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11 ORIGINAL ARTICLE / ARTÍCULO ORIGINAL

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13 HISTOLOGICAL DIAGNOSIS OF *LECITHOCHIRIUM* SPECIES PARASITIZING
14 *TRICHIURUS LEPTURUS* LINNAEUS, 1758 FROM SOUTHEASTERN BRAZIL

15
16 DIAGNÓSTICO HISTOLÓGICO DE ESPECIES DE *LECITHOCHIRIUM*
17 PARASITANDO *TRICHIURUS LEPTURUS* LINNAEUS, 1758 DEL SUDESTE DE
18 BRASIL

19
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28
29 Running Head: Histological diagnosis of *Lecithochirium* sp. in *Trichiurus lepturus*

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34

35 **ABSTRACT**

36 Histological approaches remain underexplored in the taxonomy of marine digenean
37 trematodes, despite their capacity to reveal internal morphological characters of
38 diagnostic value. In this study, we provide the first detailed histological characterization
39 and comparative analysis of two hemiurid species, *Lecithochirium microstomum*
40 Chandler, 1935 and *Lecithochirium monticellii* (Linton, 1898), parasitizing the cutlassfish
41 *Trichiurus lepturus* Linnaeus, 1758, from the southeastern Brazilian coast. Specimens
42 were processed using classical histological techniques, enabling comprehensive
43 examination of tegumental, muscular, digestive, and reproductive systems. Both species
44 exhibited a syncytial tegument covered by a thin glycocalyx, well-developed oral and
45 ventral suckers with complex fibromuscular organization, and intestinal ceca lined by a
46 simple epithelium. The reproductive system comprised testes, a compact ovary embedded
47 in a fibroelastic stroma, and a distinct hermaphroditic duct formed by the junction of the
48 ejaculatory duct and the terminal portion of the uterus. Histological differentiation
49 between species was primarily based on cirrus morphology and posterior body
50 organization. *Lecithochirium microstomum* exhibited a shorter and wider cirrus and a
51 reduced, largely internalized ecsoma, whereas *L. monticellii* presented a longer, more
52 slender cirrus and a well-developed ecsoma with a greater volume of connective tissue.
53 By documenting previously undescribed histological characters, this study establishes
54 histology as a robust and independent source of taxonomic evidence, reinforcing its value
55 as a complementary tool in integrative taxonomy and evolutionary studies of Hemiuridae.

56 **Keywords:** digenean trematodes – Hemiuridae – histology – integrative taxonomy –
57 *Trichiurus lepturus*

58

59 **RESUMEN**

60 Los enfoques histológicos permanecen poco explorados en la taxonomía de los
61 trematodos digéneos marinos, a pesar de su capacidad para revelar caracteres
62 morfológicos internos de valor diagnóstico. En este estudio, presentamos la primera
63 caracterización histológica detallada y un análisis comparativo de dos especies de

64 hemiúridos, *Lecithochirium microstomum* Chandler, 1935 y *Lecithochirium monticellii*
65 (Linton, 1898), parásitas del pez sable *Trichiurus lepturus* Linnaeus, 1758, procedentes
66 de la costa sudeste de Brasil. Los especímenes fueron procesados mediante técnicas
67 histológicas clásicas, lo que permitió un examen integral de los sistemas tegumentario,
68 muscular, digestivo y reproductor. Ambas especies presentaron un tegumento sincitial
69 recubierto por un glicocálix delgado, ventosas oral y ventral bien desarrolladas con una
70 organización fibromuscular compleja, y ciegos intestinales revestidos por un epitelio
71 simple. El sistema reproductor comprendió testículos, un ovario compacto inmerso en un
72 estroma fibroelástico y un conducto hermafrodita bien definido, formado por la unión del
73 conducto eyaculador con la porción terminal del útero. La diferenciación histológica entre
74 las especies se basó principalmente en la morfología del cirro y la organización de la
75 región posterior del cuerpo. *Lecithochirium microstomum* presentó un cirro más corto y
76 ancho y un ecsoma reducido y en gran parte internalizado, mientras que *L. monticellii*
77 exhibió un cirro más largo y delgado y un ecsoma bien desarrollado, con mayor volumen
78 de tejido conjuntivo. Al documentar caracteres histológicos previamente no descritos,
79 este estudio establece la histología como una fuente robusta e independiente de evidencia
80 taxonómica, reforzando su valor como herramienta complementaria en la taxonomía
81 integrativa y los estudios evolutivos de Hemiuridae.

82 **Palabras clave:** Hemiuridae – histología – taxonomía integradora – trematodos digéneos
83 – *Trichiurus lepturus*

85 INTRODUCTION

86 The genus *Lecithochirium* Lühe, 1901 (Digenea: Hemiuridae) comprises
87 digenean parasites of marine fishes and is characterized by a smooth tegument, a
88 prominent or weakly developed ecsoma, a tubular pars prostatica, and vitelline follicles
89 arranged in two lateral fields. The type species is *Lecithochirium rufoviride* (Rudolphi,
90 1819) Lühe, 1901 (Gibson & Bray, 1979; Gibson *et al.*, 2002). Currently, 132 species are
91 recognized within the genus (WoRMS, 2025).

92 *Lecithochirium microstomum* Chandler, 1935 was originally described from
93 *Trichiurus lepturus* Linnaeus, 1758 (Actinopterygii: Trichiuridae) in the United States
94 (Chandler, 1935). In Brazil, this species has been reported from a broad range of marine
95 fish hosts, reflecting its wide ecological distribution (Kohn *et al.*, 2007; Pantoja & Kudlai,
96 2022).

97 *Lecithochirium monticellii* (Linton, 1898) Skrjabin & Guschanskaja, 1955, originally

98 described as *Distomum monticellii* from *Remora remora* (Linnaeus, 1758) in the United
99 States (Linton, 1898), has also been recorded from several marine fishes along the
100 Brazilian coast (Kohn *et al.*, 2007; França *et al.*, 2020; Fonseca *et al.*, 2022).

101 Despite the taxonomic relevance of internal morphology, descriptive histological
102 approaches remain underutilized in helminth systematics. Histology enables direct access
103 to internal structural organization and tissue differentiation, providing diagnostic
104 characters that are often unavailable through whole mounts or surface-based techniques,
105 including scanning electron microscopy. When integrated with conventional
106 morphological analyses, histological data offer independent and complementary
107 evidence, expanding the resolution of taxonomic interpretations (Machado *et al.*, 2024a;
108 Machado *et al.*, 2024b).

109 In this context, the present study aims to provide the first detailed histological
110 description and comparison of *L. microstomum* and *L. monticellii* collected from *T.*
111 *lepturus* off the coast of Rio de Janeiro State, southeastern Brazil. By documenting
112 previously unexplored histological characters, this work highlights the taxonomic value
113 of histology and contributes to the advancement of integrative approaches in the study of
114 marine digenean trematodes.

115

116 **Materials and Methods**

117 **Host and Parasite Collection:**

118 A total of 13 specimens of *T. lepturus* were obtained from artisanal fishers at local
119 markets in the state of Rio de Janeiro, southeastern Brazil, between 2024 and 2025. This
120 sample size was considered representative for histological analyses, given the consistency
121 of internal morphological features observed among specimens and the objective of
122 detailed tissue-level characterization. Fish were taxonomically identified according to
123 Menezes & Figueiredo (1985).

124 Digestive tracts were carefully removed, opened longitudinally, and washed in
125 saline solution. The contents were rinsed through a 150 µm mesh sieve, and the retained
126 material was examined under a stereomicroscope for parasite recovery. Digenean
127 trematodes and nematodes were collected and fixed immediately in 10% neutral buffered
128 formalin, ensuring adequate preservation of internal tissues prior to histological
129 processing.

130 **Histological Processing and Analysis:**

131 Helminths were processed following standard histological protocols, allowing
132 detailed assessment of internal morphology complementary to classical whole-mount and
133 surface-based analyses. Fixed specimens were dehydrated through a graded ethanol series
134 (70%, 80%, 90%, and 100%), cleared in xylene, and embedded in paraffin. Longitudinal
135 sections, 5 μm thick, were obtained using a rotary microtome (Bancroft & Gamble, 2013).

136 Histological sections were stained with hematoxylin–eosin (H&E) for general
137 tissue architecture, Gomori’s trichrome (GT) to differentiate connective and muscular
138 components, and orcein to evidence elastic fibers (Abrahamsohn, 2016). Slides were
139 examined and photomicrographed using an Olympus BX51 light microscope equipped
140 with Capture 2.4 image analysis software, enabling detailed documentation of
141 tegumental, muscular, digestive, and reproductive structures.

142 **Ethic aspects:** All applicable institutional, national, and international guidelines for the
143 care and use of animals were strictly followed.

144

145 **Results**

146 Based on 13 specimens of *L. microstomum* (Fig. 1) and 18 specimens of *L.*
147 *monticellii* (Fig. 2), both recovered from *T. lepturus*, the two species exhibited a largely
148 conserved histological organization, while presenting consistent characters that allow
149 reliable interspecific differentiation.

150 In both taxa, the tegument was composed of flattened cells arranged in a single
151 layer, supported by a thin underlying connective tissue layer (Figs. 1c, 2c).
152 Subtegmentary musculature consisted of small bundles of striated muscle fibers, more
153 pronounced at the anterior and posterior extremities, resulting in localized thickening of
154 the body wall (Figs. 1a, 2d). The oral and ventral suckers exhibited a complex muscular
155 architecture, formed by large longitudinal muscle bundles interspersed with collagen and
156 elastic fibers and externally covered by a thin epithelial layer (Figs. 1a, 1b, 2a). A shallow
157 tegumentary invagination between the genital pore and the ventral sucker was
158 consistently observed in *L. monticellii* (Fig. 2a), whereas it was less conspicuous in *L.*
159 *microstomum* (Fig. 1b). In both species, the intestinal ceca were lined by flattened cells
160 arranged in a single layer and exhibited a uniformly smooth luminal surface (Figs. 1e,
161 2c).

162 The reproductive system was well developed in both species. In *L. microstomum*,
163 the testes were arranged along the longitudinal axis of the body (Figs. 1c, 1d, 1f), whereas
164 the ovary consisted of germ cells at different developmental stages embedded in a

165 fibroelastic stroma with associated muscle cells (Fig. 2c). The seminal vesicle, positioned
166 in close proximity to the ventral sucker, was enclosed by fibromuscular stroma and
167 contained abundant spermatozoa (Figs. 1a, 2a, 2b). The cirrus was enclosed within a
168 cirrus sac lined by an epithelium slightly thicker than that of the copulatory organ itself
169 and surrounded by well-developed musculature, reflecting the structural specialization of
170 the male copulatory apparatus (Fig. 2b). The junction between the ejaculatory duct and
171 the terminal portion of the uterus formed a distinct hermaphroditic duct. The uterus was
172 lined by a simple squamous epithelium and contained eggs embedded in a matrix with
173 modest elastic content (Figs. 1c, 1e).

174 Histochemical analysis using Gomori's trichrome enabled clear differentiation
175 between connective and muscular components, with collagen fibers staining green and
176 musculature staining red (Fig. 1a). In contrast, hematoxylin and eosin staining highlighted
177 intensely basophilic nuclei and eosinophilic cytoplasm, facilitating detailed assessment
178 of tissue organization and cellular architecture (Figs. 1b–f, 2a–d).

179 Comparative synthesis:

180 Although the overall histological organization was conserved between species,
181 marked interspecific differences were observed in the posterior body region and male
182 copulatory structures, which are of clear taxonomic relevance. *Lecithochirium*
183 *microstomum* exhibited a shorter and more robust body, with a reduced and partially
184 internalized ecsoma (Fig. 1f), whereas *L. monticellii* displayed a well-developed ecsoma,
185 representing a diagnostically informative character (Fig. 2d). No evidence of histological
186 sexual dimorphism was detected beyond the expected differentiation of reproductive
187 structures, indicating that the observed variations primarily reflect species-level
188 morphological divergence rather than intraspecific variation.

189

190 **DISCUSSION**

191 - Corroboration of previous knowledge

192 Histological analysis contributes substantially to the understanding of helminth
193 morphology and physiology, refining taxonomic descriptions and supporting functional
194 interpretations. The histological features observed in *L. microstomum* and *L. monticellii*
195 corroborate classical descriptions based on external morphology and morphometry
196 (Chandler, 1935; Linton, 1898; Fonseca *et al.*, 2022; Pantoja & Kudlai, 2022), while
197 providing internal anatomical confirmation through a methodological approach not
198 previously applied to these taxa.

199 Both species exhibited a syncytial tegument covered by a glycocalyx, robust oral and
200 ventral suckers, and a well-developed reproductive system, consistent with histological
201 patterns reported for other digenean trematodes (Halton & Dermott, 1967; Machado *et*
202 *al.*, 2024a, b). The dense subtegumentary fibrous network likely contributes to protection
203 against host digestive enzymes and provides mechanical resistance, supporting earlier
204 functional interpretations of the tegument. Similarly, the muscular architecture of the
205 suckers, characterized by densely packed longitudinal fibers, corroborates their role in
206 firm attachment within the host intestine, where peristaltic forces are intense (Bosei *et al.*,
207 2022).

208 The organization of the testes, ovary, and seminal vesicle also aligns with histological
209 descriptions reported for other digeneans (Hanna, 2015; Silva *et al.*, 2005; Panyarachun
210 *et al.*, 2013), reinforcing the presence of conserved morphofunctional traits within
211 Hemiuridae.

212 - Novel histological findings

213 Beyond corroboration, the present study provides previously undocumented
214 histological data for *L. microstomum* and *L. monticellii*. The combined use of
215 hematoxylin–eosin, Gomori’s trichrome, and orcein staining allowed a detailed
216 assessment of tissue composition and spatial organization that is inaccessible through
217 whole mounts or surface-based techniques alone.

218 The thin, uniformly organized intestinal ceca, lined by flattened cells arranged in
219 a single layer, were shown to be continuous along the body, refining earlier anatomical
220 descriptions and confirming patterns observed in other digeneans (Lakshmi & Rao,
221 1978). The ovary, embedded in a fibroelastic stroma, exhibited a compact histological
222 organization, adding novel information on its internal composition and mechanical
223 support during gametogenesis.

224 Most notably, the present study documented clear histological differences in the
225 copulatory apparatus between the two species. The cirrus of *L. microstomum* was shorter
226 and wider, whereas that of *L. monticellii* was longer and narrower, differences that had
227 been previously inferred from external morphology but not confirmed histologically. This
228 internal differentiation provides independent evidence supporting species-level
229 divergence.

230 - Taxonomic and evolutionary implications

231 The histological differences identified here have direct taxonomic relevance. The
232 morphology of the copulatory organ and the organization of the posterior body region,

233 particularly the presence of a well-developed ecsoma in *L. monticellii* and its reduction
234 or absence in *L. microstomum*, represent reliable diagnostic characters. The histological
235 confirmation of these traits strengthens species delimitation and reduces ambiguity in the
236 identification of closely related taxa.

237 Comparative analysis with other hemiurids, such as *Aponurus laguncula* (Looss,
238 1907) (Machado et al., 2024b), and with digeneans from other families, including
239 *Prosogonotrema bilabiatum* (Vigueras, 1940) (Machado et al., 2024a), suggests the
240 existence of conserved histological patterns within Digenea. These patterns likely reflect
241 evolutionary constraints associated with a shared intestinal niche, where efficient
242 attachment, nutrient absorption, and resistance to host digestive processes are essential.

243 At the same time, the subtle but consistent histological differences between *L.*
244 *microstomum* and *L. monticellii* indicate that evolutionary divergence within
245 *Lecithochirium* is expressed not only externally but also in internal anatomical
246 organization. Such differences may reflect adaptive responses to microhabitat variation
247 or host-related selective pressures, as previously suggested by ecological studies
248 (Carvalho & Luque, 2011; França et al., 2020).

249 By integrating histology with traditional morphology, ecology, ultrastructure, and
250 molecular approaches (Pantoja & Kudlai, 2022), the present study demonstrates that
251 histological characters constitute robust, independent taxonomic markers. This
252 integrative perspective enhances taxonomic resolution, deepens understanding of parasite
253 functional biology, and provides a solid morphological framework for future evolutionary
254 and phylogenetic studies of *Lecithochirium* and related hemiurid trematodes.

255 The histological evidence presented here demonstrates that tissue-level characters
256 provide reliable diagnostic information that complements traditional morphological
257 approaches and enhances species delimitation. By documenting the internal organization
258 of key structures—particularly the tegument, musculature, and reproductive and digestive
259 systems—this study highlights histology as a robust and independent source of taxonomic
260 evidence. These findings reinforce the role of histological analysis within an integrative
261 taxonomic framework and underscore its relevance for understanding morphological
262 differentiation and evolutionary patterns in Hemiuridae.

263 - Methodological limitations

264 The limitations of the present study are mainly related to the inherent difficulties
265 associated with the histological processing of small-bodied digenean platyhelminths of
266 the genus *Lecithochirium*, whose reduced size, delicate tegument, and highly compact

267 internal organization impose technical challenges during fixation, embedding, sectioning,
268 and staining.

269

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278

279 **Author contributions: CRediT (Contributor Roles Taxonomy)**

280 **PSO** = Patrícia Silva de Oliveira

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285 **Data curation:** PSO

286 **Formal Analysis:** PSO, ABM, JLL

287 **Funding acquisition:** PSO, ABM, JLL

288 **Investigation:** PSO, ABM, JLL

289 **Methodology:** PSO, ABM, JLL

290 **Project administration:** JLL

291 **Resources:** PSO

292 **Software:** PSO, ABM, JLL

293 **Supervision:** JLL

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295 **Visualization:** PSO, ABM, JLL

296 **Writing – original draft:** PSO, ABM, JLL

297 **Writing – review & editing:** PSO, ABM, JLL

298

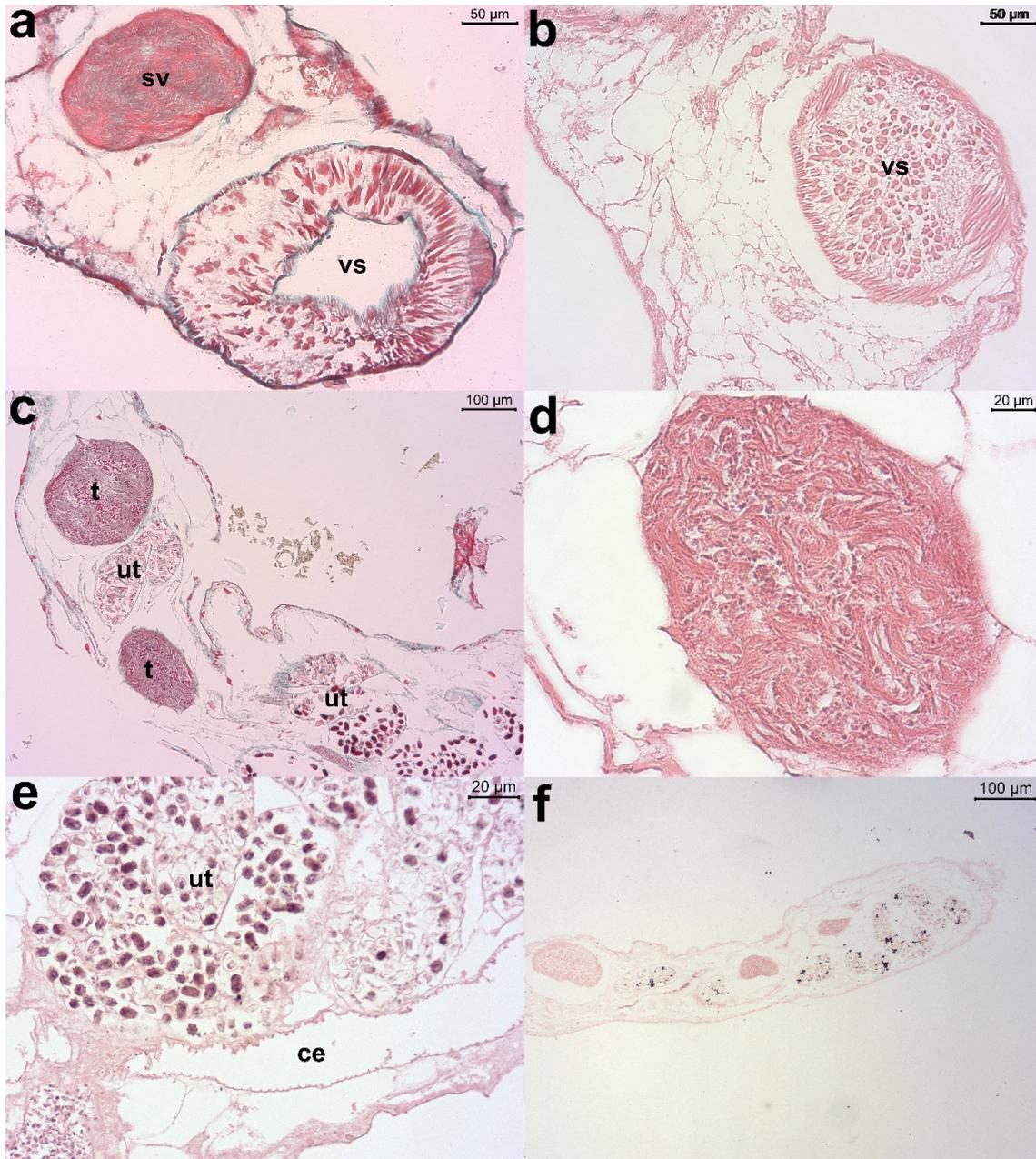
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382

383 **Figure 1.** Histological longitudinal sections of *Lecithochirium microstomum*.

384 Figure 1a shows the ventral sucker stained with Gomori's trichrome. Figures 1b–f

385 corresponds to sections stained with hematoxylin and eosin (H&E), illustrating the ventral

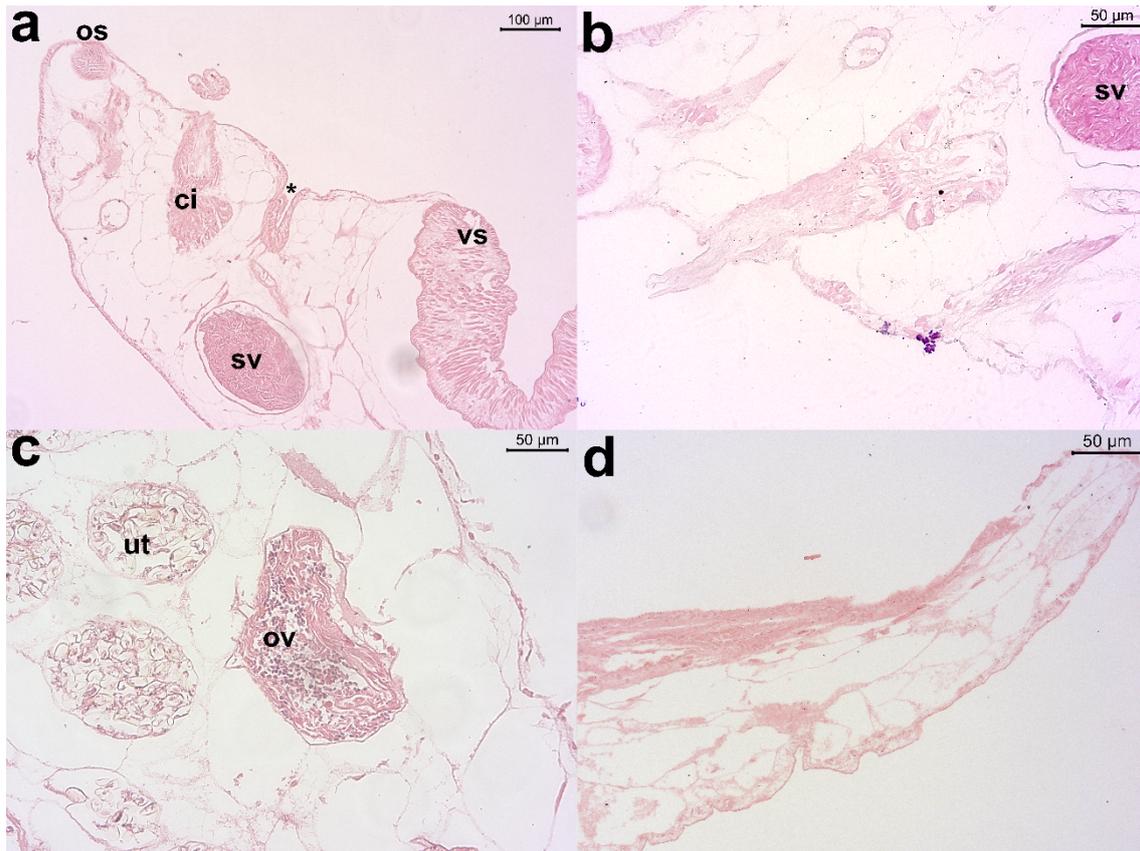
386 sucker at a deeper tissue level (Fig. 1b), reproductive structures (Fig. 1c), the seminal

387 vesicle in detail (Fig. 1d), the intestinal ceca in detail (Fig. 1e), and the posterior extremity

388 (Fig. 1f). Abbreviations: vs, ventral sucker; sv, seminal vesicle; t, testicle; ut, uterus filled

389 with eggs.

390



391

392 **Figure 2.** Histological longitudinal sections of *Lecithochirium monticellii*.
 393 (a) Anterior extremity. (b) Cirrus and associated structures in detail. (c) Female
 394 reproductive structures and intestinal ceca in detail. (d) Posterior extremity.
 395 Abbreviations: os, oral sucker; vs, ventral sucker; sv, seminal vesicle; ci, cirrus; ut, uterus
 396 filled with eggs; ov, ovary.
 397 Note: An asterisk (*) indicates a small tegumentary invagination.