

# 1 **A novel mantle-margin gland system in *Tectura virginea* (Patellogastropoda)**

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## 22 **Abstract**

23 Glandular defensive systems remain poorly understood in many marine invertebrates. Here,  
24 we investigated the anatomy and chemical composition of mantle margin glands in the true  
25 limpet *Tectura virginea*. These glands produce a persistent, thread-like secretion that  
26 emerges from the exposed mantle edge in response to mechanical stimulation. Light and  
27 electron microscopy revealed large glands, each dominated by a single voluminous secretory  
28 cell surrounded by quiescent precursors and ring musculature, suggesting a holocrine  
29 expulsion mechanism. Liquid chromatography–mass spectrometry identified over 80  
30 compounds, including disulphides, sulfonates, and organic acids. Their presence suggests  
31 that the secretion may act as a chemical barrier against microbial colonization or small  
32 invertebrate predators. Several major compounds, such as 1-(propylsulfanyl)-1-  
33 (propylsulfinyl)propane, have potential defensive roles. The anatomical position of the glands  
34 and the biochemical diversity of their products suggest a defensive role. Our findings support  
35 the interpretation of these mantle margin glands as a novel repugnatorial system,  
36 representing a unique adaptation among patellogastropods. These findings highlight the  
37 potential for secretory and defensive functions in the mantle-margin glands *Tectura virginea*  
38 underscoring the broader relevance of such glands in less-studied lineages.

39

## 40 **Introduction**

41 Across terrestrial and aquatic ecosystems, herbivorous invertebrates have developed  
42 strategies to defend themselves against predation, often by secreting chemical compounds  
43 that they either produce themselves or acquire from their diet and later store in specialized  
44 structures [1], such as glands. Molluscs produce and sequester a wide variety of compounds  
45 in their body, including terpenes, polypropionates, and nitrogenous compounds, which serve  
46 not only in defence, but also in communication, reproduction, competition, and predation  
47 [2,3]. Several reviews have focused on the isolation and characterization of these  
48 substances, particularly in three major classes: Gastropoda, Cephalopoda, and Bivalvia [3–  
49 5]. The evolution of glandular chemical defences in molluscs is frequently associated with the  
50 reduction or loss of the shell, or with increased mantle exposure, as seen in cephalopods  
51 and gastropod slugs, but this correlation is not absolute [6,7]. Within Gastropoda, most  
52 research has been focused on heterobranch species, which are well known for  
53 kleptochemistry (the sequestration of chemical compounds from prey or food sources) [8]. A  
54 broader sampling of clades is critical to understanding the evolution of chemical interactions  
55 in molluscs.

56 Limpet-shaped molluscs, a body form that has independently evolved multiple times across  
57 Mollusca, typically rely on their conical, low-profile shells to adhere tightly to substrates,  
58 thereby minimizing exposure to predators [9–11]. Many rely on aggressive behaviours such  
59 as physically dislodging predators or competing invertebrates [12,13]. Nonetheless, certain  
60 heterobranch limpets such as siphonariids and trimusculids secrete acidic mucus combined  
61 with other compounds, which likely serve as deterrents against predators [14,15]; whereas  
62 the true limpet *Lottia limatula* (Carpenter, 1864) produces limatulone, a triterpenoid that is  
63 produced as a defence against predatory fishes [16]. The limpet *Tectura virginea* (Müller,  
64 1776) has been reported to possess a distinctive group of white glands arranged along the  
65 mantle margin, which secrete a substance packaged in thread-like filaments [17]. Fretter and  
66 Graham [18] first described these structures and referred to them as “repugnatorial glands”  
67 due to their resemblance to defensive glands found in other gastropod species. Despite this  
68 early observation, no subsequent studies have investigated the ultrastructure or functional  
69 properties of these glands, which are visually striking and distinctly different to any other  
70 limpet.

71  
72 Although numerous molluscan glands have been described as defensive, their ultrastructure  
73 and the identity of their secreted compounds remain unverified. In *T. virginea*, the presence  
74 of distinctive mantle margin glands presents an opportunity to fill this gap. Therefore, this  
75 study aims to investigate both the anatomical organization and chemical nature of the unique  
76 glands of *T. virginea*, and to understand the mechanisms of secretion and release of their  
77 products. To achieve this, we combined observations of living animals, histology, and

78 electron microscopy to examine gland ultrastructure, and performed chemical analyses to  
79 identify the secreted compounds. This has enabled us to shed some light on the  
80 “repugnatorial” nature of these glands and to infer some of their potential ecological roles.

## 81 **Material and methods:**

### 82 *Specimen handling, gland extraction, sample collection*

83 Specimens of *T. virginea* were collected by hand on the rocky shores of Strangford Lough at  
84 Portaferry, N. Ireland, on 25 August 2021. The animals are approximately 6-12 mm long and  
85 are commonly found on cobble in the mid to low intertidal, usually living on small boulders  
86 with encrusting coralline algae. Limpets were transferred to the lab (Queen’s University  
87 Marine Laboratory, Portaferry) and observed under the stereomicroscope. Living specimens  
88 were held in ventral view to facilitate examination of external body parts. The mantle margin  
89 of some limpets was handled using forceps, which triggered secretion from the  
90 “repugnatorial” glands. This behaviour was recorded and photographed.

91

### 92 *Chemical analysis of glandular secretions*

93

94 The glandular secretions of two individuals were extracted by mechanical stimulation with  
95 sterilised forceps to the mantle tissue of live animals in chilled seawater or distilled water,  
96 and the excretion was removed with a glass Pasteur pipette with a minimum volume of the  
97 medium. The strings were allowed to settle to the bottom of the volume in the pipette and  
98 then moved in one drop of medium into a glass vial of methanol (MeOH). These were  
99 transported on dry ice to Royal Botanic Gardens, Kew, for further analyses. Three  
100 independent samples were obtained — one collected in seawater and two in distilled water  
101 — representing replicate extractions from different individuals. Samples were placed in  
102 Eppendorf tubes containing 2 mL of 100% MeOH (HPLC grade) to extract the chemicals.  
103 Tubes were shaken, left in the dark for 12 h at room temperature for extraction; then, 1 mL  
104 was transferred to LC-MS vials and then stored at -20°C until chemical analysis.

105

106 The chemical profiles of the glandular secretion were recorded on a Vanquish UHPLC  
107 system coupled to a 100 Hz photodiode array detector (PDA) and an Orbitrap Fusion Tri-  
108 hybrid high-resolution tandem mass spectrometer (Thermo Fisher Scientific, Waltham, MA,  
109 USA). Chromatography was performed on 5 µl sample injections onto a 150 mm × 3 mm,  
110 3 µm Luna C-18(2) column (Phenomenex, Torrance, CA, USA) using the following 400 µl/min  
111 mobile phase gradient of 90:10 to 10:90 [methanol + 0.1% formic acid (A): water + 0.1%  
112 formic acid (B)] over 20 min at a flow rate of 400 µL min<sup>-1</sup>. Blank samples (methanol only)

113 were run as controls to discard potential contaminant compounds. Mass spectrometry was  
114 performed at high resolution MS1 spectra ( $m/z$  125–1800) in both positive and negative  
115 modes, and data dependent MS2 and MS3 spectra in both modes using the linear ion trap.  
116 The software Compound Discovery (Thermo Scientific) was used for tentative identification  
117 using MS/MS data and comparing our results against several databases such as  
118 ChemBioFinder, Chempider, Kegg, LipidBank, LipidMaps, Metlin and NIST. To increase  
119 confidence in the predicted chemical formula and tentative chemical identification, the  
120 predicted chemical formula is calculated in a high-resolution mode with error of less than 5  
121 ppm. Furthermore, MS2 should match those from the databases in a value greater than or  
122 equal to 0.8 of a dots product. Only compounds consistently detected across all three  
123 samples were retained for inclusion in the final table of identified compounds.

124

### 125 *Histology*

126

127 Animals were relaxed in 7.5% magnesium chloride ( $MgCl_2$ ) for approximately 2 hours and  
128 fixed in 4% paraformaldehyde solution (PFA) in phosphate-buffered saline (PBS). Fixation,  
129 embedding, and sectioning, follow the protocols of Ruthensteiner [19]. Prior to embedding,  
130 the selected specimen was decalcified using ethylenediaminetetraacetic acid (EDTA)  
131 overnight and subjected to a graded dehydration process with acetone. It was then  
132 embedded in epoxy resin and sectioned using a HistoCore AUTOCUT R microtome fitted  
133 with a HistoJumbo 8 mm diamond knife.

134

135 Semi-thin serial sections 1.5  $\mu m$  were stained with Richardson stain to enhance tissue  
136 contrast and imaged under a Leica DM 2000LED light microscope equipped with a Leica  
137 Flexacam C1 camera at 40x magnification. The full set of histological slides is deposited in  
138 the malacological collection of the Senckenberg Research Institute and Natural History  
139 Museum Frankfurt (SMF 366936), and the full body reconstruction has been published  
140 separately [17]. Image processing, including sharpening, contrast adjustment, and grayscale  
141 conversion, was carried out in IrFanView v. 4.62 (Irfan Skiljan). The images were then  
142 realigned and compiled into a volumetric image stack in Amira v. 2020.2 (Thermo Fisher  
143 Scientific). Final segmentation and three-dimensional reconstruction were conducted using  
144 Dragonfly v. 2022.2.0.1409 (Object Research Systems).

145

### 146 *Transmission Electron Microscopy*

147 Pieces of the mantle were removed from an additional specimen fixed as above and these  
148 were used for TEM. Ultrathin sections with silver interference colour (70–75 nm thick) were  
149 prepared using a Diatome Ultra 45° diamond knife. Sections were mounted on Formvar-

150 coated, single-slot copper grids and stained with 2% uranyl acetate (E22400; Science  
151 Services) followed by 2.6% lead citrate (E17810; Science Services) using an automated TEM  
152 stainer (QG-3100; Boeckeler Instruments). Imaging was performed with a ZEISS EM 10CR  
153 transmission electron microscope equipped with photostimulable phosphor plates (Ditabis).

## 154 155 **Results**

### 156 *Observations of secretions*

157 Secretion from the repugnatorial glands (figure 1a-c) was not visibly triggered by  
158 dislodgement of the limpet nor by manipulation of its foot, but only in response to direct  
159 mechanical stimulation of the mantle margin using forceps (supplementary video 1, 2).  
160 Secretions were limited to glands in the area directly stimulated. The secretions were not  
161 triggered readily but only after extended contact of several seconds. When triggered, the  
162 glands released thin white threads. When these threads were pipetted onto a glass slide for  
163 observation under higher magnification, they were observed to consist of densely packed  
164 granules or droplets (figure 1d). These droplets slowly dissolved or dissipated, and the fluid  
165 surrounding the thread displaying active Brownian motion, and the droplets progressively  
166 decreased in size as they dissolved into the surrounding medium. Approximately 10 minutes  
167 after initial secretion, a single thread had lost about half of its volume (figure 1e,  
168 supplementary video 3).

### 169 170 *“Repugnatorial” gland structure*

171 A ring of distinctive white glands is arranged radially along the mantle margin in *T. virginea*  
172 (figure 1a). These structures, previously referred to as “repugnatorial glands” [18], are the  
173 only glands visible externally. In one specimen (~1.4 mm), approximately 640 of these glands  
174 were counted. Upon mechanical stimulation, the glands expel thread-like filaments of a white  
175 substance, which gradually dissolves in seawater. No other gland types are discernible under  
176 stereomicroscopy or from external view.

177 Histological and ultrastructural analyses revealed additional complexity. The white  
178 repugnatorial glands are large, subepidermal, sac-like structures embedded beneath a layer  
179 of mucous-secreting epidermal cells, each measuring around 78  $\mu\text{m}$  in diameter. These  
180 glands are situated just beneath the epidermis and are surrounded by mucous-secreting  
181 epidermal cells (figure 1f, g, 2a, c, 3). Transmission electron microscopy revealed that each  
182 gland is multicellular and rests on a distinct basal lamina (figure 2).

183 The repugnatorial glandular structure is dominated by a single, voluminous secretory cell  
184 occupying the majority of the gland's interior. This large cell exhibits numerous vacuoles and  
185 vesicles of varying sizes and electron densities (figure 2b), consistent with a highly active  
186 secretory state. The nucleus of the active cell is conspicuously large, with a prominent  
187 nucleolus (approximately 3  $\mu\text{m}$  in diameter) and lacks visible heterochromatin, indicative of  
188 high transcriptional activity (figure 2f). In contrast, smaller neighbouring cells—presumably in  
189 a quiescent or precursor state—are located peripherally along the gland wall and possess  
190 compact nuclei with denser chromatin (figure 2f). These smaller cells appear to serve as  
191 replacement cells that become active upon the depletion or expulsion of the central secretory  
192 cell.

193 No intercellular junctions were observed between the large secretory cell and the adjacent  
194 quiescent cells, suggesting minimal adhesion and potential for entire-cell discharge. The  
195 repugnatorial gland is surrounded by a thin, circumferential layer of muscle fibres —  
196 sometimes appearing as two closely spaced layers (figure 2g) — which presumably  
197 contracts to facilitate the forceful ejection of the glandular contents. Given the paucity of  
198 organelles in the central cell and the complete filling of the cytoplasm with secretion vesicles,  
199 it is likely that the entire cell is ruptured and expelled during discharge.

200 The secretion appears to be synthesized basally, where the cytoplasm is densely packed  
201 with small vesicles (figure 2b). As the secretion matures, vesicles become more electron-  
202 dense and fuse into larger vacuoles toward the central region of the cell. Distally, near the  
203 apical surface of the gland, the vacuoles appear electron-lucent and contain no discernible  
204 material (figure 2a, b, 3). Beneath the ring musculature lies a network of muscle fibres and  
205 neurites innervating the gland, likely coordinating the expulsion mechanism (figure 2e).

206

### 207 *Chemical analyses*

208 A total of 86 peak features were detected in the extracts, 55 of which were tentatively  
209 identified (see supplementary table 1). Seven compounds (table 1) represent almost 90% of  
210 the total relative amount of the identified chemicals, six of which are shown in figure 4.  
211 However, the most abundant peaks overall, accounting for more than 80% of the total signal  
212 intensity, remained unidentified. The identified chemicals therefore represent only about 10%  
213 of the total chemical concentration (see supplementary table 1).

214

### 215 **Discussion**

216 Our study identified a novel glandular system along the mantle margin of *Tectura virginea*,  
217 characterized by unusually large glands that release thread-like secretions upon sustained  
218 mechanical stimulation. The gland's anatomical position and secretory mechanism imply a  
219 defensive function. The chemical composition of the secretion further supports this  
220 interpretation, given the presence of compounds known from other biological systems for  
221 their antimicrobial, cytotoxic, and irritant effects (see below). These results confirm and  
222 expand the initial description by Fretter and Graham [18], who first suggested a repugnatorial  
223 role for these mantle-margin structures but did not explore their chemical nature or functional  
224 mechanisms. The ecological and evolutionary implications of these findings, particularly in  
225 the context of defensive strategies among molluscs, are discussed below.

226

### 227 *Diversity of defensive secretions*

228

229 Glands with defensive functions are well described in some aquatic invertebrates [2]. In  
230 cephalopods, for instance, the ink gland is a specialized internal organ that secretes a dense  
231 mucus, which is used to facilitate escape by creating a smokescreen and disrupting the  
232 predator's senses [20]. Various sea hares (order Aplysiida) bear an ink and an opaline gland  
233 [21], which secrete chemical substances that deter and disrupt predators' sensory systems  
234 [22,23]. These are recognised mainly for the visual phagomimicry effect, but the secretions  
235 also have chemical effects that may be equally relevant to their function in terms of the target  
236 predator. Glands appear with highly variable placement and function. Other animals, such as  
237 the scallop *Limaria hians*, bear glandular epidermal cells located in the tentacles, which  
238 secrete substances that deter predators [24,25].

239 The presence of glands in the mantle tissue of limpets is consistent with the diversity of  
240 glandular structures observed across molluscs. However, in *T. virginea*, these glands are  
241 larger and more prominent than in other patellogastropods, making them unique within this  
242 clade. In related lottiids [26–28], and other patellids [29], the marginal mantle glands form  
243 agglomerations of small pear-shaped or vacuolated secretory cells along the mantle edge  
244 and show no evident muscular association, resembling more the typical mucous mantle  
245 glands of *T. virginea*. In the latter species by contrast, the mantle glands are compact,  
246 composed of large secretory cells and associated with musculature.

247 Although glandular functions in molluscs, including those in mantle tissue, are diverse, this  
248 variability previously prevented deducing the chemical nature of the secretions without direct  
249 analysis. Our results now provide evidence to propose a potential function. The glandular  
250 extract of *T. virginea* contains several compounds classified as sulfur-containing and  
251 oxidized lipids derivatives, including 1-(propyldisulfanyl)-1-(propylsulfinyl) propane and  
252 geranyl quinone, respectively. These chemical classes have been associated in other

253 organisms with antipathogens and deterrent properties [30–33]. While functional inference  
254 remains speculative, anatomical information and the gland contents give support to the  
255 original description of these structures as “repugnatorial” glands.

256 The presence of glands in the mantle tissue of a limpet is not wholly surprising when  
257 compared to any other patellogastropod. However, they are unique in their relative size and  
258 prominence. Similar structures have not been reported in other *Tectura* species, although  
259 this may reflect limited anatomical studies rather than true absence. Several distinctive  
260 features of *T. virginica*, particularly in the mouthparts and sperm morphology, differ from the  
261 typical patterns observed in the superfamily Lottioidea [17,34]. The presence of repugnatorial  
262 glands further distinguishes this taxon, representing not only a potential synapomorphy  
263 separating it from other Lottioidea, but also a unique adaptation within Patellogastropoda as  
264 a whole. However, the evolutionary significance of these features remains unclear. Whether  
265 they represent retained plesiomorphic traits or more recently derived novelties is still  
266 unresolved.

#### 267 *Evolution of defensive secretions*

268 The defensive potential of the repugnatorial glands found at the mantle margin in *T. virginica*  
269 can be inferred from their anatomy, their stimulus-dependent discharge and comparisons to  
270 similar structures in other invertebrates. Positioned at the margin of the mantle, these glands  
271 are likely to be among the first tissues contacted during an attack. Their innervation suggests  
272 a controlled response to mechanical stimuli, while the presence of thin musculature may  
273 facilitate holocrine secretion upon activation [35]. Similar muscular arrangements are found  
274 in other defensive gland systems in heterobranch gastropods, such as the subepidermal acid  
275 glands in *Berthellina* species [36], the ceratal and acid glands in some nudibranchs [37,38],  
276 and the defensive glands in *Onchidella* [39]. In *T. virginica*, secretion occurred only in  
277 response to strong mechanical stimulation. A similar pattern is observed in *Aplysia* spp.,  
278 where ink release is triggered more reliably by firm contact than by brief tactile stimuli [23].  
279 This suggests that in both cases, although in unrelated a very different systems, the  
280 glandular discharge is more likely to be provoked by a sustained or forceful interaction, such  
281 as a predator’s grasp, rather than by incidental touch.

282 Several compounds were identified in the glandular extract of *T. virginica*, each with potential  
283 ecological or physiological relevance. Among the most abundant identifiable was 1-  
284 (propylsulfanyl)-1-(propylsulfinyl)propane, which has been previously reported in onion  
285 species (*Allium* spp.) [40–42]. Related disulfides are known for antimicrobial and  
286 immunomodulatory properties [43], indicating a potential role in defence through microbial  
287 inhibition or predator deterrence. Ribonic acid, a sugar acid and product of carbohydrate  
288 metabolism [44] may instead reflect an excretory function of the gland, involved in eliminating

289 metabolic by-products. Another metabolite identified, 4-undecylbenzenesulfonic acid,  
290 previously found in other marine organisms, exhibits fungicidal and antibacterial activity [45],  
291 further supporting its potential role in microbial defence. Sulfated L-fucan is present in a  
292 number of different brown algae and has antiviral activity [46], while geranyl quinone,  
293 previously isolated from tunicates and algae [47], has also shown cytotoxicity and toxicity  
294 toward insect larvae [48], possible acting as a chemical deterrent. Finally, tartaric acid, a  
295 strong organic acid, has been implicated in pain-inducing mechanisms, such as those found  
296 in the stinging hairs of the hairy nettle (*Urtica* spp.) [49] and could function as a chemical  
297 irritant, deterring predators through discomfort or tissue irritation upon contact.

298 While the chemical characterization focused on the identified compounds, these represent  
299 only a small fraction of the total chemical profile of the secretion, and other abundant peaks  
300 in our dataset remain unidentified. Such a pattern is common in studies of natural products,  
301 given the vast chemical diversity of marine metabolites and the frequent discovery of new  
302 molecules. These unidentified compounds together account for approximately 90% of the  
303 total signal intensity (see supplementary table 1), suggesting that the secretion may include  
304 additional, potentially novel metabolites with functions not yet understood. Further chemical  
305 analyses, including compound isolation and structure elucidation using Nuclear Magnetic  
306 Resonance (NMR), will be essential to fully resolve the biochemical complexity and possible  
307 multifunctional roles of this glandular secretion.

308 The current function of certain molluscan glands may represent an adaptation of structures  
309 that evolved with a different role. The main compound of cephalopod ink is melanin, which  
310 has a high affinity for metals and could represent a potential means of detoxification [50],  
311 although its current function is primarily defensive. Similarly in sea hares, the ink gland was  
312 reported to have evolved to process pigments from their red algal diet [21]. Following this  
313 pattern, it is possible that the mantle margin glands of *T. virginica* originated as excretory or  
314 detoxification structures involved in the elimination of metabolic by-products. Although no  
315 close relatives of *T. virginica* are known to possess homologous glands, or any glands with  
316 clearly characterized alternative functions, nonetheless the presence of compounds such as  
317 disulphides, organic acids, and sulfonated molecules suggests that these glands may follow  
318 a broader trend of functional repurposing in molluscan exocrine systems, where  
319 physiologically derived secretions are co-opted for defensive roles under ecological pressure.

320 In line with this interpretation, the composition and deployment of the *T. virginica*  
321 repugnatorial secretion indicate a biologically active mixture, potentially acting against  
322 microbial colonization or small invertebrate predators. The localization of the glands at the  
323 exposed mantle edge, and the thread-like, persistent nature of the secretion, further support  
324 a barrier function. While originally excretory, this system may have been functionally

325 repurposed for defence [51]. *T. virginia* is known to feed on diatoms, endolithic, and coralline  
326 red algae [18,52,53]. Whether these or other dietary items provide some of the identified  
327 compounds remains untested, but is a possibility.

### 328 *Ecology and function of the repugnatorial glands*

329

330 Gastropods that secrete acids from epidermal glands in the mantle buffer them using mucus  
331 to prevent rapid dispersion and protect their own cells [54–56]. This may also be the case in  
332 *T. virginia*, as the secretion did not dissolve quickly, and may serve to concentrate the dose  
333 or adhere to predators' feeding structures. Typical limpet predators can include birds, crabs,  
334 sea stars and worms [57–61]. Given the small size of the limpets and the thread-like nature  
335 of the secretion, it is possible that the primary targets of this defence are small predators  
336 such as worms.

337

338 In particular, polyclad flatworms (Platyhelminthes) and nemerteans are common in the same  
339 intertidal habitats as *T. virginia* and include genera known to prey on limpets [62]. When  
340 nemerteans and flatworms feed, they could make direct contact with the mantle edge,  
341 triggering glandular discharge. The thread-like nature of the secretion, persistent and  
342 concentrated, might function as a surface-deployed irritant, potentially coating the predator  
343 feeding structures. Although direct predation events and ecological interactions involving *T.*  
344 *virginia* remain undocumented, the ecological presence and feeding behaviour of these  
345 worms make them compelling candidates as selective agents for the evolution of this  
346 defence.

347

348 Within Patellogastropoda, chemical defences have been sporadically reported. By combining  
349 ultrastructural and chemical analyses, we clarified the anatomy and potential function of the  
350 mantle margin glands in *T. virginia*, revealing their exocrine nature. The thread-like secretion  
351 is persistent in seawater and chemically enriched with several compounds. These  
352 substances are associated with antimicrobial, cytotoxic, or irritant properties in other systems  
353 and may also function as a deterrent barrier against antagonists in *T. virginia*. We propose  
354 that these glands may have originally evolved for the excretion of metabolic by-products and  
355 were later possibly co-opted for defence, representing an example of apparent functional  
356 repurposing in molluscan gland evolution. This study reveals a previously unrecognized  
357 defensive capability in a limpet-shaped gastropod and provides insight into the broader  
358 evolutionary plasticity of molluscan secretory systems.

359

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- 536

537 Table 1. Chemical compounds identified in the extracts of the substances released by the  
 538 repugnatorial glands. The full list is given in supplementary table 1.

539

Chemical compound	Chemical Formula	Calculated molecular weight	Relative concentration (% of identified compounds)	Relative concentration (% of total compounds)
1-(Propyldisulfanyl)-1-(propylsulfanyl)propane	C <sub>9</sub> H <sub>20</sub> OS <sub>3</sub>	240.0673	30.18	2.75
Ribonic acid	C <sub>5</sub> H <sub>10</sub> O <sub>6</sub>	166.0481	25.63	2.34
4-Undecylbenzenesulfonic acid	C <sub>17</sub> H <sub>28</sub> O <sub>3</sub> S	312.176	12.13	1.1
Sulfated L-fucan	C <sub>7</sub> H <sub>14</sub> O <sub>7</sub> S	242.0461	8.07	0.73
Geranyl quinone	C <sub>16</sub> H <sub>20</sub> O <sub>2</sub>	244.1463	6.32	0.58
Tartaric acid	C <sub>4</sub> H <sub>6</sub> O <sub>6</sub>	150.0168	5.16	0.47
alpha-CEHC	C <sub>16</sub> H <sub>22</sub> O <sub>4</sub>	278.1518	2.16	0.2
Citramalic acid	C <sub>5</sub> H <sub>8</sub> O <sub>5</sub>	148.0372	1.88	0.17
Pentenedioic acid	C <sub>5</sub> H <sub>6</sub> O <sub>4</sub>	130.0266	1.83	0.17
4-Amino-1-((2E)-5-O-(((2R)-2-((10Z,13Z,16Z)-10,13,16-docosatrienoyloxy)-3-(palmitoyloxy)propoxy})(hydroxy)phosphoryl)oxy)(hydroxy)phosphoryl]-β-D-threo-pentofuranosyl)-2(1H)-pyrimidinone	C <sub>50</sub> H <sub>87</sub> N <sub>3</sub> O <sub>15</sub> P <sub>2</sub>	1031.557	1.72	0.16
UDP-GlcNAc	C <sub>17</sub> H <sub>27</sub> N <sub>3</sub> O <sub>17</sub> P <sub>2</sub>	607.0818	1.46	0.13
Pyroglutamic acid	C <sub>5</sub> H <sub>7</sub> NO <sub>3</sub>	129.0426	1.28	0.12
Quillaic acid 3-[galactosyl-(1->2)-xylosyl-(1->3)]-glucuronide] 28-[glucosyl-(1->3)-[glucosyl-(1->3)-xylosyl-(1->4)]-rhamnosyl-(1->2)]-4-acetyl-fucosyl] ester	C <sub>78</sub> H <sub>122</sub> O <sub>43</sub>	1746.732	0.87	0.08
13-L-Hydroperoxylinoleic acid (2S)-1-[(4Z,7Z,10Z,13Z,16Z,19Z)-4,7,10,13,16,19-Docosahexaenoyloxy]-3-(pentadecanoyloxy)-2-propanyl tetracosanoate	C <sub>18</sub> H <sub>32</sub> O <sub>4</sub> C <sub>64</sub> H <sub>112</sub> O <sub>6</sub>	312.2302 976.8438	0.72 0.63	0.07 0.06

540

541 **Figure captions**

542 Figure 1. Mechanical stimulation of the mantle margin causes visible secretion from distinct  
543 mantle glands. Limpet shell length  $\approx$  12 mm (a–c). Glands are identified (a), touched with  
544 tweezers (b), and respond by releasing thread-like secretions (c). The secretion is observed  
545 under the microscope immediately after release (d) and after 10 minutes (e), dissolving in the  
546 medium. A cross section of the mantle margin reveals the internal structure of the glands (f).  
547 A 3D histological reconstruction highlights the position of these glands within the mantle  
548 margin (g). Abbreviations: mg, mantle gland; nf, nerve fibre; rg, “repugnatorial” gland.

549

550 Figure 2. Ultrastructure of the repugnatorial gland (rg) and surrounding mantle tissue of  
551 *Tectura virginea* (a–g). (a) Section through the apical region of the rg, where secretory  
552 vesicles have largely fused into large vacuoles. (b) Section closer to the basal region of the  
553 rg, showing numerous small, electron-dense vesicles; quiescent cells (qc) are visible along  
554 the glandular wall. (c) Overview showing two rgs with adjacent mucosecretory mantle glands  
555 (mg) and muscle cells (mc) located between them. (d) Detail of the glandular lining: white  
556 arrows mark the extracellular matrix; the boundaries between the active gland cell and  
557 adjacent quiescent cells are visible, but lack prominent intercellular junctions. (e) Neurites  
558 (ne) and periglandular muscles surrounding the rg. (f) Nuclei of the active ( $n^*$ ) and quiescent  
559 (n) gland cells, illustrating the marked size difference; note the large nucleolus and absence  
560 of heterochromatin in  $n^*$ . (g) Glandular lining with surrounding ring musculature; arrowheads  
561 mark spot desmosomes between muscle cells. Abbreviations: *cm*, cell membrane; *mc*,  
562 muscle cell; *mg*, mantle gland; *n*, nucleus;  $n^*$ , nucleus of the active secretory cell of *rg*; *ne*,  
563 neurite; *qc*, quiescent cell; *rg*, repugnatorial gland.

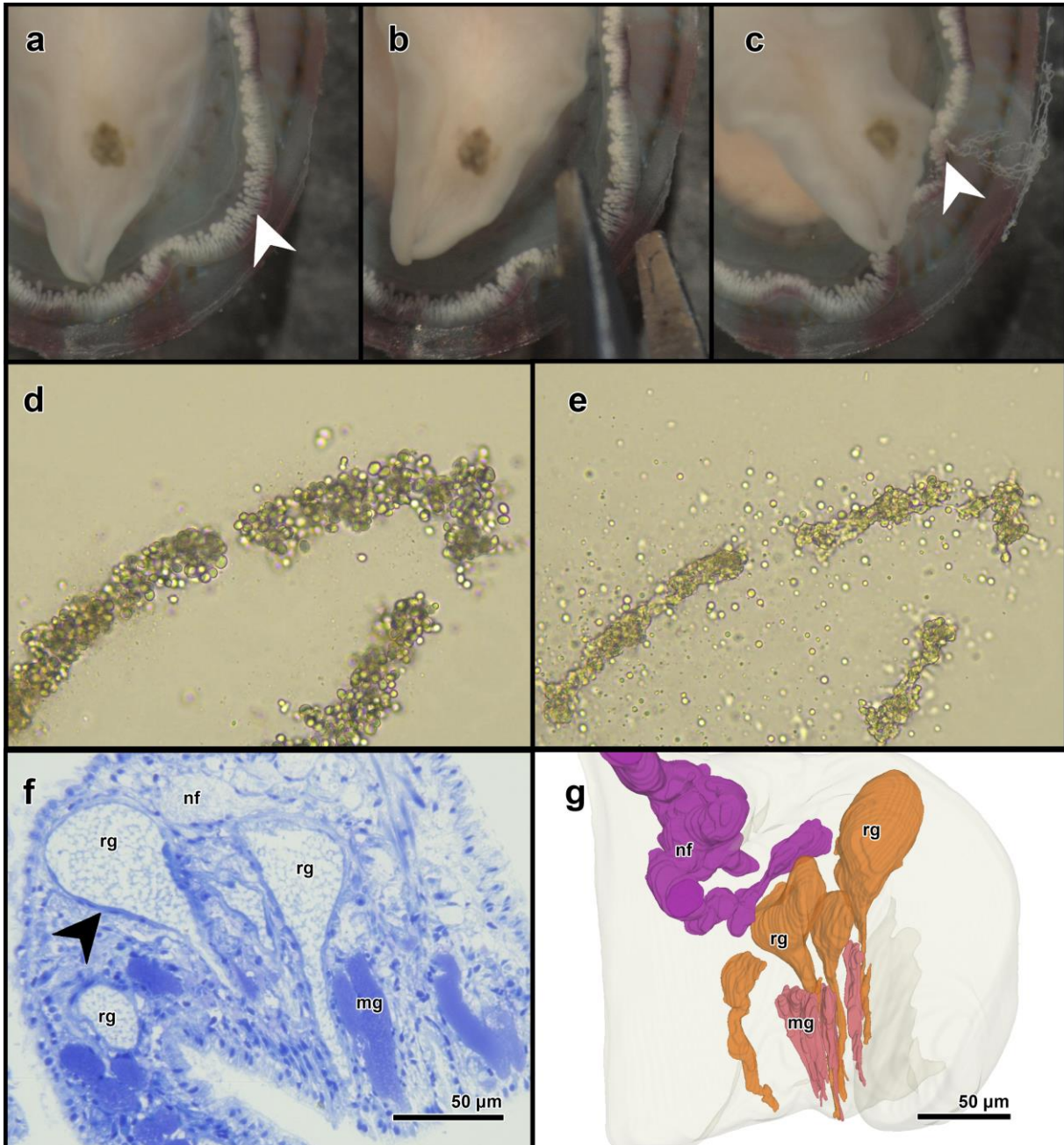
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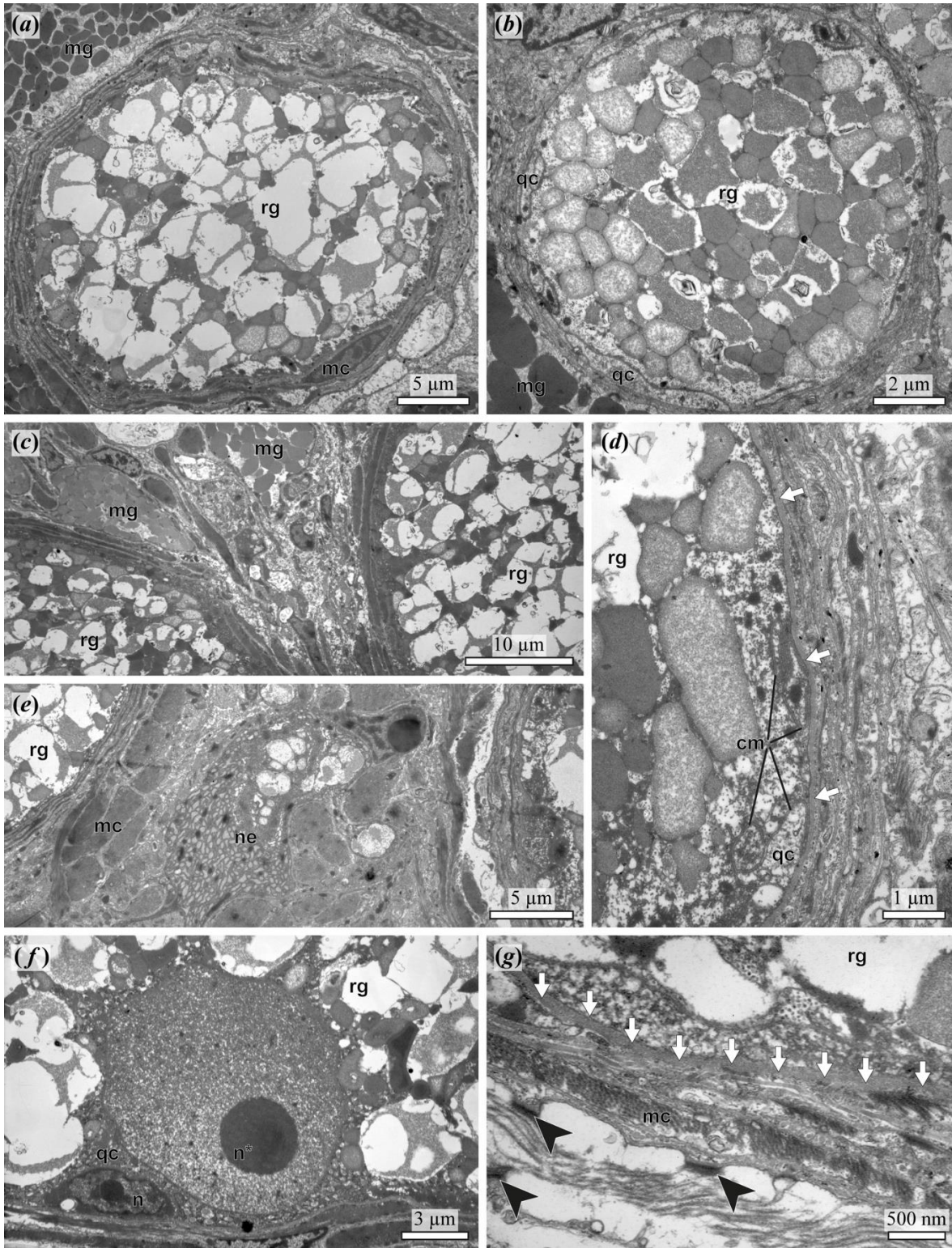
565 Figure 3. Schematic representation of the repugnatorial gland (*rg*) and surrounding mantle  
566 tissue. Epidermal cells (*ec*), mantle glands (*mg*), and quiescent cells (*qc*) are illustrated in  
567 their respective positions. Nuclei are shown in brown. Muscle cells are shown in red. The  
568 periglandular ring muscles are indicated by white dots, and the basal lamina is marked with a  
569 blue line. Abbreviations: *ec*, epidermal cell; *mg*, mantle gland; *n*, neurite; *qc*, quiescent cell;  
570 *rg*, repugnatorial gland.

571

572 Figure 4. Chemical structures of the six most abundant compounds identified in the glandular  
573 secretion of *Tectura virginea*: 1-(Propyldisulfanyl)-1-(propylsulfinyl)propane, Ribonic acid, 4-  
574 Undecylbenzenesulfonic acid, Sulfated L-fucan, Geranyl quinone, Tartaric acid.

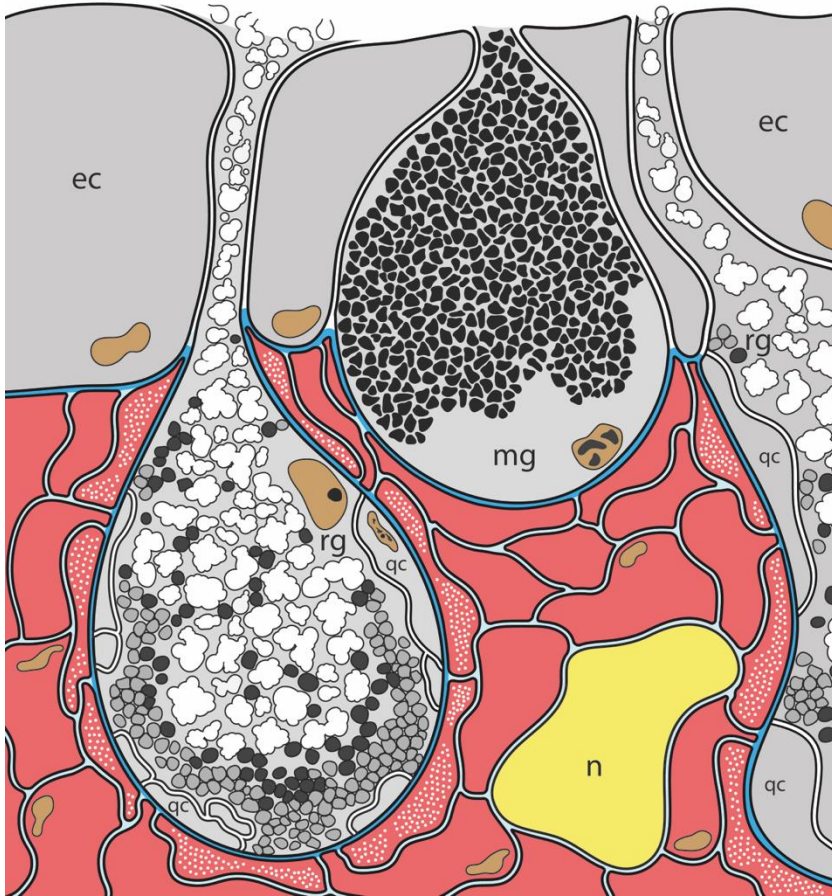
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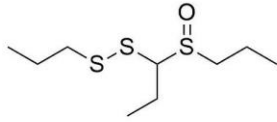
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580 Figure 2.

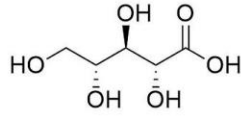


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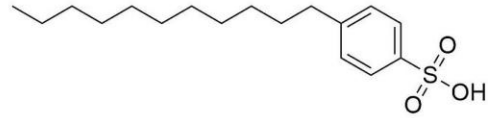
582 Figure 3.



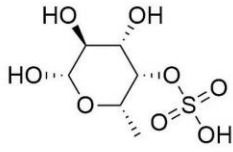
1-(propyldisulfanyl)-1-(propylsulfinyl)propane



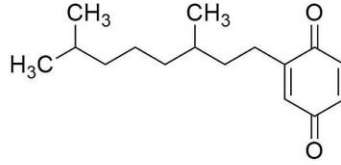
ribonic acid



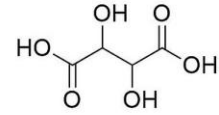
4-undecylbenzenesulfonic acid



sulfated L-fucan



geranyl quinone



tartaric acid

583

584 Figure 4.