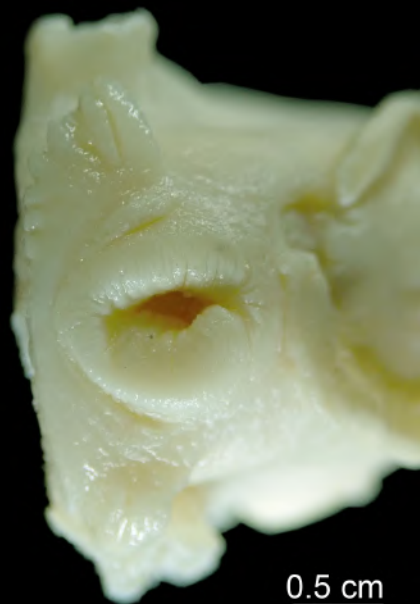


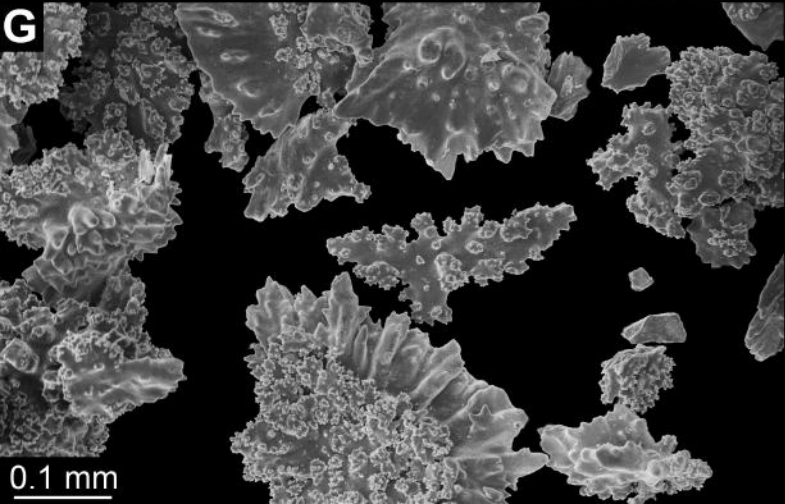
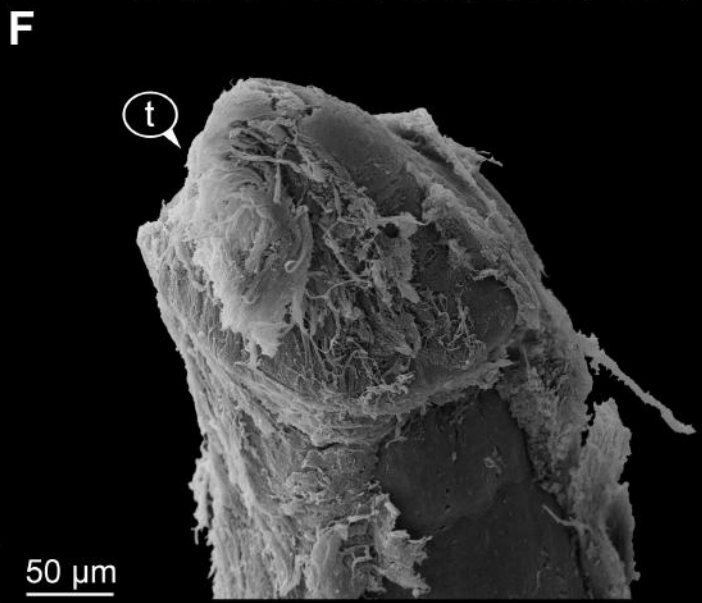
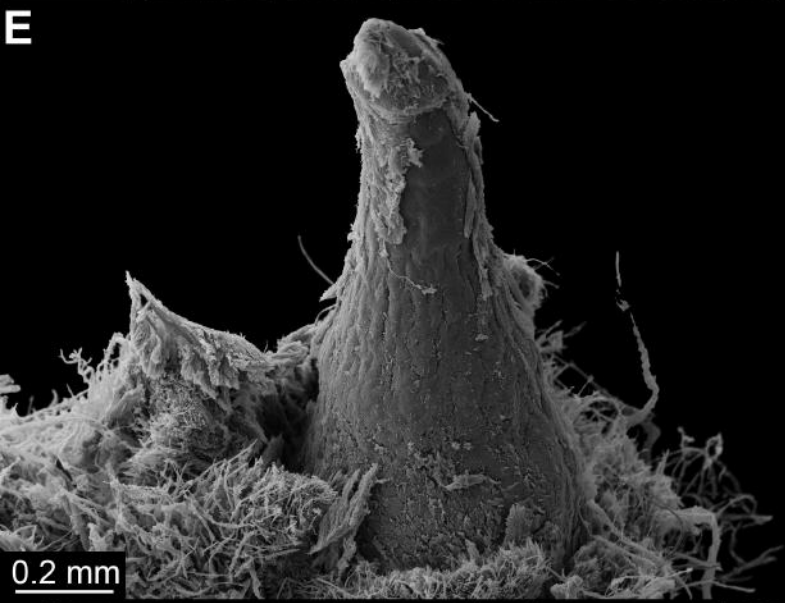
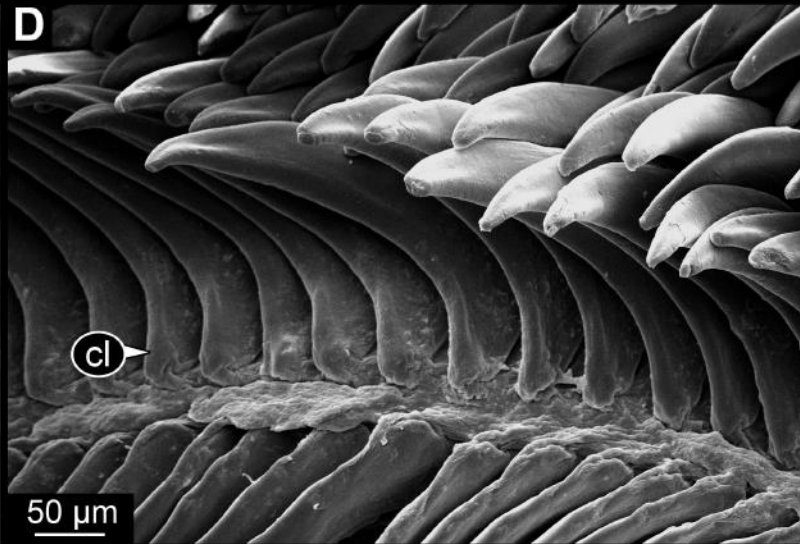
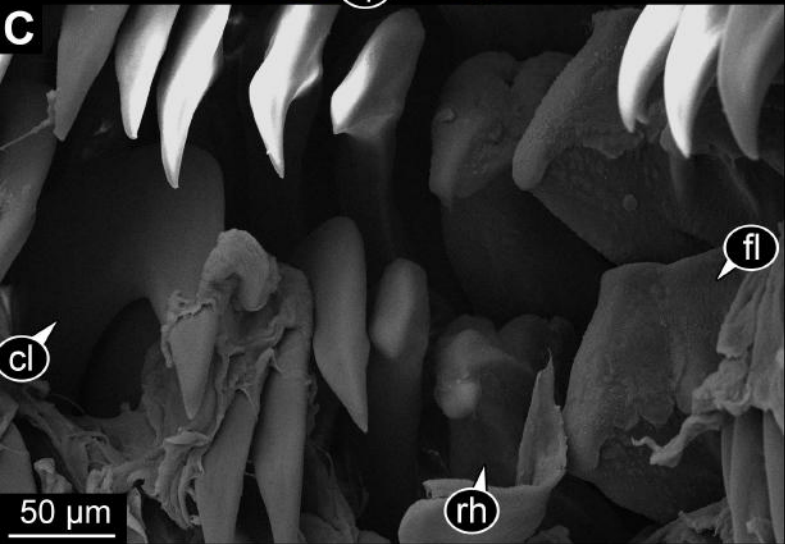
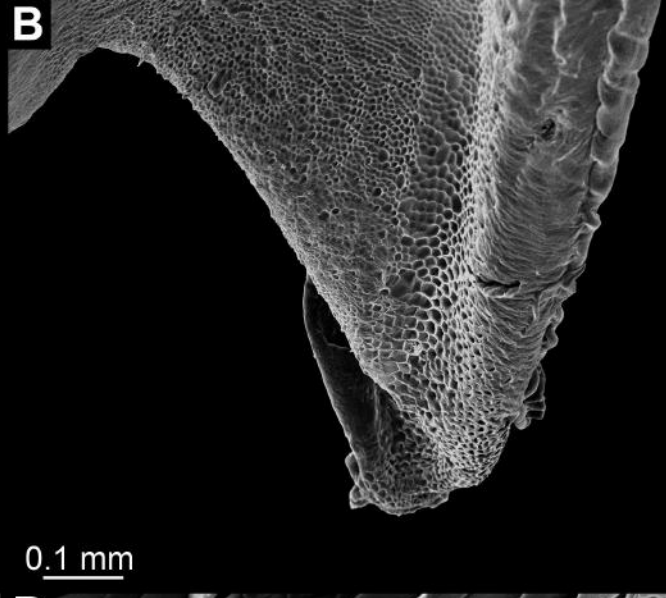
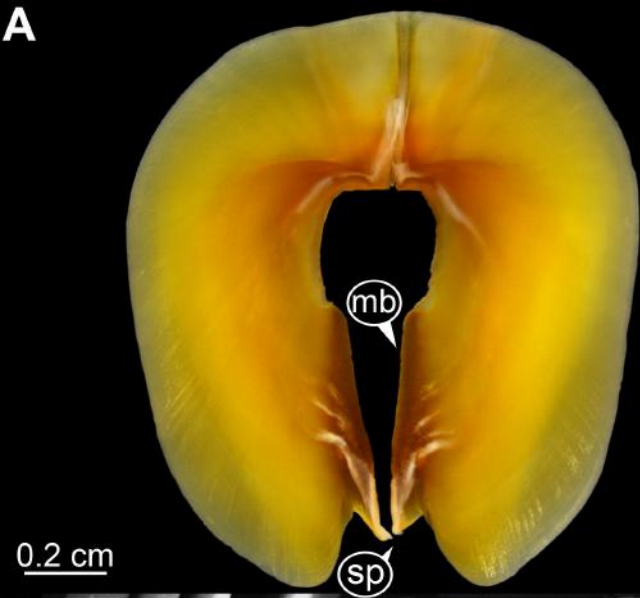




A**B****C****E****D**0.5 cm1.0 cm1.0 cm0.5 cm

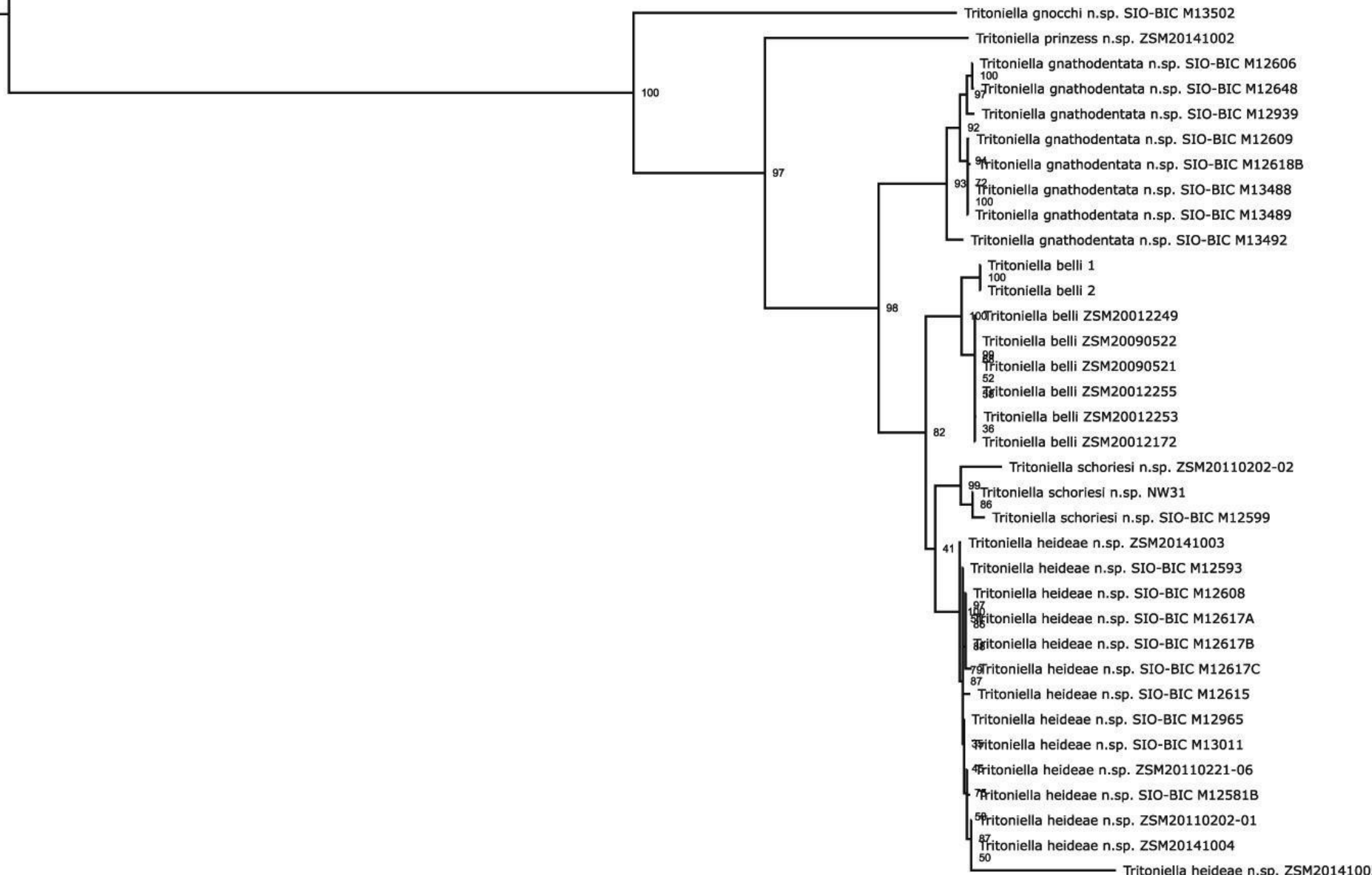


A0.5 cm**B**0.5 cm**C**1.0 cm**D****E**0.5 cm



Tochuina gigantea BFHL-2218

Tochuina nigritigris LACM3553



0.04

